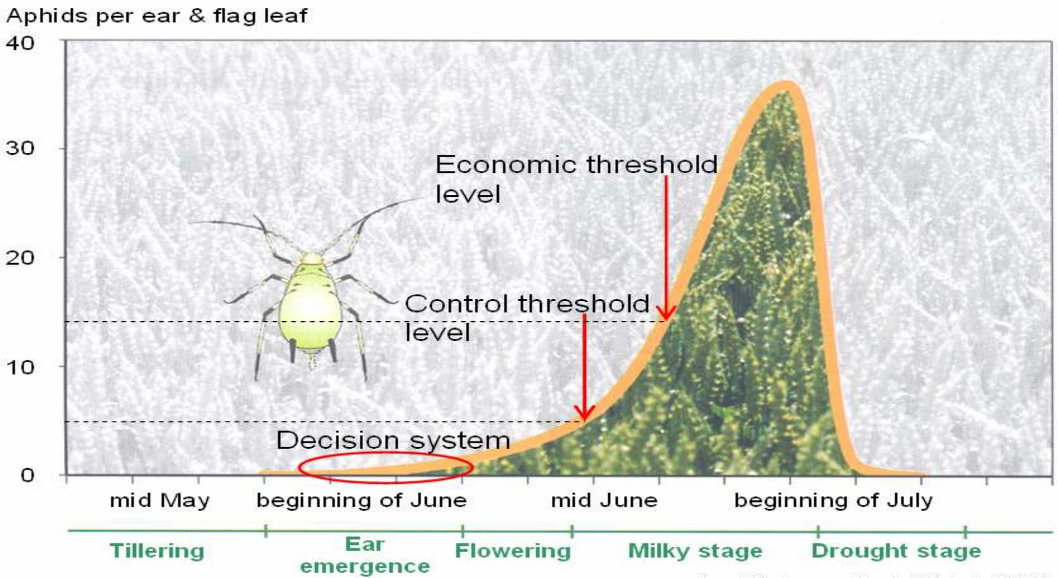
Migration and early population development of aphids (Hemiptera: Aphididae) in winter cereals

Von der Naturwissenschaftlichen Fakultät
der Gottfried Wilhelm Leibniz Universität Hannover
zur Erlangung des akademischen Grades

Doktor der Gartenbauwissenschaften
Dr. rer. hort.

genehmigte Dissertation von
Dipl.-Ing. agr. A. Michael Klüken, geboren am 15.09.1973 in Krefeld
Hannover, Januar 2008



(modified according to Wetzel, 2004)

1. Referent:	Prof. Dr. B. Hau
2. Referent:	Prof. Dr. B. Freier
Tag der Promotion (mündlichen Prüfung):	27.02.2008

Soli Dei Gloria

Eidesstattliche Erklärung

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Arbeit selbstständig angefertigt habe und keine anderen als die angegebenen Quellen und Hilfsmittel verwendet habe, sowie dass diese Arbeit noch keiner anderen Prüfungskommission als Diplomarbeit oder ähnlicher Prüfungsarbeit vorgelegt worden ist.

Hannover, 07.01.2008

A. Michael Klüken

Table of contents

TABLE OF CONTENTS V

LIST OF ABBREVIATIONS XII

SUMMARY XIV

RESUME XVI

ZUSAMMENFASSUNG XIX

GLOBAL INTRODUCTION 23

IMPORTANCE OF CEREAL APHIDS 23
THRESHOLD LEVEL CONCEPTS AND THEIR PROBLEMS 24
POPULATION MODELS 26
MIGRATION 27
EVALUATION OF CEREAL APHID POPULATIONS 30
LANDSCAPE STRUCTURE AND POPULATION GENETICS 31
HOST PLANT SPECIALISATION 32

OBJECTIVES AND CHAPTER TITLES 34

CHAPTER 1: COMPARISON AND VALIDATION OF POPULATION MODELS FOR CEREAL APHIDS 36

ABSTRACT 36
INTRODUCTION 37
MATERIALS AND METHODS 39

FIELD EVALUATION 39
MODEL SIMLAUS 40
MODEL LAUS 41
MODEL GETLAUS01........ 42
VALIDATION AND STATISTICAL ANALYSIS........ 43
RESULTS 44
GENERAL RESULTS 44
MODEL SIMLAUS 44
MODEL LAUS 47
MODEL GETLAUS01........ 48
DISCUSSION 54
MODEL SIMLAUS 55
MODEL LAUS 56
MODEL GETLAUS01........ 58
CONCLUSIONS........ 62
Acknowledgements 62

CHAPTER 2: FORECASTING GRADATION OF CEREAL APHIDS (HEMIPTERA: APHIDIDAE) IN WINTER WHEAT AT EAR EMERGENCE........ 64

ABSTRACT........ 64
INTRODUCTION 65
MATERIALS AND METHODS 67
FIELD DATA EVALUATION 67
SUCTION TRAP SAMPLES........ 67
METEOROLOGICAL PARAMETERS........ 69
DEFINITION OF VARIABLES........ 69
STATISTICAL ANALYSES 69
LOGISTIC REGRESSION ANALYSES (LOG RA) 70
LINEAR DISCRIMINANT ANALYSES (LIN DA) 71
MODEL VALIDATION........ 72
RESULTS 73
GENERAL RESULTS 73
LOGISTIC REGRESSION ANALYSES (LOG RA) 74
LINEAR DISCRIMINANT ANALYSES (LIN DA)........ 81
EXAMPLES FOR LIN DA AND LOG RA 83
MODEL VALIDATION........ 84

DISCUSSION 85
GENERAL DISCUSSION 85
ESTABLISHMENT OF “WINTER CONDITIONS” AND “REAL MIGRATION” SUBMODELS 86
COMPARISONS OF METHODS 87
COMPARISON OF LOCATIONS 89
MODEL CONSTRAINTS 90
IMPORTANCE OF THRESHOLD LEVELS 91
CONCLUSIONS 92
Acknowledgements 92

CHAPTER 3: FORECASTING MIGRATION OF CEREAL APHIDS (HEMIPTERA: APHIDIDAE) IN AUTUMN AND SPRING 94

ABSTRACT 94
INTRODUCTION 95
MATERIALS AND METHODS 97
FIELD DATA EVALUATION 97
SUCTION TRAP SAMPLES 98
METEOROLOGICAL PARAMETERS 98
STATISTICAL ANALYSES 99
DEFINITION OF VARIABLES 99
CORRELATION AND LINEAR REGRESSION ANALYSES 100
LOGISTIC REGRESSION ANALYSES 100
LINEAR DISCRIMINANT ANALYSES 100
MODEL VALIDATION 102
RESULTS 103
GENERAL RESULTS 103
COMPARISONS OF SUCTION TRAP CATCHES AND FIELD POPULATIONS 104
IMPORTANCE OF INFLUENCING PARAMETERS 105
DEVELOPMENT OF MODELS FOR MIGRATION 109
EXAMPLES OF FORECASTING MODELS 110
VALIDATION OF MODELS 111
DISCUSSION 113
INFLUENCING VARIABLES 113
PERFORMANCES OF MODELS 115
COMPARISONS OF STATISTICAL METHODS 116
DENSITY EFFECTS 117

MULTITUDE OF FACTORS INFLUENCING MIGRATION 118
CONCLUSIONS 120
Acknowledgements 121

CHAPTER 4: THE IMPORTANCE OF PROXIMITY BETWEEN WINTER AND SUMMER HOSTS ON IMMIGRATION AND EARLY POPULATION DEVELOPMENT OF HOST-ALTERNATING APHIDS IN CEREAL FIELDS 122

ABSTRACT 122
INTRODUCTION 123
MATERIALS AND METHODS 125
LARGE-SCALE EXPERIMENTS 125
SMALL-SCALE EXPERIMENTS 126
GENOTYPIC ANALYSIS OF R. PADI POPULATIONS ON WINTER HOSTS AND WHEAT FIELDS 127
STATISTICAL ANALYSES 128
ANALYSES OF GENETIC DATA 129
RESULTS 130
LARGE-SCALE EXPERIMENTS 130
SMALL-SCALE EXPERIMENTS 133
GENOTYPIC ANALYSIS OF R. PADI POPULATIONS ON WINTER HOSTS AND WHEAT FIELDS 137
DISCUSSION 140
LARGE-SCALE EXPERIMENTS 140
SMALL-SCALE EXPERIMENTS 143
GENOTYPIC ANALYSIS OF R. PADI POPULATIONS ON WINTER HOSTS AND WHEAT FIELDS 145
CONCLUSIONS 148
Acknowledgements 148

CHAPTER 5: ATTRACTIVENESS AND HOST SUITABILITY OF WINTER WHEAT CULTIVARS FOR CEREAL APHIDS (HEMIPTERA: APHIDIDAE) 150

ABSTRACT 150
INTRODUCTION 151
MATERIALS AND METHODS 152
EXPERIMENTAL DESIGN 152
WINTER WHEAT CULTIVARS 152
CEREAL APHIDS 153
ANTIBIOSIS EXPERIMENTS 153

SETTLEMENT EXPERIMENTS 154
INFESTATION LOSS RELATION EXPERIMENTS 154
STATISTICAL ANALYSES 155
RESULTS 155
ANTIBIOSIS EXPERIMENTS 155
SETTLEMENT EXPERIMENTS 159
INFESTATION LOSS RELATION EXPERIMENTS 161
DISCUSSION 162
ANTIBIOSIS EXPERIMENTS 162
SETTLEMENT EXPERIMENTS 163
INFESTATION LOSS RELATION EXPERIMENTS 164
IMPORTANCE FOR POPULATION AND MIGRATION MODELS 165
IMPORTANCE FOR INTEGRATED PEST MANAGEMENT 166
Acknowledgements 167

CHAPTER 6: COMPARISON OF TECHNIQUES TO SURVEY POPULATIONS OF CEREAL APHIDS (HEMIPTERA: APHIDIDAE) IN WINTER CEREALS DURING AUTUMN AND SPRING WITH SPECIAL CONSIDERATION OF SAMPLE SIZE 168

ABSTRACT 168
INTRODUCTION 169
MATERIALS AND METHODS 171
FIELD SAMPLING 171
VISUAL COUNTS 172
PLANT SAMPLING 172
D-VAC SAMPLING 172
SAMPLING TECHNIQUES FOR WINGED APHIDS 173
STATISTICAL ANALYSIS 173
METHODS AND PRECISION OF SAMPLE SIZE ESTIMATION 174
RESULTS 176
GENERAL POPULATION DEVELOPMENT 176
COMPARISON OF SAMPLING TECHNIQUES 176
COEFFICIENT OF VARIATION 181
RELEASE AND RECAPTURE EXPERIMENTS 181
CALCULATION OF SAMPLE SIZE 183
DISCUSSION 184
COMPARISON OF SAMPLING TECHNIQUES 184

COEFFICIENT OF VARIATION 186
CALCULATION OF SAMPLE SIZE 187
CONCLUSIONS 190

GLOBAL DISCUSSION 192

MODEL COMPARISONS 192
CEREAL APHID GRADATION 193
IMPLICATIONS FOR PRACTICE AND ECONOMIC FRAMEWORK 196
MIGRATION MODELS 198
COMPARISON OF LOCATIONS 199
IMPROVEMENT OF MIGRATION MODELS 199
VALIDATION METHODS FOR THE DEVELOPED MODELS 202
DISPERSAL AND MIGRATION IN THE CONTEXT OF POPULATION GENETICS 203
HOLOCYCLIC VS. ANHOLOYCLIC LIFE STRATEGIES 204
DISPERSAL BEHAVIOUR 204
POPULATION GENETICS - SUBPOPULATIONS 205
MIGRATION MODELS 206
HOST PLANT INTERACTIONS 207
MEAN RELATIVE GROWTH RATE (MRGR) 208
GENOTYPIC HETEROGENEITY 208
EVALUATION TECHNIQUES FOR INSECT POPULATIONS 209
CEREAL APHID POPULATION DYNAMICS 209
EFFECTS OF NATURAL ENEMIES 211
FUTURE PROSPECTS 213
CLOSING STATEMENTS 214

REFERENCES 216

ACKNOWLEDGEMENTS 238

CURRICULUM VITAE (ENGLISH) 240

CURRICULUM VITAE (DEUTSCH) 242

List of abbreviations

a = intercept

ANOVA = analysis of variance

ANCOVA = analysis of co-variance

b = slope

BYDV = barley yellow dwarf virus

cl = confidence interval

cv = coefficient of variation

D = distance

d = level of precision

dd = degree day

df = degree of freedom

DNA = deoxyribonucleic acid

D/V = D-VAC to visual catch ratio

D-VAC = Dietrick-Vacuum insect net

DWD = Deutscher Wetter Dienst (German Weather Service)

FN = false negative

FP = false positive

GIS = geographic information system

G/N = gene diversity / genotypic diversity

GS = growth stage

HPLC = Hochleistungsflüssigkeitschromatographie
(engl.: high performance liquid chromatography)

IPM = integrated pest management

IPP = Institut für Pflanzenkrankheiten und Pflanzenschutz

Isern. = Isernhagen (location of a case study)

ISIP = Information System Integrated Plant Protection

K = number of distinct populations

Lin DA = linear discriminant analysis

Log RA = logistic regression analysis

LRT = likelihood ration test

m = mean

MRGR = mean relative growth rate

N, n = sample size (basic and sub populations)

nLS = northern Lower Saxony

PCR = polymerase chain reaction

p_p = prior probability

p_{pf} = prior probability for field data

p_{ps} = prior probability for suction trap data

p_{po} = posterior probability

ps = preliminary survey

P/V = plant sampling to visual catch ratio

R5.10, R5.50 = loci isolated from *Rhopalosiphum padi*

R = coefficient of correlation

R^2 = coefficient of determination

$\mathrm{r_m}$ = intrinsic rate of natural increase

ROC = receiver operating characteristic curves

RP = Rheinland Palatinate

S16b, S17b = loci, isolated from *Sitobion miscanthi*

s, s^2 = standard deviation, squared standard deviation

SA = Saxony Anhalt

sBR = southern Brandenburg

SD, SE = standard deviation, standard error

sLS = southern Lower Saxony

SPRP = sample size with percentage relative precision

SPS = sample size according to preliminary survey

SR = sample size according to regression

ST-93 = Strube-type 93-11-21

T = tally threshold

TGW = thousand grain weight

TN = true negative

TP = true positive

VOC = volatile organic compounds

wb = winter barley

ww = winter wheat

z = discriminant function

z_α = standard normal deviate

Summary

Cereal aphids occasionally cause economically relevant yield losses in winter cereals, particularly when optimal abiotic and biotic factors for the pest are present. The lack of precise knowledge about the migration (immigration) of the aphids to the plants is a critical bottleneck for early-season simulation of cereal aphid population development (i.e. till the end of flowering). There are considerable gaps in knowledge about autumn and spring immigration and the early population development that ensues. The central aim of the present three-year project was therefore to analyse and characterise the migration and early population development of cereal aphids and to use this information to construct models of relevance to aphid control practice.

Cereal aphids were collected daily from aerial plankton (using suction and yellow water traps) and evaluated weekly in cereal crops (winter wheat and winter barley) at different locations in Germany during the 2003/2004 to 2005/2006 growing seasons. Moreover, historical datasets from field evaluations, suction traps, and yellow water traps were also assessed. Detailed meteorological data for each study location were obtained from the German Weather Service (DWD) and from the Information System Integrated Plant Protection (ISIP) service.

Comparison and validation of the SIMLAUS, LAUS, and GETLAUS01 models showed low (LAUS) to high (GETLAUS01) predictive accuracy, as determined by comparison with field data. SIMLAUS predicted accurately the type of hibernation of *S. avenae* and *R. padi*, but failed to correctly forecast the population dynamics in autumn. Systematic errors, differences in reliability between case studies, and the possibility of model extensions were discussed in terms of improving simulation models for decision support systems in integrated pest management.

Forecasting models for cereal aphid outbreaks (i.e. gradations) in winter wheat were developed using different statistical techniques in order to set-up rules for early decision making for insecticide treatments at ear emergence. This should meet the demands of farmers much better then the current late threshold level. The four different models are dependant on either temperature-derived predictor variables (submodel “winter conditions”) or suction trap-derived predictor variables (submodel “real migration”), showing high levels of accuracy with different validation methods.

Six migration models based on meteorological parameters (focussing on the light hours of a given day) were likewise developed using amount-specific or species-specific features to characterise days with or without cereal aphids caught in suction traps in autumn (September 22nd to November 1st) and spring (May 1st to June 9th). The number of cereal aphids caught in suction traps increased with increasing temperature, global radiation, and duration of sunshine, and decreased as precipitation, relative humidity, and wind speed increased. The models achieved diverse levels of (low) accuracy; they may be helpful for assessing the start and amount of aphid immigration into cereal crops, which is most important for field monitoring.

The contribution (density dependence) of available winter hosts on the shift (immigration) and the early population development of host-alternating cereal aphid species in cereal crops was assessed in small-scale (i.e. one field) and large-scale (at landscape level) field trials. Significant higher counts of *R. padi* and *M. dirhodum* in cereal crops were observed in landscapes with higher numbers of winter hosts. Concerning small-scale experiments, cereal fields adjacent to a large hedge with several winter hosts were directly influenced by distance between winter and summer hosts in the case of the former, but not the latter species. After tracking aphid movements at the field scale (using four microsatellite markers), no spatial genotypic structure was found for winged *R. padi*.

The effects of eight current winter wheat cultivars on cereal aphid immigration and early population development were evaluated in terms of antibiosis, aphid settlement behaviour, and the infestation yield loss relation. Whereas the cultivar Hybnos I significantly reduced numbers of offspring of caged *M. dirhodum* and *S. avenae* at seedling stages (growth stage 13, in laboratory), no significant differences in aphid development were observed among cultivars during later crop growth stages (GS 30/32 and 65/69). None of the cultivars proved to be superior to the others, neither in terms of settlement behaviour (immigration) nor in terms of yield (i.e. crop yield, hectolitre weight, protein content). Moreover, no striking indications for different aphid susceptibilities could be found in the set of cultivars tested.

Our assessment of the efficiency of different techniques for cereal aphid surveying in autumn and early spring showed that the highest numbers of aphid instars per m² were detected by plant sampling (i.e. collecting whole plants from fields for evaluation in the laboratory). Visual counts (i.e. *in situ*) were most effective for producing a rough and quick estimate of the overall population density (i.e. for management strategies). The mobile D-VAC suction sampler turned out to be the least effective technique and was found to be unsuitable for the collection of cereal aphids in autumnal crops. We also compared minimum sample size estimates obtained by different calculation methods (Feng & Nowierski, 1992; Greenwood & Robinson, 2006) using numerical, visual counts at several levels of precision (i.e. 50%, 30%, 20%, and 5% precision). The results demonstrate the importance of sample size and sampling technique for cereal aphid surveys performed in winter wheat and in winter barley in autumn and early spring.

Keywords:

Population dynamics, population models, migration models, winter-to-summer host ratio, distance regulation, microsatellite genotyping, density dependence, sample size, sampling techniques

Resumé

Les pucerons de blé provoquent occasionnellement des pertes de rendement de grain de blé d'hiver, particulièrement quand les facteurs abiotiques et biotiques sont optimaux pour le développement des ravageurs. La détermination précise de la migration (immigration) s'avère critique pour une simulation saisonnière précoce du développement des populations des pucerons de blé (avant la fin de la fleuraison de blé d'hiver). Cependant, il y a d'importantes lacunes en matière de migration aussi bien automnale que printanière, ainsi que pour le développement des populations suivantes. Sur ce, le principal objectif de ce projet de trois ans était d'analyser et de déterminer la migration et le développement des populations, de même que la construction des modèles correspondants avec une relevance pratique.

Les pucerons de blé étaient journellement collectés du plancton aérien (en utilisant des pièges à succion et des pièges jaunes à eau) et évalués hebdomadairement dans les champs des céréales (le blé d'hiver et l'orge d'hiver) dans différents sites en Allemagne pendant les saisons agricoles de 2003/2004 à 2005/2006. En outre, les donnés historiques des évaluations visuelles au champ, des évaluations des pièges à succion et des pièges jaunes à eau étaient exploitées. Pour chaque site d'étude, les paramètres météorologiques détaillés étaient disponibles à travers le Service Météorologique Allemand (DWD) et le service du Système Informatique pour la Protection Intégrée des Plants (ISIP).

Les comparaisons et validations des modèles SIMLAUS, LAUS, et GETLAUS01 ont montré une précision pronostique faible (pour le modèle LAUS) ou forte (pour le modèle GETLAUS01) par rapport aux données du champ. Le modèle SIMLAUS a fourni une prédiction précise du mode d'hibernation de *S. avenae* et de *R. padi* pendant que la dynamique des populations d'automne n'avait pas pu être prédite par ce model. Les erreurs systématiques, les différences en fiabilité entre les études des cas, et la possibilité d'élargissement des modèles ont été discutées en vue d'une amélioration des modèles de simulation pour des systèmes de décision en lutte intégrée contre les ravageurs.

Des modèles prédictifs de l'envahissement intense des champs le blé d'hiver par les pucerons (gradation) sont développés avec des techniques statistiques différentes en vue de mettre au point des règles pour la prise de décisions précoce en terme d'application des insecticides à l'épiaison. Ces modèles répondent mieux aux attentes pratiques des paysans plus que ne le permet le concept actuel des valeurs de seuil. Les quatre modèles différents sont dépendants soit des variables prédictives dérivées de la température (modèle inférieur « condition d'hiver ») soit du pièges à succion (modèle inférieur « migration réelle »). Ces modèles présentent un niveau de précision élevée avec des méthodes de validation différentes.

De même, six modèles de migration basés sur des paramètres météorologiques (en considérant la durée d'éclairage d'un jour donné), ont été développés, spécifique soit par nombre ou par espèce, pour caractériser des jours avec ou sans pucerons de blé capturés dans les piège de succion en automne (de 22/09 en 01/11) ou au printemps (de 01/05 en 09/06). Avec l'élévation des températures, avec le rayonnement global et les durées d'insolation plus en plus longues, le nombre des pucerons de blé collectés dans les pièges de succion a augmentait, pendant que leur nombre diminuait avec l'augmentation des précipitations, d'humidité relative ou de la vitesse du vent. La performance des modèles a montré des différents niveaux (bas) de précision. Ces modèles seraient particulièrement utiles pour l'estimation du début d'infestation et du nombre des pucerons immigrés dans les champs de céréales; ce qui est très important pour la suivie au champ.

La contribution (dépendant de la densité) des hôtes d'hiver disponibles pour le changement (immigration) et le développement précoce de population de pucerons de blé (espèces alternants les hôtes) a été examinée en culture céréalière à petite échelle (au niveau du champ) ou à grand échelle (au niveau du paysage). Au comptage, le nombre de *R. padi* et *M. dirhodum* en cultures céréales était significativement plus élevé dans les paysages comportant plusieurs hôtes d'hiver. Pour ce qui concerne les essais à petite échelle, les champs céréales proches d'une grande haie avec plusieurs hôtes d'hiver ont montré une influence directe de la distance entre les hôtes d'hiver et d'été pour la première l'espèce, mais pas pour la dernière. En suivant les mouvements à l'échelle champêtre, aucune structure génotypique spatiale était trouvée pour des *R. padi* ailé (en utilisant quatre markers microsatellites).

Les influences de huit cultivars de blé d’hiver par rapport à l’immigration et au développement précoce des populations ont été évaluées en terme d’antibiose, du comportement de colonisation et des relations entre les pertes de rendement et les infestations. Le cultivar Hybnos I a provoqué une réduction significative du nombre de descendants de *M. dirhodum* et de *S. avenae* encagés sur les jeunes plants (phase de développement 13, au laboratoire). En outre, aucune différence significative n’a été observée dans le développement des pucerons sur les plantes en stade de développement avancé (phase de développement 30/32 et 65/69) pour les différents cultivars examinés. De même, aucune supériorité d’un cultivar n’a été observée, ni dans le comportement de colonisation (immigration), ni dans les réductions des pertes de rendement (rendement des épis au champs, des poids de hectolitre, du teneur de protéine). Dans l’ensemble, aucune différence n’a pu être démonstrée pour la susceptibilité aux pucerons des différents cultivars de blé qui ont fait l’objet de l’étude.

L’étude de l’efficacité de diverses techniques de collecte des pucerons de blé en automne et au début printemps a révélé un nombre significativement élevé des aspects de pucerons par m² en utilisant un échantillonnage de plantes entièrement collectées au champ et évaluées au laboratoire. Le comptage visuel (*in situ*) s’est révélé la méthode la plus efficace, si une estimation approximative et rapide de la densité de population était nécessaire. Par contre, le piège mobile de succion (D-VAC) s’est révélé le moins efficace et était inutilisable pour la collecte des pucerons de blé sur les plantes cultivées en automne. Pour l’évaluation des pucerons de blé, les échantillons minima sont comparés par rapport aux différentes méthodes (Feng & Nowierski, 1992; Greenwood & Robinson, 2006) en utilisant des comptages numériques et visuels avec différents niveaux de précision (i.e. 50%, 30%, 20%, et 5% niveaux de précision). Les résultats ont indiqué l’importance de la taille des échantillons et de la technique de comptage des pucerons de blé sur le blé d’hiver et l’orge d’hiver en automne et au début printemps.

Des mots clés:

Dynamique des populations, modèles de population, modèles de migration, ratio des hôtes d’hiver aux été, régulation de distance, structure génotypique spatiale par microsatellites, dépendance de densité, taille des échantillons, techniques de collecte

Zusammenfassung

Relevante Ertragsverluste durch Getreideblattläuse werden nur dann in Wintergetreide hervorgerufen, wenn abiotische und biotische Faktoren im Optimum für die Entwicklung der Schädlinge vorliegen. Als ein kritischer Punkt für die Simulation der Populationsentwicklung von Getreideblattläusen zu einem frühen Zeitpunkt in der Saison (d.h. bis zum Ende der Winterweizenblüte) wird die präzise Determinierung der Migration (besonders der Immigration) angesehen. Jedoch gibt es bemerkenswerte Wissenslücken bzgl. der Herbst- und Frühlingsimmigration und der sich anschließenden, frühen Populationsentwicklung. Deshalb ist die Analyse und Determinierung der Migration und der frühen Populationsentwicklung, für die praxisrelevante Modelle entwickelt werden sollen, das zentrale Ziel dieser dreijährigen Studie.

Getreideblattläuse wurden täglich im Luftplankton mittels Saug- bzw. Gelbschalen und wöchentlich in Getreidefeldern (Winterweizen und Wintergerste) an verschiedenen Standorten in Deutschland in der Vegetationszeit zwischen 2003/2004 und 2005/2006 gesammelt. Darüber hinaus wurden historische Datensätze von Feldbonitierungen und aus Saug- bzw. Gelbschalenfängen eruiert. Für jede Kombination aus Standort und Jahr (entspricht einer Fallstudie) standen detaillierte meteorologische Parameter durch den Deutschen Wetterdienst (DWD) und das Informationssystem Integrierter Pflanzenschutz (ISIP) zur Verfügung.

Der Vergleich und die Validierung der Modelle SIMLAUS, LAUS und GETLAUS01 zeigte geringe (z.B. Modell LAUS) bis hohe (z.B. Modell GETLAUS01) Vorhersagegüten im Vergleich mit Felddaten. Das Modell SIMLAUS sagte sehr genau den Überwinterungstyp von *S. avenae* und *R. padi* vorher, jedoch versagte das Modell, die Populationsdynamik im Herbst richtig zu simulieren. Systematische Fehler, Unterschiede in der Verlässlichkeit zwischen verschiedenen Fallstudien und die Möglichkeit von Modellerweiterungen wurden diskutiert in Bezug auf die Verbesserung von Simulationsmodellen für entscheidungsunterstützende Systeme im Integrierten Pflanzenschutz.

Vorhersagemodelle für Getreideblattlausgradationen (d.h. hohe Populationsniveaus) im Winterweizen wurden entwickelt unter Verwendung von verschiedenen statistischen Methoden mit dem Ziel, zeitige Entscheidungsregeln für eine Insektizidbehandlung zum Ähreschieben aufzustellen, welche wesentlich besser an die Bedürfnisse der Landwirte angepasst sind als das aktuelle Bekämpfungsschwellenkonzept zum Ende der Winterweizenblüte. Die vier unterschiedlichen Modelle, die entweder mit temperaturabhängigen (Untermodell „Winterbedingungen“) oder von Saugfallenfängen

(Untermodell „Tatsächliche Migration“) abgeleiteten Prädiktoren berechnet werden, zeigen hohe Vorhersagegüten in verschiedenen Validierungsmethoden.

In ähnlicher Weise wurden sechs Migrationsmodelle entwickelt, die auf meteorologischen Parametern (bezogen auf die Lichtzeiten eines gegebenen Tages) basierend entweder anzahlspezifisch oder artenspezifisch im Herbst (22.09. bis 01.11.) bzw. im Frühling (01.05. bis 09.06.) die Tage mit und ohne Flugaktivitäten der Getreideblattläuse (in Saugfallen gefangen) charakterisieren. Mit zunehmender Lufttemperatur, Globalstrahlung und Sonnenscheindauer stieg die Anzahl der Getreideblattläuse in Saugfallenfängen, wohingegen geringere Mengen gefunden wurden, wenn Niederschlag, relative Luftfeuchtigkeit und Windgeschwindigkeit zunahmen. Das Modellbetriebsverhalten zeigte unterschiedliche (geringe) Genauigkeiten, so dass die Verwendung besonders für den Start und den Umfang der Blattlausimmigration in Getreidekulturen geeignet ist, welche wiederum besondere Bedeutung im Feldmonitoring haben.

Der Beitrag (Dichteabhängigkeit), den vorhandene Winterwirte auf die Verlagerung (Immigration) und die frühe Populationsentwicklung der wirtswechselnden Getreideblattlausarten in Getreidekulturen haben, wurde in kleinräumigen (innerhalb eines Feldes) und großräumigen (auf Landschaftsebene) Feldversuchen abgeschätzt. Signifikant höhere Anzahlen von *R. padi* und *M. dirhodum* wurden in Getreidefeldern in solchen Landschaften beobachtet, in denen auch viele Winterwirte vorhanden waren. Bezogen auf die kleinräumigen Versuche zeigten Getreidefelder, die an eine breite Hecke mit mehreren Winterwirten angrenzten, einen direkten Einfluss der Entfernung zwischen Winter- und Sommerwirten für die erstgenannte, jedoch nicht für die letztgenannte Aphidenart. Beim Verfolgen der Bewegungen im Feldmaßstab konnte für geflügelte *R. padi* keine genotypische Struktur unter Verwendung von vier Mikrosatellitenmarkern gefunden werden.

Der Einfluss von acht Winterweizensorten auf die Immigration und frühe Populationsentwicklung von Getreideaphiden wurde hinsichtlich der Antibiosiswirkung, des Besiedelungsverhaltens und der Befalls-Ertragsverlust-Relation untersucht. Während die Sorte Hybnos I die Anzahl des Nachwuchs von aufgekäfigten *M. dirhodum* und *S. avenae* im Sämlingswachstum (Wachstumsstadium 13, im Labor) signifikant reduzierte, konnten in späteren Pflanzenentwicklungsstadien (Wachstumsstadien 30/32 und 65/69) keine signifikanten Unterschiede zwischen den Sorten erkannt werden. Darüber hinaus zeigte sich keine Überlegenheit einer Sorte, weder bzgl. des Besiedelungsverhaltens (Immigration) noch bzgl. reduzierter Erträge (Kornerträge, Hektolitergewichte, Proteingehalte). Keine bemerkenswerten Anhaltspunkte für unterschiedliche Aphidenanfälligkeit konnte unter den getesteten Sorten gefunden werden.

Bei der Abschätzung der Effizienz von unterschiedlichen Erfassungstechniken für Getreideblattläuse im Herbst und zeitigem Frühjahr zeigte sich, dass die signifikant höchsten Anzahlen von Aphidenerscheinungsformen pro m² mit den Pflanzenproben (d.h. dem Sammeln von ganzen Pflanzen im Feld für die Bonitierung im Labor) gefunden wurden. Visuelle Zählungen (*in situ*) stellten sich als besonders effektiv heraus, wenn eine ungefähre und besonders schnelle Schätzung der allgemeinen Populationsdichte gebraucht wurde (z.B. für Managementstrategien). Der mobile D-VAC Saugapparat hingegen war am wenigsten effektiv und somit ungeeignet, um Getreideblattläuse in herbstlichen Kulturen zu sammeln. Bezüglich der Bonitierungen von Getreideaphiden wurden minimale Stichprobengrößen verglichen, die mit unterschiedlichen Methoden (Feng & Nowierski, 1992; Greenwood & Robinson, 2006) unter Verwendung von numerischen, visuellen Zählungen bei verschiedenen Präzisionsgüten (50%, 30%, 20% und 5% Präzision) errechnet wurden. Die Ergebnisse zeigen die besondere Bedeutung der Stichprobengröße und der verwendeten Erfassungstechnik für die Beobachtung von Getreideaphiden in Winterweizen- und Wintergerstenfeldern im Herbst und im zeitigen Frühjahr.

Schlüsselwörter:

Populationsdynamiken, Populationsmodelle, Migrationsmodelle, Winter- zu Summerwirt Relation, Entfernungsregulation, Mikrosatelliten Genotypisierung, Dichteabhängigkeit, Stichprobe, Sammeltechniken

“Aphids have fascinated and
frustrated man
for a very long time”

A. F. G. Dixon, 1998

Global Introduction

Importance of cereal aphids

Today, cereal aphids represent the most important pests of winter cereals causing substantial yield losses. On the one hand, cereal aphids transmit as vectors harmful viral plant diseases, with patho-types of the Barley Yellow Dwarf Virus (BYDV) being most relevant in winter barley but also in winter wheat. On the other hand, cereal aphids directly cause damage as phloem feeders including the excretion of carbohydrate rich faeces solutions (so-called honey-dew). The sucking activity with removal of assimilates is of particular economic importance in winter wheat during the growth stages (GS) of grain development.

The increasing damage potential during the last 30 years in northern and western Europe was related to the continuously increased agricultural management of grains. Yields in winter cereals increased on average more then 40% and are approx. 160% above the worldwide level with an average of 6.600 kg per ha today (European agricultural statistics, 2008). With the first gradation in 1968, cereal aphids came into focus and constitute up to the present the most relevant wheat pests in central Europe. In this context, the term “gradation” referred to cereal aphid outbreaks (i.e. exceptional high population levels) in winter wheat after flowering as defined according to Ohnesorge (1991).

Important factors, supporting cereal aphid development, have been identified: The development of late ripening and high yielding cultivars, enhanced nitrogen fertilisation, increased proportion of cereals in the crop rotation, dense crop stands on extended areas, the intensive control of competing fungal diseases as well as a decreasing impact of natural enemies due to the side effect of insecticides and habitat changes. Convenient host plants of high nutritional quality for cereal aphids, which allow intensive reproduction and multiple generation cycles, are widely available (Hasken & Poehling, 1995; Richter, 2000). Therefore, cereal aphids can build-up large populations, and accordingly, they bring about yield losses, which can exceed 60% in winter barley and 20% in winter wheat (Rabbinge & Vereijken, 1979; Wratten & George, 1985; Niehoff & Stäblein, 1998).

Regarding abundance (in crops) and damage potential, *Sitobion avenae* F., *Metopolophium dirhodum* Walk., and *Rhopalosiphum padi* L. are the most important species in central Europe. Direct damage and the responding yield losses caused by *S. avenae*, which prefers to feed on the ears, amount about double the loss, which results from an even infestation of the leaves, e.g. by *M. dirhodum* (Niehoff & Stäblein, 1998). *R. padi*, however, is most dominant migrating species, especially significant as virus vector for early BYDV-infection of emerging winter cereals in autumn. This species can normally be found on the lower leaves and attains high population levels, especially when infestation starts early and the weather is moderately cold and humid (Wiktelius, 1992; Ekbom et al., 1992).

Risks for cereal yields can be roughly divided in aphid vector activities for virus transmission and damage associated with nutrient uptake. Whereas the epidemiology of the virus diseases is mainly a function of aphid seasonal activity pattern (infection time and secondary distribution) and here, even single sucking events can led to severly damage of the whole plants, the sucking damage with nutrient uptake is strongyl density realted. Cereals tolerate or might even be stimulated from few aphid individuals per tiller by enabling a disproportionate increase of photosynthetic activity (Wetzel, 2004). However, at higher population densities the loss of assimilates cannot be overcompensated. Though yield losses rise with increasing pest density, the yield loss per aphid, which may range between 0 and 0.4 mg yield loss per aphid day, decreases (Niehoff & Stäblein, 1998). The high variability of feeding induced yield losses in relation to aphid infestation levels results from the different sensitivity of the host plant between the flowering (GS 69) and early drought stage of winter wheat (GS 83). Hence, the amount of yield losses does not only dependent on aphid peak densities but also on time and duration of infestation of cereal aphid species (Rappaport, 1998).

The population dynamics of cereal aphids depends on a number of factors, both abiotic (e.g. temperature, precipitation) and biotic (e.g. intraspecific density effects, host plant quality, interspecific competition by predators, by parasitoids, but also by fungi or virus colonizing the same host plant). Therefore, cereal aphid gradations with economically relevant yield losses only occur in seasons with especially impact of single important key factors or of combinations of several minor regulating factors.

Threshold level concepts and their problems

Integrated control strategies for cereal aphids are mainly based on threshold levels and forecast models. Classical integrated pest management (IPM) should be based on the concept of economic thresholds, which have been defined for cereal aphids. However, in most seasons this critical thresholds are reached during the period of exponential growth of aphid populations and even short delays in application of pesticides can result in strong overrun of that limits. To avoid risks for farmers, control thresholds were specified from series of field studies, distinctly lower than the “real” economic threshold (Holz & Wetzel, 1989; Basedow et al., 1994; Holz et al., 1994; Rappaport & Freier, 2001). The philosophy behind such control thresholds is that if cereal aphid populations exceed a control threshold level, the probability is high that the economic threshold level will be reached soon after. Moreover, in classical terms of IPM thresholds based on economical evaluations should consider not only the pest induced yield losses, but flexible calculate the relation expected between yield losses and expenses for control. That implies to consider fluctuating prices for the produce on one hand and for variable and fixed costs for the management on the other hand. Actually, however, practical management is far away from such sophisticated post management strategies, and plant protection services recommend control decisions according to simple and fixed control threshold levels. A fixed threshold level of more than three aphids per ear and flag leaf is most widespread recommended by plant protection services (Basedow et al., 1994; Rappaport, 1998; F. Burghause, B. Freier, E. Jörg, S. Krüssel, P. Matthes, pers. comm.).

The dilemma of improved and much more sensitive threshold levels, which have been developed by different scientific studies, is their low acceptance in practice. The main reason for this is the increasing labour input. Important steps towards more flexible thresholds would be to consider species-specific threshold levels, since the damage potential of the main aphid species is quite different and furthermore, the assessment of the important regulating potential of natural enemies is most relevant (Rappaport & Freier, 2001). However, such improved models will only be implemented, if the effort for the farmers to raise input values will be paid-off. Furthermore, the broad acceptance and large-scale implementation in practice of the recent threshold level concept (Basedow et al., 1994; Rappaport & Freier, 2001) is hindered by the effective seasonal date of its application. Previous concepts only become effective after flowering of winter wheat (GS 69).

For economic reasons, the practical use of insecticides against aphids in winter wheat is often combined with the use of fungicides, as so-called final treatment or ear treatments, following the ear emergence (GS 55). These treatments against aphids are mostly of prophylactic character, since at that time in most seasons aphid densities are low and the threshold level concepts mentioned above are not adjusted for decisions that early. The reasons of final treatments are mainly fungal infestation of wheat (e.g. powdery mildew *Blumeria graminis* Speer ex DeCandolle, Septoria leaf blotch *Septoria tritici* Rob. ex Desm., and Fusarium head blight *Fusarium graminearum* Schwabe), which may cause fast decay of leafs. Especially the flag leaf is most relevant as source organ of assimilates for the time of ear filling (and subsequently for yield), legitimating application of fungicides. The secondrank added insecticides and the resulting combined applications implement action targeted at economic working.

Prophylactic treatments, however, are undesirable from an economical as well as from an ecological point of view. First of all, aphid infestation does not reach the economic threshold level in all locations and all years (Basedow et al., 1994). Multiple case studies (i.e. research activities in a given location and year) in Magdeburger Börde during the last years (1970-2007) showed that gradations of cereal aphids in winter wheat occurred approx. every third to fourth year. Subsequently, an insecticide treatment was simply waste of money in remaining 73% of case studies (Freier et al., 2002). Secondly, the use of insecticides against cereal aphids can cause adverse effects on natural regulation (Dixon, 1998). Most active agents actually used are of limited selectivity regarding the broad and diverse spectrum of natural enemies. Side effects by acute toxicity are unavoidable and can strongly influence the build-up of effective antagonist populations. This effect can be amplified by too early deprivation of aphids as necessary prey or host, notably for specialized predators or parasitoids. Unfortunately, aphids often recover faster after insecticide treatments, due to their high reproduction and immigration rates, leading to disproportional prey-predator or host-parasite relationships with disturbed balance and synchronisation between aphids and their competitors. In spite of all, about 30% of the wheat area in all Germany has been prophylactic treated in the past (European agricultural statistics, 2008). Locally, however, the intensity of insurance spraying can be much higher (> 50%), because very typical differences in the aphid infestation of wheat may regionally arise, which is related to the climate, the intensity of the culture treatment (and yield expectations), and also to the structure of the rural area.

The whole problem of early insecticide applications can be considerably improved, if the potential economic damage of aphids can be assessed at an earlier time point, when in the majority of cases regular fungicide treatments at GS 55 are applied. Hence, there is a strong interest by field advisers and farmers to have a reliable early decision support to use insecticides in winter wheat much more targeted.

Population models

Since the beginning of the eighties, several simulation models have been developed to calculate and forecast the population development of the most important cereal aphid species, and in some cases they can also be used to estimate yield losses. The models partly considered many different factors, which influence the population development of aphids, such as weather (e.g. temperature), appearance of antagonists, and nitrogen supply. Simulation models do exist for *S. avenae, M. dirhodum*, and *R. padi* (Friesland, 1986; Kleinhenz, 1994; Ma, 2000; Gosselke et al., 2001) and detailed simulation runs reproduced the dynamics of field situations correctly in summer populations (i.e. à posteriori; Gosselke et al., 2001; Freier et al., 2002). However, models describing the population dynamics in great detail in autumn or in spring and early summer (i.e. before GS 69) are lacking. In some cases, high variations between the population dynamic simulated by vague models and the real field situation were observed. A major drawback is doubtless that models do not consider in detail the immigration of cereal aphids into the crops, which might be of particular importance for the early population development in autumn or after wintertime. Validated models for predicting the spring migration (e.g. immigration) of cereal aphids are not available at the moment, but are already being developed for e.g. aphids in salad (Tatchell, 2007). A weak point in modelling attempts for early population developments (in autumn and spring) in general, and for the migration of aphids in particular, is a sound validation of the models. The confidence in population models is a vital point in their application, interpretation, and integration in decision support systems. Due to limited financial support, most developed models were only rough and short time verified and validated (Knudsen & Schotzko, 1999; Ma, 2000). Moreover, for the validation usually only a few datasets from limited locations were available (Friesland, 1986; Kleinhenz, 1994; Gosselke et al., 2001). A more broad validation of existing models could help to identify weak points or missing parameters to be considered. Models could be improved and, including corrected substructures, could be adjusted for more sophisticated population models valid during the whole season.

Migration

A critical bottleneck for an early season simulation of aphid development seems to be the precise determination and evaluation of the migration of aphids, especially of immigration phases into cereal crops. Particularly, the timing of aphid arrival on new hosts can influence plant health and yield. This could form a main parameter for the improvement of decision support systems with respect to early warning systems. However, there are considerable gaps in knowledge for both, the spring and autumn seasons, concerning the migration of aphids and the relation of the migration time and intensity to the population build-up in the crop. At present only contradictory and non-statistically proved statements are available, even though considerable research activities have been carried out in Europe. One main problem to illustrate the relation between migration events and population curves is definitely the high temporal and spatial variability in the migration events, so that sound statements can only be made on the basis of long term studies, and by comparison of multiple datasets from several years of investigation. The situation is aggravated by diverse aphid morphs and life stages (polymorphism, polyphenism) that redistribute themselves differently in response to intrinsic and extrinsic factors. Winged cereal aphids have only a considerable small window to fly (i.e. one to five days), which opens shortly after the final moult to adult stage and closes with the beginning of autolysis of wing muscles. Furthermore, flight initiation is primarily restricted to daylight hours and to instances when atmospheric conditions favour take-off. Following the both aspects, migratory events were perceived by some researchers as minimal, and were frequently understated concerning the ecological consequences on profound economic impact aphids have. Aphids move from its source to sink either by unintentionally (i.e. externally forced) or by intentionally (i.e. intrinsic or extrinsic forced) transport mechanisms. After take-off, aphids usually ascend into the surface boundary layer, where they are frequently enabled to considerably control their flight including descending and landing for host search. For such flights, Wenks (1981) used the term “appetitive dispersal” (e.g. secondary, targeted dispersal or “Befallsflug”), which is discriminated from “real” migration (so-called alighting flight or “Distanzflug”) neither by the distances travelled, nor by the mode of transport, but by the “motivating force” behind. For example, an aphid actively seeking a resource item during dispersal, may encounter atmospheric conditions (e.g. thermals winds), where it is then subjected to horizontal translocation, e.g. by low-level-jet streams. This aphid may move over the same distance as a migratory aphid that was just actively flying towards an ultraviolet light source after take-off. Subsequently, suction trap catches or field counts cannot be doubtless referred to the one or other flying movement (Taylor, 1986; Loxdale et al., 1993; Dixon, 1998). Loxdale et al. (1993) found that migration is the exception and that “flying aphids” are most frequently conforming to the appetitive dispersal. However, the importance of long distance to short distance migration is difficult to assess. Extrinsic cues that stimulate for dispersal might be of physical origin, of natural perturbations, host plant mediated or according to crop management practices. But sometimes it may even occur without any apparent external stimulus, just due to the innate strategy to make the best use of a plant resource (Hodgson, 1991). Leaving an undesired host and seeking a new one includes per definition the seeking for an overwintering primary host as well as seeking a secondary host in early spring. This is corroborated by Mackenzie & Dixon (1991), claiming that winged adults produced on a primary host generally do not need to travel by migration (over long distances) to find suitable secondary host plants (i.e. dispersal is sufficient). Given the evidence that migratory cereal aphids most often colonize crops, both modes of movement (i.e. the dispersal and the migration) are equally important. According to the study’s topic, the migration and early population development of cereal aphids are taking the central stage during our investigations. Due to the fact that the expression “migration” is most popular, we use this term not in the restricted, originally way (*sensu stricto*), but including the appetitive (secondary) dispersal. Moreover, we must consider that flying movements of aphids observed during our studies would primarily refer to dispersal, because migration - *sensu stricto* - rarely appeared before mid June in cereals (Loxdale et al., 1993).

For the observation of the flying activity of aphids in general and especially of cereal aphids, fixed suction traps were erected for the first time in 1965 in Europe (in Rothamsted, England) and in 1983 in U.S.A. Today, corresponding suction traps are used in 19 European countries (Harrington et al., 2007). In the “Euraphid” association, the E.U. sponsored several meetings on aphid monitoring. In 2000, the E.U. Thematic Network EXAMINE (EXploitation of Aphid Monitoring systems IN Europe) was set up in order to exchange data from several case studies on an integrated database and to facilitate Europe-wide analyses (Harrington et al., 2004; P. Verrier, pers. comm.).

It has been shown that during the spring and summer migration, for *R. padi* (and partial for *M. dirhodum*), there is normally a strict time synchronisation between the development of winged stages on winter hosts and the first flying activity in spring. The flying activity, which can be recorded e.g. with the help of fixed suction traps, is significantly correlated with the first colonisation of the cereal hosts (Veenker et al., 1998). A corresponding relation could not be found for *S. avenae*, a species not changing its host (i.e. all-season on gramineous plants). Several studies on *S. avenae* in Germany tested single individuals under laboratory conditions for their life-cycle (Weber, 1985; Hoeller, 1990). It has been proven that anholocyclic clones were present in northern Germany, but usually the rather cold winters are likely to eliminate these clones during wintertime (Hoeller, 1990; Williams & Dixon, 2007). It was postulated that these clones might have immigrated from milder climate, as it was observed for entire anholocyclic species like *Rhopalosiphum maidis* (Fitch) that were also found in northern Germany, or *S. avenae* in Sweden or in China (Wiktelius, 1984; Dong et al., 1987). That indicates the basically different hibernation and migration behaviour of *S. avenae*. However, to complicate the situation even more, nothing is really known about the local hibernation and early spring dispersal behaviour of that species. Presumably, *S. avenae* may evolve from very scattered and small subpopulations of circumjacent gramineous habitats, which may contribute than to large summer populations in winter wheat, e.g. in northern Germany (Hoeller, 1990). Apart from density and distribution of sources, climatic conditions seem to be the most important driving forces for cereal aphid population development. Important evidence has become available concerning the influence of weather parameters on the spring migration, because the start of spring migration of cereal aphids was delayed but not prevented with colder temperatures (Walters & Dixon, 1984), which, however, also depended on the geographical latitude (Walters & Dewar, 1986). Veenker et al. (1998) confirmed the influence of the winter temperature on the start of the spring migration. The colonization of cereals began at the end of March or beginning of April after mild winters (e.g. less than 72 freezing days) with a large part of anholocyclical hibernation (Veenker et al., 1998). However, these studies were not aimed to improve decision models for control of summer populations in wheat, but stressed the most problematically spread of BYDV with early immigration or internal crop movement of aphids.

Evaluation of cereal aphid populations

The studies carried out by MeyerZuBrickwedde & Poehling (1996) and Veenker (2000) have so far not been able to identify any significant correlation between the number of aphids caught in the suction traps and their early colonisation density in cereals. This was also the case for earlier studies carried out by Latteur & Nicolas (1987). The missing dependencies are at least also a problem of the often very low numbers caught in spring in fields (Jarosík et al., 2003). Low numbers and aggregated distribution pattern cause severe problems for finding significant and reliable correlations. The selection of sufficient numbers of samples for random sampling strategies and the particular method of collection are extremely crucial.

Previous comments concerning the migration and population development referred primary to early immigration period in spring and subsequent early population development in winter wheat after wintertime. However, the cropping season of winter cereal starts in September and October, and hence, immigration and settlement of aphids during that period can be a key factor for the determination of size and dynamics of locale population development. Moreover, intensive autumn infestation, reproduction, and spread may legitimate control strategies even before winter, particularly regarding the complex of BYDV problems. Up to now, however, neither in-depth studies of the autumn population dynamics, nor scientifically based or founded control thresholds exist. Reliable descriptions of autumn and winter population dynamics and the development and implementation of thresholds suffer mainly from methodological constrains concerning in particular sampling techniques and intensity in the field. A critical comparison of different sampling techniques and appropriate sample sizes is therefore a pending issue.

Landscape structure and population genetics

Besides parameters such as temperature directly driving aphid development and flight activity, the diversity of the agro-ecosystem and so the landscape structure came more and more into focus recently. The three main aspects discussed are the density and distribution (i) of wind-breaking elements, (ii) of potential infestation sources such as winter hosts, and (iii) of the spatial and temporal distribution of refuges or source habitats for natural enemies responsible for important conservation of bio-control for aphid populations. Firstly, landscape structures including hedges and small forests are important in terms of migration. Alighting aphids are attracted to shape size and colour of possible host plants (i.e. the landing targets). Increased numbers of aphids landing on the leeward side of wind-breaking barriers, such as hedgerows, were perceived to result from behavioural attraction to these contrasts and the enhanced physical control over flight direction, when aphids approach to the surface (Isard & Gage, 2001). Secondly, nothing is known about the direct effects of winter host availability for host-alternating aphids towards the immigration and early population development in cereals in Germany. Higher population peaks of *R. padi* in cereal crops have been reported from locations with higher numbers of winter hosts in northern Europe (Leather et al., 1989). However, recent studies from the same locations did not detected clear distribution pattern to the summer population peak (Bommarco et al., 2007). The contribution of winter host densities and distributions has been inadequate under examination concerning the immigration and the early population development, neither in large- nor in small-scale experiments. Thirdly, concerning the population development of cereal aphids, high diversity of landscape structures (e.g. with expanded and connected field margins and hedgerows) promoted the abundance and diversity of predators and parasitoids, and led subsequently to lower peak populations of cereal aphids. Observed significant correlations between structural diversity and reduced aphid performances were attributed to changed predator-prey or host-parasite densities (Roschewitz et al., 2005; Tscharntke et al., 2005; Rossing et al., 2006). The spacious capture and assessment of landscape structures might be therefore an important factor influencing the immigration and early population development of cereal aphids.

Host plant specialisation

As reported above, differences in host plant colour, shape, crop density, and nutrition quality (including plant resistance factors) exert different directed landing and subsequent settlement behaviour. Likewise, literature reviews often referred to varying population levels of cereal aphids in different cultivars of winter wheat in spring and summer. Reports (based on non-statistically proved observations) have been made on different preferences during “attack flight” (Befallsflug) and on the subsequent development potential related to different cultivars (Rappaport, 1998). Moreover different studies on antixenxosis and antibiosis showed that cultivars can influence the performance of aphids (i.e. the attractiveness, growth rates, and development; Escobar et al., 1999; Hesler & Tharp, 2005). However, such results were mainly derived from laboratory examinations or from small-scale experiments, without consideration of actually cultivars grown under natural conditions in the fields. The possible influence of actual cultivars on the population dynamics of the cereal aphids has little been studied up till now (Thieme & Heimbach, 1996), and accordingly, it has not been integrated into the population models (Gosselke et al., 2001). Yearly, several new winter wheat cultivars are licensed on the market, but so far none of them was assessed for resistance characteristics towards most important cereal pests, i.e. *S. avenae* and *M. dirhodum* (Havlickova, 2001; Bundessortenamt, 2006).

Objectives and chapter titles

The present study deals with migration and early population development of aphids in winter cereals and aims to improve decision making for insecticide treatments in order to reduce prophylactic spraying in winter wheat. A three-year field study was intended to clarify the following aspects:

1. The validation of currently available population models for cereal aphids and their possible integration into decision support systems.
2. The evaluation of the possibility to forecast the gradation of cereal aphids in winter wheat at an early growth stage (i.e. before flowering).
3. The evaluation of the possibility to forecast the migration (immigration) of cereal aphids in autumn and spring.
4. The relative importance of proximity between winter and summer hosts on colonisation and early population development of host-alternating aphids in winter cereals.
5. The influence of different cultivars on the settlement (immigration) and (early) population development of cereal aphids in winter wheat.
6. The evaluation of collection methods in autumnally cereals and the significance of the random sample sizes.

Parts of the chapters are prepared or submitted for reviewed journal publications under the following titles:

Chapter 1: Klüken A.M., Hau B., Freier B., Kleinhenz B., Friesland H. & Poehling H.-M. 2008: Comparison and validation of population models for cereal aphids. *Ecological Modelling* (submitted).

Chapter 2: Klüken A.M., Hau B., Freier B. & Poehling H.-M. 2008: Forecasting gradation of cereal aphids (Hemiptera: Aphididae) in winter wheat at ear emergence. *Ecological Modelling* (submitted).

Chapter 3: Klüken A.M., Hau B. & Poehling H.-M. 2008: Forecasting migration of cereal aphids (Hemiptera: Aphididae) in autumn and spring. *Ecological Modelling* (prepared).

Chapter 4: Klüken A.M., Simon J.-C., Hondelmann P., Mieuzet L., Gilabert A., Warmke C., Poehling H.-M. & Hau B. 2008: The importance of proximity between winter and summer hosts on immigration and population development of host-alternating aphids in cereal fields. *Agricultural and Forest Entomology* (prepared).

Chapter 5: Klüken A.M., Hau B. & Poehling H.-M. 2008: Attractiveness and host suitability of winter wheat cultivars for cereal aphids (Hemiptera: Aphididae). *Journal of Plant Disease and Protection* (submitted).

Chapter 6: Klüken A.M., Hau B., Koepke I. & Poehling H.-M. 2008: Comparison of techniques to survey populations of cereal aphids (Hemiptera: Aphididae) in winter cereals during autumn and spring with special consideration of sample size. *European Journal of Entomology* (submitted).

The interested reader may await to the above-mentioned, reviewed papers or refer to further publications of the author group (see curriculum vitae section). Subsections related to the problem of migration and early population development were worked out by T. Bornwasser (B.Sc. thesis, 2005; M.Sc. thesis, 2007), S. Hermus (B.Sc. thesis, 2005), I. Koepke (Diploma thesis, 2006), C. Scholz (B.Sc. thesis, 2006), and C. Warmke (B.Sc. thesis, presumably: 2008).

It is important to notice that each chapter represents one independent part of the thesis. Hence, the reader should not be confused, if meanings of a given letter, number, or variable possibly differ among the chapters.

Chapter 1: Comparison and validation of population models for cereal aphids

A. Michael KLÜKEN[1]*, Bernhard HAU[1], Bernd FREIER[2], Benno KLEINHENZ[3], Hans FRIESLAND[4] & Hans-Michael POEHLING[1]

[1] Institut für Pflanzenkrankheiten und Pflanzenschutz (IPP), Leibniz Universität Hannover, Herrenhäuser Str. 2, 30419 Hannover, Deutschland.
[2] Institut für Integrierten Pflanzenschutz, BBA, 14532 Kleinmachnow, Deutschland.
[3] Zentralstelle der Länder für EDV-gestützte Entscheidungshilfen und Programme im Pflanzenschutz, Rüdesheimer Strasse 60-68, 55545 Bad Kreuznach, Deutschland.
[4] Deutscher Wetterdienst, Agrarmeteorologische Forschung und Beratung, Bundesallee 50, 38116 Braunschweig, Deutschland.

Abstract

Comparison and validation of population models for cereal aphids are a rare but necessary pre-requisite for their use and improvement. Comparison and validation of the models SIMLAUS, LAUS, and GETLAUS01 were carried out for several years in different German locations with considerable different agro-climatic conditions. Therefore, evaluation of cereal aphids and their antagonists was carried out in winter wheat and winter barley fields with density dependent sample sizes. In 96% of simulation runs, the model SIMLAUS predicted accurately the type of hibernation of *S. avenae* and *R. padi* in winter wheat and winter barley fields. In eight of 52 case studies (i.e. locations and years), the model predicted anholocyclic hibernation, though it was not detected in the field. Model employments to forecast the population dynamics of cereal aphids in autumn are not appropriate, because SIMLAUS failed to reliable predict either the population level or changes of a given population. The model LAUS predicted accurately (à priori) the population dynamics of *S. avenae* in spring and early summer in 12 of 35 case studies ($R^2 > 0.36$, $p < 0.05$). Intercepts and slopes differed significantly from zero and one in 2.9% and 83% of case studies, respectively. Improvements of results were obtained for 89.9% of case studies after the adjustment of starting values according to population development (à posteriori). In 82% of simulation runs with the scientific model GETLAUS01 (à posteriori), close relationships between observed and predicted summer population dynamics of all cereal aphids in winter wheat were observed ($R^2 > 0.47$, $p < 0.05$). In 12 case studies, slopes differed significantly from one ($b = 1$), whereas no significant differences from zero were obtained for intercepts ($a = 0$). Systematic errors, differences in reliability between case studies, and the possibility of model extensions are discussed in terms of improving simulation models for decision support systems in integrated pest management.

Introduction

Population models for cereal aphids (Hemiptera: Aphididae) are important tools for several reasons: Firstly, they help to simulate the population development of aphid species in terms of decision making for plant protection measures (Rossing, 1991; Leclercq-LeQuillec et al., 2000). The implementation of well-directed monitoring systems, reliable prediction, and biological or economically-justified control strategies against cereal aphids are the most important targets (Kleinhenz & Jörg, 1998). Secondly, models can help to understand the complex dependencies and interactions between different trophic levels, and enhance our knowledge on the importance of key factors (e.g. sensitivity analysis; Freier et al., 1996). Similar to laboratory experiments (but sometimes even quicker or more economically), models are capable to run experiments with different biotic and abiotic factors involved (e.g. the cereal aphid species; Topping & Sunderland, 1994; Freier et al., 2002). Thirdly, benefits lay in illustrative material and knowledge storage, because quickly generated diagrams and reports of interactions and population developments show interested users the different parameters and prognoses quite plainly (Bianchi & VanDerWerf, 2003, 2004; Parry et al., 2006).

Within the trophic system, winter cereals - cereal aphids - aphid antagonists, several simulation models have been developed over the last decades (Freier & Wetzel, 1980; Carter, 1985; Pierre & Dedryver, 1985). Starting with simple regression attempts in the eighties (Rautapäa, 1976; Entwistle & Dixon, 1987), considerable improvements in aphid system modelling were achieved over the last few years (Zhou & Carter, 1989; Rossing, 1991; Hansen, 1999). For example, Gosselke et al. (2001) defined more than 13 submodels for wheat-aphid-antagonist interactions for the simulation model GETLAUS01. Other models are being constructed to assess how changes in environmental conditions affect cereal aphids (particularly CO_2 concentrations; Wolf et al., 1996; Newman et al., 2003), GIS based spatial models try to explain the influence of landscape structures on spatial distribution (and development) of cereal aphids (Bianchi & VanDerWerf, 2003, 2004; Parry et al., 2006), and migration models try to explain the effect of host-alternation of aphids on seasonal population development (Lushai & Loxdale, 2004; Malloch et al., 2006). Further modelling approaches are focusing on the occurrence and relationships of different aphid clones (i.e. sexual vs. asexual lineages), in order to forecast the spread of barley yellow dwarf virus (BYDV) in winter cereals (Papura et al., 2003; Llewellyn et al., 2004). Whatever the aims, confidence in the performance and reliability of models can be improved by validating them in different regions and in different seasons, covering broad spectrums of weather conditions.

A close agreement between model results and evaluated data within the validation process could lead to confidence in the ability of models. An additional benefit is that the concepts and assumptions underlying each model are scientifically analysed and scrutinised. Tests of very detailed population models (including several species and a certain time span) have to fulfil three requirements. First of all, data used for validation must be independent of those used to develop the model (Passioura, 1973). Otherwise the process is logically circular. Secondly, for most detailed population models it is not sufficient to use only single point data, such as final population peaks, for validation, since a detailed population model should also simulate accurately the population dynamics (Porter et al., 1992). Finally, validation data must have been monitored with sufficient frequency in time during growth and development e.g. of cereal aphids to be reliably.

Cereal aphid population models have been developed for widely varying climatic conditions (Skirvin et al., 1997; Knudsen & Schotzko, 1999; Newman, 2004) and different objectives (Kleinhenz, 1994; Ma, 2000). This has led to completely different models, varying in their description of various processes, input requirements and sensitivities to environmental conditions. Furthermore, the description of processes and the parameters in models are often highly related to their conditions encountered during data generation, which could be rather specific (i.e. seasonal and regional effects) and not universally valid (Porter et al., 1992). Due to limited financial support, most developed models were only roughly and hastily verified and validated (Knudsen & Schotzko, 1999; Ma, 2000). Furthermore, only a few datasets from few locations were used for the validation (Friesland, 1994; Kleinhenz, 1994; Gosselke et al., 2001).

Comparisons and validations of three population models for cereal aphids, developed for the conditions in Germany, were carried out over several years in different locations of Germany with different agro-climatic conditions. The aim of the present study was to verify and review the performance of the models SIMLAUS (Kleinhenz, 1994), LAUS (Friesland, 1994) and GETLAUS01 (Gosselke et al., 2001) in order to compare the models and suggest improvements with respect to the usefulness of models for decision support systems in integrated pest management.

Materials and methods

Field evaluation

Multiple sets of field data on aphid and antagonist densities were used for the validation of models. Field evaluations were conducted in a two ha large, insecticide-free “window” in fields of winter wheat and winter barley in several locations of Germany. Our investigations included weekly counts from October to December and from March until the harvest of the crops during the years 2004 to 2006. On each evaluation day, the numbers of the three most important cereal aphids *Sitobion avenae* Fabr., *Metopolophium dirhodum* Walk., and *Rhopalosiphum padi* L. and their antagonists were evaluated visually (per plant or tiller) or by means of D-VAC suction sampler (per m²; Dinter, 1995). *R. maidis* L. is of minor importance in Germany (Basedow et al., 1994) and usually occurring only in late autumn. For evaluation, reliable distinctions between *R. padi* and *R. maidis* could not continuously be made in all locations, and hence both species were counted together as *R. padi*-group. Sample size per evaluation day varied according to aphid density and ranged from 700 to 35,000 plants (i.e. 4 to 150 m² for D-VAC) in autumn and from 100 to 8,000 tillers in spring and summer. Counts of different forms of aphids and antagonists (e.g. eggs, larvae, pupae, adults and their different forms) per subsample (i.e. per plant, per tiller, or per D-VAC sample) were transformed into area values according to the numbers of tillers or plants per square meter. Additionally, several sweep net catches (sub-sample of 100 hits) were taken in winter barley and winter wheat throughout June to estimate the abundances of antagonists during the phase of rapid aphid population increase in winter wheat (e.g. in growth stage (GS) 51 to 71; Tottman & Broad, 1987).

Tab. 1 gives a summary of datasets and the numbers of locations available for the comparison and validation procedure of the different models, whereas evaluations from a given location and year (i.e. at harvest time of the crop) represent one case study. The growth stages of the crops were evaluated at each time based on the mean of several tillers or plants. The location of each field was chosen according to close proximity of next weather stations (< 20 km). The meteorological data were provided by the German Weather Service (DWD) in Excel tables and compatible files for each of the models. All agronomic practices were carried out according to good agricultural practices in each of the study locations.

Tab. 1: Numbers of datasets available to validate each model: one year at each location represents one validation run per crop. Datasets were taken in winter wheat fields, in case of SIMLAUS additional datasets from winter barley fields were used (sLS = southern Lower Saxony, SA = Saxony-Anhalt, RP = Rhineland Palatinate, nLS = northern Lower Saxony, sBR = southern Brandenburg).

			Total number	Numbers of validation runs		
Region	Location	Year	of fields (*n*)	SIMLAUS	LAUS	GETLAUS01
sLS	Isernhagen	2004-2006	6	6	2	3
sLS	Jeinsen	2004-2005	4	4	1	2
sLS	Hiddestorf West	2004-2006	6	6	3	3
sLS	Hiddestorf East	2004-2005	2	0	0	2
SA	Magdeburg	1993-2002* 2004-2006	16	6	11	3
SA	Bernburg	2004-2006	6	6	2	3
RP	Wörth	2004-2006	6	6	1	3
RP	Wahlbach	2004-2006	6	6	1	3
nLS	Bensersiel	2004-2006	6	6	2	3
nLS	Carolinensiel	2004-2006	6	6	2	3
sBR	Fläming	1993-2002*	10	0	10	0
		Σ	74	52	35	28

*Asterisks indicate datasets collected by working group of Freier (Freier et al., 2002).

Model SIMLAUS

The simulation model SIMLAUS was developed in order to estimate the possibility of anholocyclic hibernation of *S. avenae*, *R. padi* and *R. maidis* in winter barley and winter wheat (Kleinhenz, 1994). The population dynamics of the aphids are forecasted from autumn to early spring (including estimations of possible BYDV outbreaks). Furthermore, decision support for control of aphids and best timing of pesticide application is made. The model takes into account the temperature and precipitation, which are based on the current and predicted values from the weather stations. The submodels of SIMLAUS are based on extended LESLIE-matrices, which describe the age-specific structure of populations in terms of possible transition, reproduction and survival rates. Since temperature was regarded as the most important factor for the development, development rates of instars, probabilities of reproduction and survival of the three cereal aphid species were described with temperature-depended mathematical models. Based on laboratory experiments, basis temperature values for each of the four larval instars served as limits to model their development. Nutrition uptake in dependency on temperature was included to determine the age- and temperature-specific survival probabilities. Based on field observations, mortality rates due to precipitation were additionally determined and integrated in the simulation models.

The model SIMLAUS is available in the Internet (www.isip.de) and currently used by federal plant protection services, where it attained a certain regionally importance (e.g. in Rhineland Palatinate, Hessian and Saxony) to forecast the possible survival of anholocyclic cereal aphid populations during wintertime. The program allows two modes of calculations depending on different input variables. Firstly, observed data from field evaluations may be entered as referred to evaluation time (so-called “crop specific”). Therefore, specifications of observed cereal aphid densities at a certain location and time are needed. Secondly, standard values based on experimental and historical datasets are automatically calculated depending on the location and the date of leaf emergence (GS 7 to 10), necessarily specified for a given crop in a certain region (so-called “region specific”). However, the model aims are not changed using either mode of calculation (see above).

Model LAUS

The simulation model LAUS was developed by Friesland (1986) at the German Weather Service (DWD) in Braunschweig. The basic aphid evaluations stem from the working group on cereal pests (Basedow et al. 1989), in which the developer participated. Therefore the model is based on many case studies from divers parts of Germany. The model simulates and predicts population development of *S. avenae* in winter wheat from April 1st to hard dough stage (GS 87). Whereas the meteorological input variables from daily updated datasets (including regional forecasts) are automatically involved, the users' interface requires (only at the first time in a given season) the input of location, growth stage of winter wheat on April 1st, and (optionally) the calendar day of the first field evaluation (as counts per tiller). The module for phenology of winter wheat excludes cultivar effects and is computed as non-linear function of several weather parameters. Standard values of temperature and relative humidity of the closest weather station are empirically transformed to model crop climate and phenology. Both weather modules are important control factors influencing the population dynamics of *S. avenae* and its antagonists. Birth-rates of aphids are generated with temperature- and age-dependent development functions following the boxcar-train procedure (DeRoos et al., 1990). As representatives for all antagonists, the model takes into account the population dynamics of the ladybeetle *Coccinella septempunctata* L., the parasitoids (i.e. *Aphidius* spp.) and the development of entomopathogenic fungal infections (e.g. *Pandora neoaphidis* Humber) and calculates their killing potential by assuming simplified averaged mortality rates. Whereas meteorological and crop density parameters were perceived as most important influencing variables for arthropods, temperature, relative humidity, and precipitation were only incorporated in modelling infection rates of entomopathogenic fungi. Immigration rates of *S. avenae* from offside (from field boundaries and other fields) into “empty” winter wheat fields were calculated using a set-a-side function (with few categorical values for immigration rates), which describes the population density outside of the winter wheat.

The German Weather Service (DWD) in Braunschweig is in charge of the model LAUS, which has been revised several times and has gained a certain regionally importance as decision support system in pest management. Additional specifications and changes of input variables (see above) can be performed if crop parameters differ from standard calibration, e.g. assuming common fertilization levels for nitrate (180 to 225 kg per m^2), crop densities (600 tillers per m^2) and mean starting population densities (value range of 15 to 35 aphids in surrounding habitats). Firstly, model runs were performed using the standard calibration (à priori) and then in a second model run, these starting values were altered according to the actual situation (including population development) in a given case study (à posteriori).

Model GETLAUS01

The simulation model GETLAUS01 is a scientific model developed to improve the knowledge of abiotic and biotic interactions (Gosselke et al., 2001). It is not designed for aphid control decisions by the farmers or for population forecasts, but to demonstrate and to explain à posteriori:

1. the population dynamics of cereal aphids depending on several driving forces and
2. the tritrophic interactions between winter wheat, cereal aphids and their antagonists under field conditions.

The latest version of the model is the result of a long experience (starting about 25 years ago) in simulating cereal aphid populations (based on former models GTLAUS, PEST-SIMAC, etc.), including several laboratory experiments as well as detailed long-term field observations in central Germany (Freier & Wetzel, 1980; Rossberg et al., 1986; Freier & Triltsch, 1996). The model is a discrete and deterministic model structured in compartments, which contain a variable number of age classes (one age class per time increment). Several processes are internally calculated using a time step of two hours. Each submodel run is initiated by entering a wide range of starting values. The defined sequence of biological processes in GETLAUS01 is: migration, feeding, reproduction, development, and mortality. Several improvements were made to enhance the models sensitivity and power. Today, the model consists of 13 submodels and modules, simulating ontogenesis of the host plant as well as developments of the three most important cereal aphids (*S. avenae*, *M. dirhodum*, *R. padi*) and their antagonists (aphid-specific predators: ladybeetles, lacewings, and chrysopids; polyphagous predators: carabids, staphylinids, spiders; entomopathogenic fungi infestation, parasitation rates). Each program run requires the input of the duration of the simulation (start and end), meteorological data (two-hour values) and information on wheat development. Additionally, initial values for all instars of aphids and antagonists have to be specified. Furthermore, the type of migration ("early", "regular", or "late" season migration for aphids and antagonists) and information on pesticide application may also be included. Usually, the model runs are started using the initial values of the field populations at the end of flowering (GS 69).

The latest version of the GETLAUS01 simulation model can be downloaded from the Internet (www.bba.bund.de: Protecting Plants / Integrated / GETLAUS01). For details of the modules and submodels see descriptions in the Internet or in Gosselke et al. (2001).

Validation and statistical analysis

In our study, the field data were compared with data from simulated aphid population densities. Moreover, we varied input variables and starting conditions of simulation runs for model improvement and extension.

The Pearson's Chi-square test on differences (with Yates correction for small samples sizes; program StatXact) served for the validation of model SIMLAUS. Tests of equivalence were performed in order to obtain equivalence thresholds (upper and lower limits, using the program R). Datasets from autumn (SIMLAUS), spring and early summer (LAUS), and summer (GETLAUS) were analysed using linear regression analyses between observed and predicted data (prog reg, program SAS; SAS, 2008). According to Sachs (1999), the resulting linear regression lines should have intercepts not significantly different from zero and slopes not significantly different from one. Significant deviations ($p < 0.05$) of the intercept from 0 or the slope from 1 were detected using SAS increments (aplus-procedures) or calculations according to Teng (1981).

The simulation model GETLAUS01 was further validated by comparing the shapes of observed and predicted population curves according to Gosselke et al. (2001). Accordingly, a model run is defined as "successful" if differences between simulated and observed values remained within in the range of acceptance limits (25% deviation in terms of aphid infestation expressed as aphid index in aphid days per m^2 as well as 50% deviation in terms of predator occurrence measured as a predator index in predator unit days per m^2; Freier et al., 1997a; Gosselke et al. 2001).

Analysis of variance (ANOVA; proc glm, program SAS; SAS, 2008) was used to detect significant differences between observed and predicted data for single evaluation dates in order to analyse different simulation starts or levels of species.

Results

General results

In 2003/2004, no anholocyclic hibernation was observed at all locations, except in one winter barley field (location Wörth), where individuals of *S. avenae* were found very early in the year (8.3 adults per m^2 on April 8th). In winter wheat fields of most locations, first aphids occurred later in that year (at the beginning of June), but due to weather conditions and absence of antagonists (e.g. exceptionally low numbers of Coccinellids and Syrphids) *S. avenae* optimally developed leading to extremely high population values (up to 75,000 aphids per m^2) for most locations. In 2005 and 2006, no anholocyclic hibernation was detected in either location, and aphid populations reached only moderate peak levels (ca. 7,500 to 10,000 and 2,500 to 3,500 aphids per m^2, respectively). In those two years, *M. dirhodum* was the most abundant species.

Model SIMLAUS

In more than 96% of case studies, the model SIMLAUS estimated accurately the hibernation type in winter wheat and winter barley, i.e., anholocyclic hibernation was reliably predicted. No significant differences were detected between observed and predicted hibernation types (Pearson’s Chi-square test) and confidence limits of equivalence were smaller than 29% (Tab. 2). In 2003/2004 in three (5.6%), in 2004/2005 in four (4.5%), and in 2005/2006 only in one field (1.3%) the prediction of hibernation types were wrong or did not match to field observations (including region and crop specific data, Tab. 2). In all these cases, the model assumed anholocyclic hibernation of *S. avenae* and *R. padi* / *maidis*, which was not detectable in fields.

Tab. 2: Validation results for the model SIMLAUS: number of wrong classified locations, p-values from Pearson χ^2-tests on differences (with Yates correction for small samples sizes), and limits of confidence intervals to test the equivalence ($\alpha = 0.1$) of observed and predicted anholocyclic hibernation for each aphid species in several region and crop specific datasets (*n* = sample size).

Year	Aphid species	*n*	No. of wrong classified locations	Pearson χ^2 test on difference (p-value)	Confidence interval on equivalence lower limit	upper limit
2003/2004	*S. avenae*	18	1 (Wörth)	0.841	-0.26	0.15
Region specific	*R. padi*	18	2 (Wörth)	0.697	-0.29	0.07
	R. maidis	18	0	1	0.00	0.00
2004/2005	*S. avenae*	18	2 (Wörth)	0.697	-0.29	0.07
Region specific	*R. padi*	18	0	1	0.00	0.00
	R. maidis	18	0	1	0.00	0.00
2004/2005	*S. avenae*	17	1 (Wörth)	0.500	-0.09	0.21
Crop specific	*R. padi/maidis*	17	1 (Wörth)	0.500	-0.09	0.21
2005/2006	*S. avenae*	16	0	1	0.00	0.00
Region specific	*R. padi*	16	0	1	0.00	0.00
	R. maidis	16	0	1	0.00	0.00
2005/2006	*S. avenae*	15	1 (Wörth)	0.500	-0.11	0.24
Crop specific	*R. padi/maidis*	15	0	1	0.00	0.00

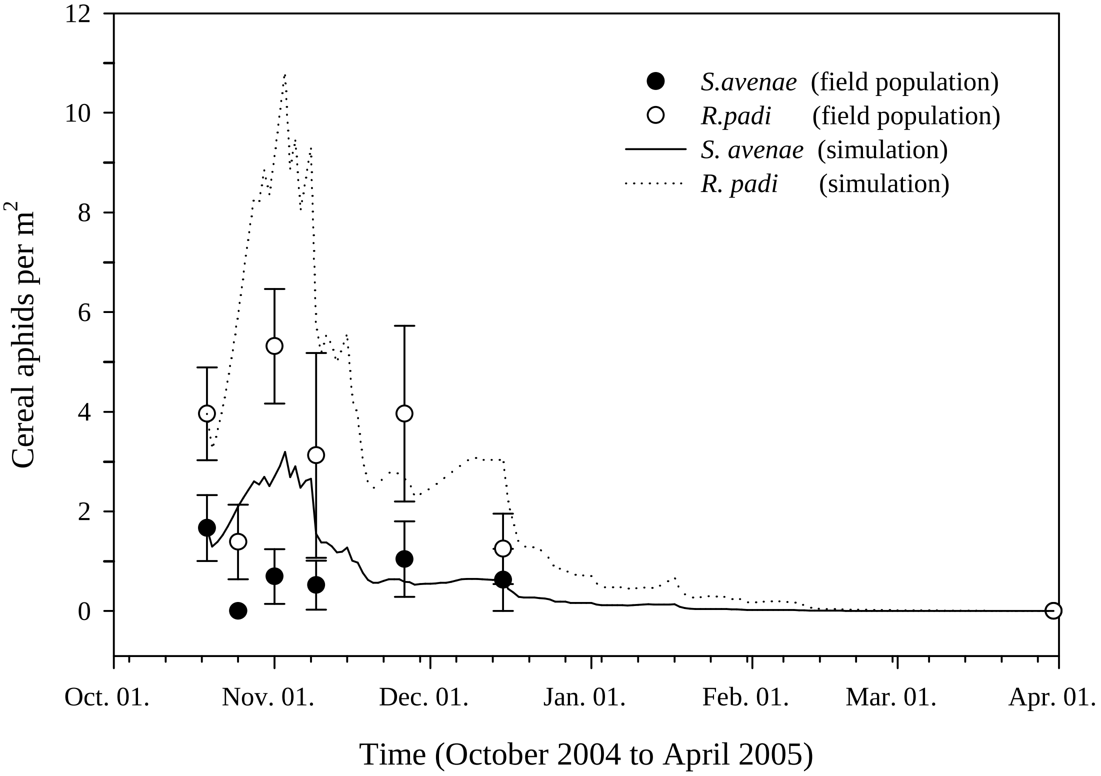


Fig. 1: Comparison between observed (field data) and predicted (SIMLAUS simulation) population dynamics of *S. avenae* and *R. padi* in a winter barley field in Hiddestorf West in 2004/2005 (representative of typical population development for several case studies, i.e. locations and years).

Weak simulations of autumn population dynamics of *S. avenae* and *R. padi* were typically obtained comparing observed and predicted data. This is shown in Fig. 1 for the location Hiddestorf West in 2004/2005, a representative case study within the data collection. Inaccurate simulations were found in most locations with regard to population dynamics (e.g. population increased, when a decrease was predicted and vice versa, Fig. 1).

Tab. 3: Validation of the model SIMLAUS in winter wheat (ww) and winter barley (wb) fields: results of linear regression between observed and predicted population levels in autumn specified for regions and years. Coefficients of determination (R^2) followed by asterisk (*) indicate significant results ($p < 0.05$), whereas y-axis intercept "*a*" and slope "*b*" followed by asterisk (*) indicate significant differences ($p < 0.05$) from 0 and 1, respectively (*n* = samples size, SD = standard deviation, sLS = southern Lower Saxony, SA = Saxony-Anhalt, RP = Rhineland Palatinate).

					S. avenae				*R. padi*	
Year	Region	Crop	*n*	R^2	*a* ±SD	*b* ±SD	*n*	R^2	*a* ±SD	*b* ±SD
2005	sLS	wb	.	.	.	.	13	0.40*	-0.10 ±1.04	1.12 ±0.40
	sLS	ww	.	.	.	.	16	0.74*	0.02 ±0.05	0.50 ±0.08*
2006	sLS	wb	13	0.81*	0.51 ±0.31	1.14 ±0.16	.	.	.	.
2005	SA	wb	.	.	.	.	13	0.46*	0.11 ±0.05*	0.54 ±0.17*
2006	SA	wb	12	0.48*	1.88 ±1.27	1.47 ±0.46	12	0.57*	0.96 ±0.28*	0.31 ±0.08*
2006	RP	wb	15	0.29*	5.49 ±1.50*	0.27 ±0.11*	.	.	.	.

The coefficients of determination were significant ($p < 0.05$) in three and four of 11 case studies for *S. avenae* and *R. padi*, respectively (Tab. 3). Coefficients of determination ranged from $R^2 = 0.29$ to $R^2 = 0.81$ for *S. avenae* and from $R^2 = 0.40$ to $R^2 = 0.74$ for *R. padi*. Significant coefficients of determination provided, intercepts and slopes were significantly different from 0 and 1 in one case study for *S. avenae*, and in two and three case studies for *R. padi*, respectively (Tab. 3).

Weak matches between observed and predicted cereal aphid populations were found in pooled datasets from different case studies from northern Lower Saxony and Rhineland Palatinate ($n = 91$, $R^2 = 0.19$, $p > 0.05$). However, a significant coefficient of determination was found, when locations from southern Lower Saxony and Saxony Anhalt were pooled ($n = 177$, $R^2 = 0.40$, $a = 0.41 \pm 0.32$, $b = 0.92 \pm 0.17$, with *a* and *b* being not significantly different from 0 and 1, respectively). Regarding the simulation results of the different species (pooled case studies and crops), the model performed better for *S. avenae* ($n = 148$, $R^2 = 0.49$, $a = 1.32 \pm 0.22$, $b = 0.52 \pm 0.05$) than for *R. padi* ($n = 125$, $R^2 = 0.07$, $a = 1.07 \pm 0.22$, $b = 0.24 \pm 0.08$), with all statistical parameters showing significant values ($p < 0.05$). Comparing the model's performances in different crops (pooled case studies and species), the model predicted population levels better in winter barley ($n = 164$, $R^2 = 0.24$, $a = 0.44 \pm 0.13$, $b = 0.81 \pm 0.20$) than in winter wheat ($n = 107$, $R^2 = 0.23$, $p > 0.05$).

Model LAUS

Since the model LAUS is designed to describe solely population dynamics of *S. avenae*, case studies without sufficient numbers of that species were not included in the validation process. Hence, the model was validated with field data of only 35 case studies using both, the standard calibration of the corresponding case study (à priori), and the adjusted calibration based on the effective population development in the case study (à posteriori; Tab. 4).

Tab. 4: Validation of the model LAUS was performed on datasets defined as à priori (standard values for model start) and à posteriori (adjustment of starting values according to population development). Results of linear regression between observed and predicted values are specified according to case studies (i.e. locations and years). Coefficients of determination (R^2) followed by asterisk (*) indicate significant results, whereas y-axis intercept "*a*" and slope "*b*" followed by asterisk (*) indicate significant differences from 0 and one 1, respectively (*n* = samples size, SD = standard deviation, $p < 0.05$).

			à priori			à posteriori		
Location	Year	*n*	R^2	*a* ±SD	*b* ±SD	R^2	*a* ±SD	*b* ±SD
Isernhagen	2004	12	.	.	.	0.70*	639 ±327	1.10 ±0.22
Jeinsen	2004	13	.	.	.	0.85*	290 ±305	1.30 ±0.16
	2006	8	0.72*	74 ±59	1.59 ±0.38	0.74*	199 ±146	4.20 ±0.95*
Fläming	1993	8	.	.	.	0.54*	182 ±394	2.76 ±0.97
	1994	7	0.64*	26 ±40	13.61±4.20*	0.87*	6 ±6	4.22 ±0.68*
	1997	9	0.44*	53 ±59	0.41 ±0.16*	0.92*	4 ±8	0.22 ±0.02*
	1998	9	.	.	.	0.78*	155 ±85	0.86 ±0.16
	1999	9	0.77*	-44 ±323	7.65 ±1.50*	0.81*	-27 ±63	1.72 ±0.29*
Magdeburg	1995	7	0.81*	138 ±306	0.47 ±0.09*	0.94*	-42 ±103	0.31 ±0.03*
	1996	8	.	.	.	0.61*	130 ±142	1.29 ±0.39
	1997	8	.	.	.	0.77*	11 ±35	0.28 ±0.06*
	1998	8	.	.	.	0.46*	775 ±445	0.52 ±0.22
	2001	8	0.65*	77 ±120	3.54 ±0.98*	.	.	.
	2004	13	0.60*	640 ±415	0.31 ±0.07*	0.90*	115 ±89	0.17 ±0.02*
Bernburg	2004	14	0.62*	1005 ±799	0.59 ±0.13*	0.75*	238 ±260	0.26 ±0.04*
Wahlbach	2004	16	0.64*	22 ±15	0.06 ±0.01*	0.50*	160 ±118	0.35 ±0.09*
Bensersiel	2004	11	.	.	.	0.63*	124 ±72	0.32 ±0.08*
	2005	17	0.36*	214 ±163	1.71 ±0.57	0.59*	143 ±126	2.12 ±0.44*
Carolinensiel	2004	11	0.83*	31 ±13*	0.02 ±0.00*	0.68*	201 ±85*	0.10 ±0.02*
	2005	16	0.47*	82 ±105	3.90 ±1.07*	0.78*	24 ±67	4.96 ±0.69*

Great variability between case studies was observed and major differences were detected between observed and predicted populations of *S. avenae* with regard to the standard calibration (Tab. 4). In 12 of 35 case studies, the coefficients of determination were significant, with $R^2 > 36\%$. Case studies with highest coefficients of determination were found at Carolinensiel ($R^2 = 0.83$, $p < 0.01$ in 2004) and at Magdeburg ($R^2 = 0.81$, $p < 0.01$ in 1995). The intercepts ranged from $a = -44$ to $a = 1005$ and were significantly different from zero in one case study. The slopes ranged from $b = 0.02$ to $b = 13.61$ and differed significantly ($p < 0.05$) from 1 in 83% of case studies. The slopes were significantly ($p < 0.05$) below and above 1 in six and four case studies, respectively (Tab. 4).

Adjusting starting values to actual population levels of a given case study (à posteriori), the coefficients of determination increased in 89.9% with 19 significant case studies showing lowest scattering ($R^2 > 0.46$, $p < 0.05$, Tab. 4). Likewise, intercepts differed significantly from zero in one case study, and values reached a similar range compared to the à priori validation results (Tab. 4). Slopes differed significantly from one 1 in 13 case studies, with eight and five cases significantly below and above 1, respectively. Moreover, the slopes rang mean values closer to 1 than in the à priori validation results ranging from $b = 0.10$ to $b = 4.96$ (Tab. 4).

Model GETLAUS01

The model GETLAUS01 was validated against field data, excluding data from years 1993 to 2002, which have been used in the model construction (Freier et al., 2002).

Fig. 2 shows a significant relationship between observed and predicted values of all cereal aphids in 2004 and 2005 (Fig. 2 excludes the five highest values of 2004 and all of 2006 to avoid scaling bias). The coefficient of determination was higher in 2005 than in 2006 ($R^2 = 0.93$ and $R^2 = 0.90$, respectively) with constant slopes of $b = 0.93$ (both not significantly different from 1). However, in 2004, when enormous peak numbers of cereal aphids were recorded in fields, the model tended to underestimate the highest observed field values ($R^2 = 0.75$, $b = 0.53 \pm 0.03$), with slopes being significantly different from 1. Regarding intercepts, they only differed significantly from 0 in 2004 ($a = 257 \pm 114$), whereas no significant differences were detected in 2005 ($a = 81 \pm 53$; Fig. 2) and 2006 ($a = 16 \pm 11$).

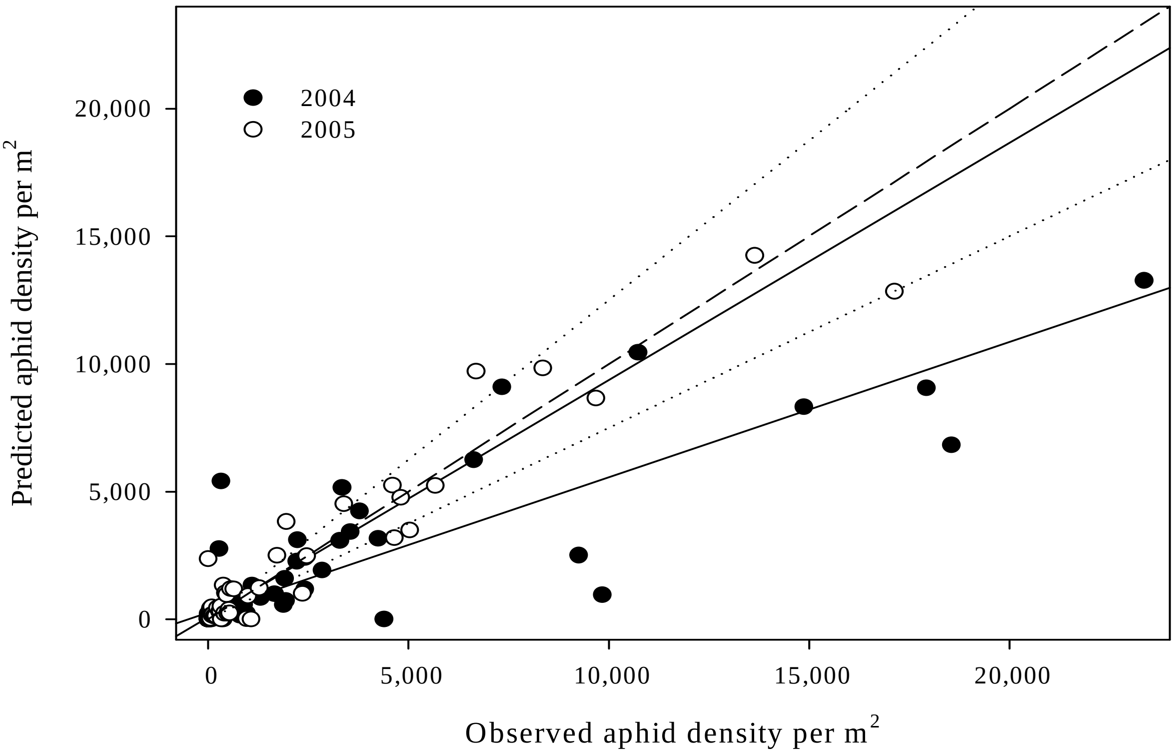


Fig. 2: Linear Regression between observed (field data) and predicted (GETLAUS01 simulation) cereal aphid density (sum of all species m^{-2}) in winter wheat in 2004 (closed circles and lower solid line, *n* = 108, R² = 0.75, p < 0.001) and in 2005 (open circles and long upper solid line, *n* = 142, R² = 0.93, p < 0.001). Bisecting line is short dashed and dotted lines symbolise the respective ±25% limits. The five highest values from 2004 were not shown to avoid scaling bias.

Case studies from northern Lower Saxony and from Rhineland Palatinate showed greater scattering with smaller coefficients of determination, which were not significant in five case studies. Fig. 3 shows weak simulations in scale and shape for Wörth 2006, a typical case study for simulation runs in northern Lower Saxony and Rhineland Palatinate. In case studies from southern Lower Saxony and Saxony Anhalt, coefficients of determination were always significant (Tab. 5, Fig. 4). In none of the case studies, the intercept was significantly different from 0. Slopes were significantly different from 1 in 39% of case studies, with all but one being significantly lower than 1 (Tab. 5).

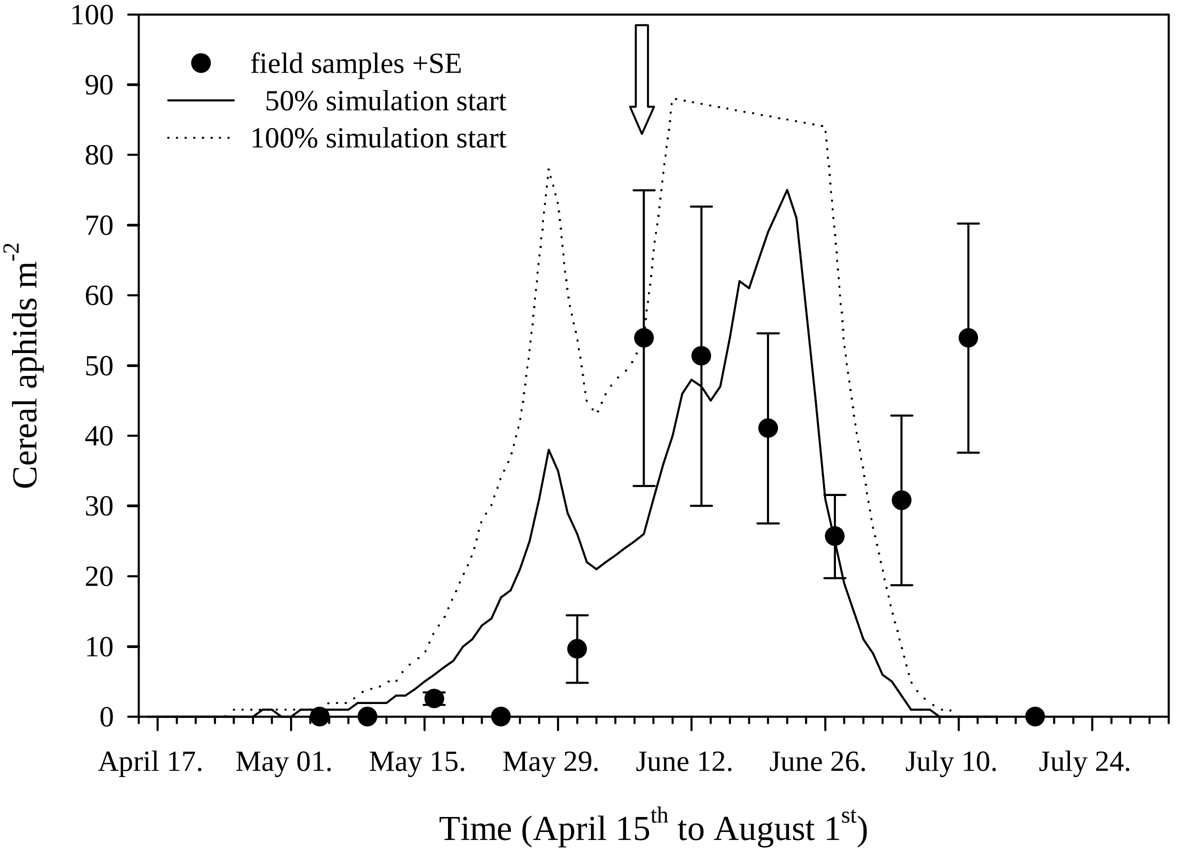


Fig. 3: Comparison between observed (field population ±SE) and predicted (GETLAUS01 simulation) population development in Wörth 2006 (as representative of typical population dynamics). Simulations were started on recommended date, June 10th (arrow), with 50% and 100% of the initial population. The model is able to calculate the population development backward to beginning of infestation.

The validation analysis according to the method used in Gosselke et al. (2001) supports the results described above, when case studies were compared among each other (Tab. 6). Good conformance was established in all simulation runs in case studies from southern Lower Saxony and Saxony Anhalt (with difference between observed and simulated values of 4.4% and 3.5%, respectively). The differences between observed and simulated values (aphid index per m²) always remained clearly below the defined acceptance limits of ±25% (Tab. 6). This is in contrast to case studies from Rhineland Palatinate and northern Lower Saxony, where 30.0% and -85.9% mean differences were obtained, respectively (Tab. 6).

Tab. 5: Validation of model GETLAUS01 in winter wheat fields: results of linear regression between observed and predicted values specified for locations and years. All coefficients of determination (R^2) are significant at the $\alpha = 5\%$ level. No significant differences ($p > 0.05$) from 0 were found for y-axis intercept "*a*" (*n* = samples size, R^2 = coefficient of determination, *a* = intercept, *b* = slope, SD = standard deviation).

Location	Year	*n*	R^2	*a* ±SD	*b* ±SD
Isernhagen	2004	12	0.97	-49 ±129	0.95 ±0.05
	2005	13	0.93	-25 ±171	0.88 ±0.07
	2006	9	0.98	13 ±16	0.97 ±0.05
Jeinsen	2004	11	0.80	610 ±473	0.93 ±0.15
	2005	11	0.89	174 ±425	1.02 ±0.11
Hiddestorf West	2004	11	0.60	235 ±253	0.85 ±0.22
	2005	8	0.99	-30 ±55	1.17 ±0.02*
	2006	9	0.99	24 ±20	0.97 ±0.02
Hiddestorf East	2004	11	0.58	76 ±71	0.44 ±0.12*
	2005	14	0.96	170 ±280	0.86 ±0.05*
Magdeburg	2004	12	0.95	183 ±211	0.43 ±0.03*
	2005	15	0.80	256 ±170	0.99 ±0.13
	2006	14	0.93	2 ±4	0.93 ±0.07
Bernburg	2004	13	0.89	540 ±472	0.59 ±0.06*
	2005	15	0.81	72 ±46	1.04 ±0.13
	2006	10	0.99	-2 ±2	1.10 ±0.04*
Wörth	2005	13	0.76	3 ±6	0.85 ±0.14
Wahlbach	2005	13	0.96	5 ±5	1.06 ±0.06
Bensersiel	2004	9	0.71	-25 ±165	0.72 ±0.16
	2006	11	0.47	17 ±13	0.25 ±0.08*
Carolinensiel	2004	9	0.49	337 ±262	0.16 ±0.06*
	2005	15	0.70	15 ±24	0.77 ±0.14
	2006	11	0.47	25 ±32	0.45 ±0.15*

* Asterisks indicate slopes *b* being significantly different from 1.

Early starting points for simulation tended to overestimate the population development in the field (data not shown). Differences between observed and predicted values were most pronounced, when the model was started four weeks earlier then recommended (Fig. 4). Several significant differences between the simulations starting on May 17th and on June 14th were detected for evaluation days in Isernhagen 2005 (as a representative of typical population dynamics of several case studies). When the simulation start was shifted two weeks earlier, the differences between observed and predicted values were not significant (Fig. 4).

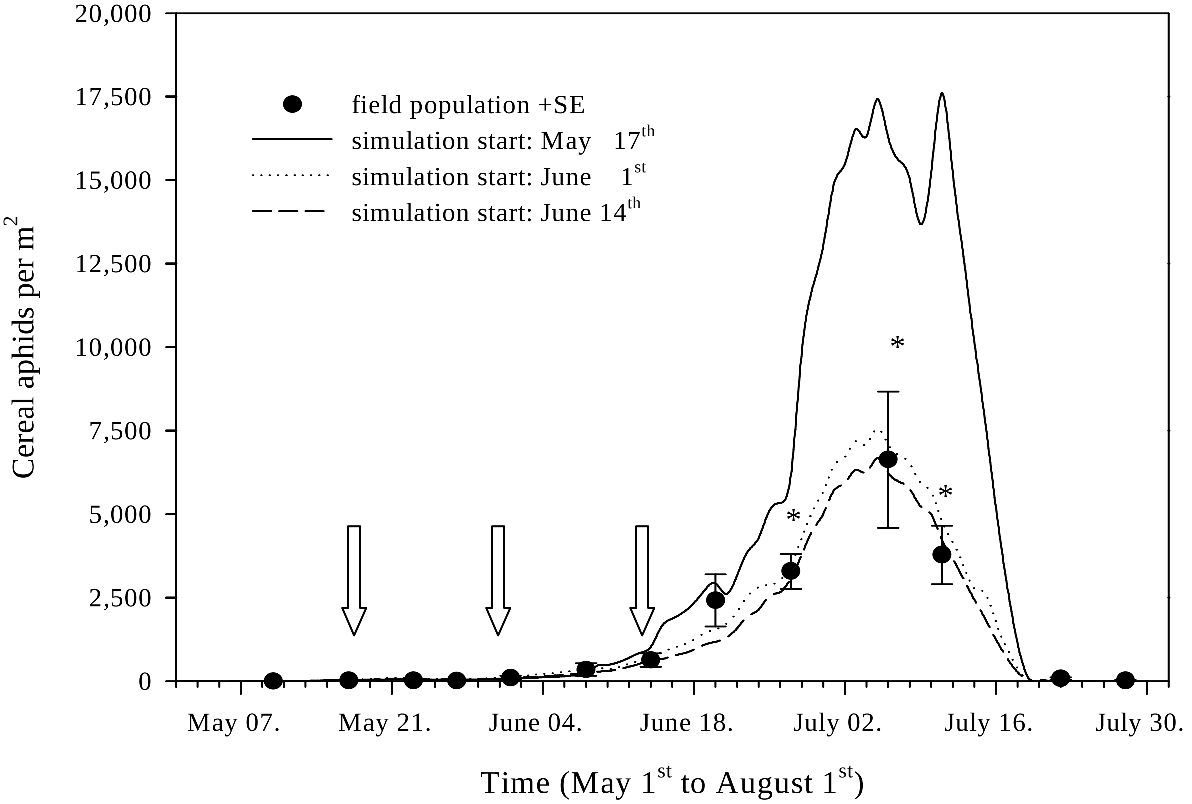


Fig. 4: Comparison between observed (field population ±SE) and predicted (GETLAUS01 simulation) population dynamics in Isernhagen 2005 (representative as typical population development for several case studies, i.e. locations and years). Simulations were started at three times (arrows): two weeks (June 1st) and four weeks earlier (May 17th) than recommended date (June 14th). The model is able to calculate the population development backward to beginning of infestation. * Asterisks indicate significant differences between observed and predicted populations when the simulation started four weeks earlier than recommended.

No significant differences between observed and predicted populations were found on the species level (Fig. 5). Concerning the absolute numbers and relative amounts of instars of *S. avenae, R. padi,* and *M. dirhodum* were equivalent to the results above or to those specified in Tab. 5. This is in contrast to the numbers of antagonists, which showed stronger variation and significant differences between observed and simulated values (data not shown). Differences between field data and model results were more pronounced using the validation method of Gosselke et al. (2001) with mean differences between 5% and 20% for cereal aphid species and 35% and 74% for antagonists (data not shown).

Tab. 6: Validation of model GETLAUS01 in winter wheat fields: results of comparisons (differences in %) between observed and predicted population development of cereal aphids (aphid index m^{-2}) in different case studies (i.e. locations and years).

	2004			2005			2006		
Location	observed	predicted	difference	observed	predicted	difference	observed	predicted	difference
	(aphid days*1000 m^{-2})		(%)	(aphid days*1000 m^{-2})		(%)	(aphid days*1000 m^{-2})		(%)
Isernhagen	73.1	74.2	1.5	111.6	98.4	-13.4	7.3	7.7	4.4
Jeinsen	114.8	140.4	18.2	127.1	110.1	-15.4	.	.	.
Hiddestorf West	17.0	18.1	5.8	143.9	165.6	13.1	25.1	24.0	-4.4
Hiddestorf East	30.0	32.3	7.2	166.7	203.1	17.9	.	.	.
Magdeburg	8.4	6.9	-22.0	16.9	16.7	-1.3	0.5	0.5	11.0
Bernburg	25.7	34.1	24.6	9.3	9.8	5.7	2.0	2.1	8.7
Wörth	7.4	21.9	66.3	2.0	1.7	-17.7	1.1	1.7	34.5
Wahlbach	8.4	8.6	2.2	3.4	3.8	10.8	1.4	8.5	84.1
Bensersiel	32.3	19.6	-64.6	7.8	9.8	20.3	5.7	1.4	-313.1
Carolinensiel	34.3	20.9	-64.1	7.3	4.7	-57.5	4.8	3.5	-36.2

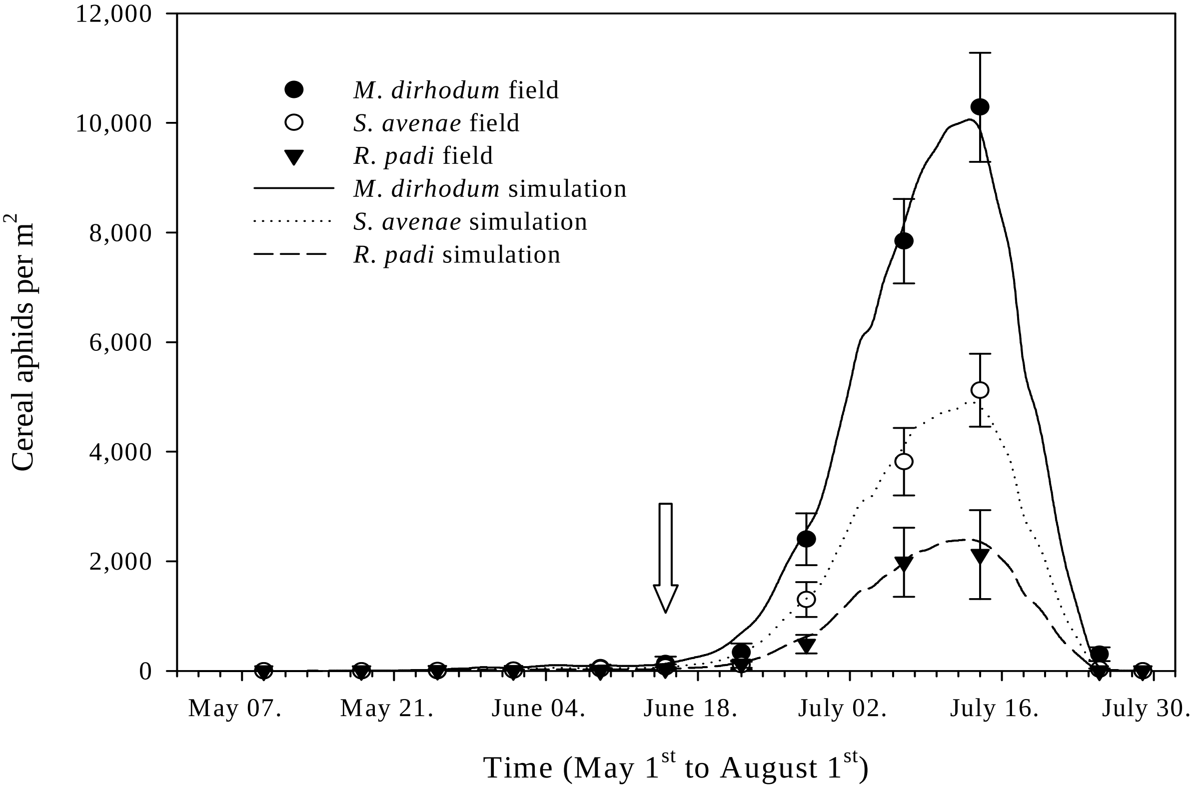


Fig. 5: Comparison between observed (field population ±SE) and predicted (GETLAUS01 simulation) population development according to cereal aphid species in Hiddestorf West 2005 (representative as typical population development for several case studies, i.e. locations and years). Simulation started on recommended date (June 15th, arrow). The model is able to calculate the population development backward to beginning of infestation.

Discussion

It is often difficult to explain the conclusions and sensitivities of different models on the basis of differences in model structure, source code and input data, as the models' structure is rather complex or unknown, and too many feedbacks are involved. Hence, the assessments of model performances are largely based on comparisons of numbers of cereal aphids between field data and model results.

Our comparisons of aphid simulation models served two purposes. The models were assessed for their ability to simulate the population growth and development for case studies not included in the calibration and development process. Secondly, and more importantly, it was possible to identify parts (e.g. submodules) in some models that produce systematic errors and require improvements.

Model SIMLAUS

Validation results of model SIMLAUS have shown the accuracy in the prediction of successful hibernation of cereal aphids in winter wheat and winter barley fields (i.e. 96% correct simulations, no significant differences between observed and predicted hibernation types, and small equivalence limits, Tab. 2). The prediction of hibernation rates is based on relatively simple connections. This is a reason for high numbers of correct simulations. However, quantitative simulation of population growth processes in spring and early summer is much more complicated. This confirms the present study. Successful anholocyclic hibernation is most often related to increased occurrence and spread of barley yellow dwarf virus (BYDV). Outbreaks of BYDV after mild winters have been reported and are considered to cause important yield reductions in winter barley and winter wheat (Kendall & Chinn, 1990; Fabre, 2006). Most patho-types of BYDV are transmitted by *S. avenae* and *R. padi*. According to our results, differences in model's performances between both species were small (Tab. 2) and the population densities after wintertime of *S. avenae* and *R. padi* or *R. maidis* were correctly predicted by SIMLAUS. Wrong simulation results were mainly obtained from location Wörth, basically situated in an agro-climatic zone with mildest winter conditions (e.g. mean temperatures of 2.3°C from December to February 2005). In this location, anholocyclic hibernation may be more frequently possible (Kleinhenz & Sengonca, 1993), which is supported by our results. However, we cannot exclude that aphids have been overlooked during early field evaluation (e.g. in March and April), but due to the high sample sizes this is not very likely. Systematically faintness in the model may explain a few wrong estimates regarding the hibernation types. Certain mild winter temperatures (threshold values) may effect the population of *S. avenae* and *R. padi* disproportionately high as reported by Kleinhenz (1994). Interestingly, the model predicted anholocyclic hibernation of *S. avenae* and *R. padi*, which was not detectable in fields (except in less than 4% of locations in 2004). The complete lack of false-negative simulations diminished the danger that insecticide control strategies are not considered in spring even though cereal aphids may have successfully overwintered in fields. Conservative risk assessments with SIMLAUS may help to promote the model's acceptance by plant protection services and farmers. Subsequently, the model's predictions can be very helpful to reduce the amount of regular stressing field controls after winter for BYDV risk assessment (e.g. secondary BYDV spread).

Even though the simple decision, whether or not anholocyclic hibernation of cereal aphids will occur, is an important output of the model SIMLAUS, a correct simulation of the course of aphid densities in autumn is desired, too (Kleinhenz, 1994; E. Jörg, pers. comm.).

Especially in years with long periods of mild temperatures and best conditions for population growth of cereal aphids, farmers demand decision support in autumn as well. Unfortunately, in the majority of case studies, the simulated population dynamics did not reflect the real autumn field populations (Tab. 3). The consequences may especially concern cases, when neither explicit holo- nor anholocyclic hibernations of cereal aphids were facilitated (i.e. location Wörth). Wrong simulations of autumnal population trends (e.g. population in- or decrease) as well as of the population levels may cause wrong assumptions for subsequent effects of winter conditions in a particular case. The discrepancies between observed and predicted values of autumn populations may be due to small sample size in the course of model construction. Kleinhenz (1994) disposed only 7 × 20 plants for population evaluation in nine case studies. The numbers of plants used in this study were 700 to 35,000 plants per evaluation date in 52 case studies. Furthermore, missing consideration of migration (e.g. immigration from time of crop emergence onwards) may explain the incorrect prediction of autumn populations in part. It seems that while comparing observed and predicted autumnal population levels taking into account weather data, precipitation has an outsized effect on the population simulation. The model calculated strong population reductions after precipitation of more than 4 l per m^2 (data not shown). These effects are questionable and need to be reviewed. Further improvements may incorporate more credible autumnal growth rates (including immigration), facilitate the user's interface (e.g. explicitly illustrating fraction of hibernation types), and include more detailed information about the necessities of insecticide applications. Interestingly, the main model results of SIMLAUS, e.g. the possibility of anholocyclic hibernation, were most often estimated correctly, although autumn populations were simulated inaccurately. Strength of winter (here mainly the variables temperatures and precipitation from December to February) seems to exert strong effects, which were not related to a given autumn population level.

In conclusion, this model allows reliable predictions of possible hibernation types (e.g. holo- or anholocyclic) for *S. avenae*, *R. padi*, and *R. maidis*. However, for further applications, the model SIMLAUS, e.g. estimations of population dynamics in autumn and subsequent decision support for autumnal insecticide applications, are not appropriate.

Model LAUS

The model LAUS predicted correctly the population dynamics of *S. avenae* in winter wheat in about 30% of case studies, but showed enormous variability in coefficients of determination (Tab. 4). Slopes often differed significantly from one, whereas the intercepts were rarely significantly different from zero. However, qualitative prediction of population development in spring was more reliable by model LAUS compared to simulation of autumn population development with model SIMLAUS. For pest control, high coefficients of determination ($R^2 > 70\%$) and slopes not significantly different from one should be aspired (Selhorst, 2000). Changing the starting conditions by taking into account the observed population level of *S. avenae* (à posteriori) improved the results of model LAUS. This became apparent in most case studies (e.g. increased levels of coefficient of determinations and higher numbers of slopes not significantly different from one, Tab. 4). Detailed specifications of population forecasts and precise adjustment of starting conditions may therefore enhance the models correctness. In this context, if parameters for offside population of *S. avenae* (see model description) and the subsequent immigration of alatae into winter wheat fields were adjusted, the most tight fitting of field-raised and simulated data could be achieved. The calibration of this variable may be improved using migration models, suction trap data, or by taking the hibernation type as result of model SIMLAUS into account.

Accurate predictions of population development were neither consistent in certain years nor in certain locations. A major disadvantage is that the model only considers the dynamics of *S. avenae* as most important cereal aphid species (in terms of yield losses). However, in 2005 and 2006, *M. dirhodum* became the predominant species in all locations. Subsequently, no validation could be performed for the simulation model LAUS in most locations. Comparing all datasets, *S. avenae* was the dominant species in only 71% of case studies with cereal aphid outbreaks. In remaining cases with cereal aphid outbreaks, *M. dirhodum*, was the dominant cereal aphid species and presumably responsible for yield losses (Basedow et al., 1994). In several locations, higher numbers of *S. avenae* appeared only very late in years with earlier predominance of *M. dirhodum*, which left the plants when flag leaves dried. It is well known that both species exert different influences on yield depending on time and density of infestation (Niehoff & Stäblein, 1998). Moreover, population models developed for *M. dirhodum* (Zhou & Carter, 1989; Ma, 2000) strongly suggest that simulation of *S. avenae* populations alone may not be sufficient to explain or predict yield effects of mixed aphid populations. Moreover, antagonistic effects between the species may influence the whole population development of cereal aphids (Dixon, 1998). Subsequently, decision support by a single species model for the control of cereal aphids may be misleading in most cases (Tab. 4). Improvements of the model are necessary for broader acceptance in practice, e.g. by including population development of *M. dirhodum*.

Model GETLAUS01

In most case studies, narrow conformity was found between observed and predicted data (i.e. significant coefficients of determination, Tab. 5). Intercepts were never and slopes only in 39% of case studies significantly different from 0 and 1, respectively. Thus, resulting lines were close to bisection line and provide further proofs for accurate model results (Fig. 2). However, simulation results were consistently worse in locations from northern Lower Saxony and Rhineland Palatinate compared to locations in southern Lower Saxony or Saxony Anhalt. Despite high grade of accuracy and similarity during all case studies, the model GETLAUS01 was not able to reproduce the population development in those regions. The model was developed and improved by means of both laboratory results and field data, taken in regions of Saxony Anhalt and of Brandenburg (Freier et al., 1998; Gosselke et al., 2001). The experience and evaluation from those regions may have led to regionally imprinting. Moreover, climatic differences between regions may have contributed to our results, because Brandenburg, southern Lower Saxony, and Saxony Anhalt are affected by continental climate, whereas the other regions are more influenced by maritime climatic conditions. Constructing a model based on meteorological data from continental climatic conditions may not perform reliably in maritime regions (Pierre & Dedryver, 1985). Landscape structures prevailing in the different regions may have contributed to further differences in the reliability of models. In Rhineland Palatinate and in northern Lower Saxony, landscape is more variably and multifunctionally structured including hedges, and copses (Backhaus, 2008; Klüken et al., unpublished data). Crop acreage of fields rarely exceeds more than 10 to 15 ha. This is in contrast to continental regions (e.g. Saxony Anhalt), where field sizes frequently exceed 80 ha, and landscape is less divers with only a few overwintering sites being available (e.g. for cereal aphids' antagonists; Hahlen, 2004; European agricultural statistics, 2008). Subsequently, this may lead to differences in arthropod community. Some studies have shown increased abundance of cereal aphid antagonists in highly divers structured regions (Holland et al., 2003; Thies et al., 2003, 2005). Fluctuations of antagonists are less consistent and more pronounced in those landscapes (Freier et al., 2002). The model seems to simulate the steady population of antagonists (and subsequently of cereal aphids) more accurately (e.g. in Saxony Anhalt and southern Lower Saxony).

While comparing the factor "years", 2004 revealed the most interesting result. Extremely high populations of cereal aphids were observed in fields, but were significantly underestimated by the model ($R^2 = 0.75$, $b = 0.53 \pm 0.03$). In 2004, the winter wheat showed an uncommon long growth period with delayed maturity favoured by weather conditions

(P. Matthes, pers. comm.). Furthermore, few antagonists in uncommon low densities were recorded in the fields. The reasons for that remain unclear. However, both events reflect the absence of important naturally limiting factors (e.g. decreasing nutritional host plant quality and increasing abundance of natural enemies to the end of the growing season) for cereal aphids and may have contributed to extreme population growth. Even when simulation runs were performed without consideration of any antagonists (not reflecting the field situation and very unlike even with comparable low densities of natural enemies), the model calculations did not reflect the high field populations observed (data not shown). In 2004, the composition of cereal aphid populations was dominated by *S. avenae*. It may be possible that the model GETLAUS01 does not reliably simulate the population dynamics of *S. avenae*. For this reason, we have additionally compared in detail the observed and simulated populations of each of the species using datasets from 2005 (Fig. 5). Interestingly, the model simulated very well the species population levels, without wrong classifications in comparison with field data for most case studies. Moreover, results of species-specific linear regression analyses did not show significant differences in observed and simulated values, and corresponded to the results in Tab. 6. Certainly, a true species-specific simulation may be most important, and is a precondition for the improvement of the model by incorporating further abiotic and biotic factors. A possible reason for the observed high population densities of *S. avenae* may be an exceptionally immigration from surrounding habitats (e.g. winter barley fields and winter rye). At the time of population increase in winter wheat fields (mid to end of June), population crash of cereal aphids was observed in winter barley fields, where relative high population densities were observed (data not shown). Therefore, including the factor migration may enhance the models performance to simulate à posteriori the high aphid populations observed in fields. At least, it may explain in part the cereal aphid population development in 2004. Nevertheless, 2004 remained exceptionally in population development (P. Matthes, pers. comm.).

The validation method of Gosselke et al. (2001) investigates, whether the general shape of the curve of field and simulated data is correct, and the quantitative conformance is reasonable. Comparing the two shapes solely (here expressed in differences of aphid days per m² between observed and predicted aphid populations), may let to biased results (Tab. 6). When differences are small, it does not necessarily mean that shapes of curves are close to or cover each other. This is possible due to parallel translation of population dynamics in time, which lead then to significant differences between field and simulated data using further validation methods. It is therefore recommended to use the method of linear regression analyses, which compares directly single values of observed and predicted population levels during the population development. Several significant differences were found when using both methods in comparison (e.g. case study at Wahlbach in 2004, or those at Bensersiel and Carolinensiel from 2004 to 2006). A problem may arise, if a few extremely high values (outlier) influence the regression line disproportionately (Sachs, 1999). This was not the case in our model comparisons and validation processes, because we have used high sample sizes with weekly counts over long periods (e.g. high numbers of evaluation days). Interestingly, in several locations slopes differed significantly from one, although their values were near to one (with relatively low standard errors, e.g. case study in Hiddestorf West in 2005). Sample size seems to be most relevant (i.e. numbers of weekly evaluation; Selhorst, 2000). The smaller the sample size, the more frequently no significant differences from one were found (Sachs, 1999; Tab. 5).

The end of flowering of winter wheat (GS 69) is the recommended date to start the model GETLAUS01. Within the validation process we altered the start of the model run. Extensions of model's simulation period (e.g. bringing forward the start time of the model) tended to result in higher population of cereal aphids (Fig. 5). Two (June 1st) and four (May 17th) weeks earlier starts of simulation runs resulted in significant differences between simulations (Fig. 5). Primary immigration (i.e. of host-alternating aphids, included in the model as threshold value) may have caused this effect, because important immigration periods for cereal aphids have often been perceived between mid and end of May (Zhou et al., 1996). During this period, first antagonists have frequently been detected, influencing the cereal aphid population dynamics at an early stage in the growing season (Veenker & Ulber, 2004). It seems that as early as four weeks before end of flowering (the recommended simulation start), factors influencing the population dynamics are rather too complex to yield good fit between observed and predicted data. Reasons may be that the primary immigration rarely ceases, and that the start and amount of secondary spread are frequently unknown as early as mid May. Moreover, fundamental and reliable studies about early population development of cereal aphids and their antagonists are rare. A major problem results from aphid dispersion characteristics early in the season. In contrast to the end of winter wheat flowering, highly aggregated distributions of cereal aphids (and of their antagonists) challenge high sample sizes and very detailed observation at early stages of winter wheat development (i.e. at GS 32-39). Shifting the model start to an earlier date allowed testing the models performances in terms of usefulness for decision support in pest management. Even though the results from two weeks earlier simulation starts seemed to be promising, a practical utilisation as decision support is very unlikely for several reasons. Firstly, large investment in very detailed field evaluation (i.e. high numbers of tillers evaluated for cereal aphids, including their antagonists) is required for the huge amount of starting variables required for the model run. Neither farmers nor plant protection services may cope with this endeavour. Secondly, reliable methods for quick estimation of antagonist densities are lacking (Mühlenberg, 1993; Southwood & Henderson, 2000). Thirdly, weather forecasts must provide reliable meteorological values (two hour values of temperature, of precipitation, etc.) for at least three weeks, a period which is actually impossible.

There is still investment needed for model supervision, because the model GETLAUS01 did not perform equally in different case studies. Summarising, the results from the present study (i.e. different performances in different agro-climatic locations; as shown above) suggest that (predictive) simulation models should include both local (e.g. host plant communities) and large-scale (e.g. landscape elements) spatial processes to describe the system (Winder et al., 2005). Incorporation of GIS-based (geo information systems) specifications about typical, regional population developments of cereal aphids (i.e. case studies from Wörth vs. from Bernburg) may lead more frequently to correct model predictions at different locations (Gosselke et al., 2001; Backhaus, 2008). At the same time, landscape characteristics (e.g. percentage of arable land, hedges etc.) may ameliorate the regional antagonist modelling (as discussed above), and yield ultimately in credible cereal aphid population levels in all cases (Thies et al., 2003, 2005). Considering GIS-based operations, information about regional soil structures may be easily incorporated, too. We found differences in ontogenesis between observed and predicted host plant development (i.e. winter wheat) in several locations within one region (e.g. Isernhagen vs. Hiddestorf; data not shown). Sandy soils in Isernhagen differed from loamy soils in Hiddestorf, which may particularly affect the water and nutrient contents of the plants (at different meteorological events). Moreover, important influences on the development of cereal aphids (e.g. wing induction) are modelled according to the entrance of certain GS during the ontogenesis of winter wheat e.g. in model GETLAUS01. However, very detailed information about the state and conditions of host plants are an essential prerequisite, because among several influencing variables (e.g. abiotic environment, maternal experiences and morph), the host plant quality and its GS affected the development of cereal aphids most directly (Watt, 1979; Zhou & Carter, 1992; Tsai & Wang, 2001). Wrong predictions of winter wheat ontogenesis (as well as yield) may lead most directly to wrong population estimates of cereal aphids. Information about the soil conditions in Germany are available (Meynen et al., 1962) and easily incorporated into GETLAUS01 using GIS (Liebig, 2001).

Conclusions

We have compared and validated three models for cereal aphids. Some aspects of the performances of the models were satisfactory (e.g. high precision of anholocyclic hibernation in model SIMLAUS), but there were also clear indications for necessary improvements (e.g. autumn population development in model SIMLAUS). It must be stressed that the validation of a model can never be absolute. In particular, expanding knowledge in biology of cereal aphids and their interactions in and with changing environmental conditions should be utilized to improve and extend cereal aphid population models.

Acknowledgements

The authors are especially grateful to members of Plant Protection Services in Lower Saxony, Rhineland Palatinate, and Saxony Anhalt, and T. Michel for practical help. The project was financially supported by the Bundesministerium für Verbraucherschutz, Ernährung und Landwirtschaft, Germany (Federal Ministry of Food, Agriculture, and Consumer Protection; project code: 01HS083).

Chapter 2: Forecasting gradation of cereal aphids (Hemiptera: Aphididae) in winter wheat at ear emergence

A. Michael KLÜKEN[1]*, Bernhard HAU[1], Bernd FREIER[2] & Hans-Michael POEHLING[1]

[1] Institut für Pflanzenkrankheit and Pflanzenschutz (IPP), Leibniz Universität Hannover, Herrenhäuser Str. 2, 30419 Hannover, Deutschland;
[2] Institut für Integrierten Pflanzenschutz, BBA, 14532 Kleinmachnow, Deutschland

Abstract

Threshold levels for cereal aphid control at the end of the flowering stage of winter wheat are hardly ever accepted in practice due to the need for labour-intensive field surveys to compare population levels with threshold levels and due to economical production constraints. Cereal aphid treatments are preferably applied together with the last fungicide treatment at the beginning of ear emergence. Models for cereal aphid outbreaks (i.e. gradation models) have been developed using simple and multiple logistic regression analyses as well as linear discriminant analyses to support decision-making on insecticide spraying at ear emergence. In the present study, datasets from field counts and suction traps were binary classified as case studies (i.e. location-years) with and without cereal aphid gradation based on the threshold level of more than three individuals per ear and flag leaf of winter wheat at the end of flowering. Ninety-two predictor variables were derived from meteorological data and suction trap catch data characterising “winter conditions” and “real migration” and their influences on subsequent gradation. In the “winter conditions” submodel, “mean temperatures in February based on daily maximum values”, “temperature sum > 0°C based on mean daily values” (November 15th and May 1st), and “numbers of days with minimum temperatures < 0°C” (November 15th and May 1st) were most significantly associated with gradation. For the “real migration” submodel, the sums of *S. avenae* and *M. dirhodum* between April 15th and June 2nd as well as 10th catch of *S. avenae* were the most significant predictor variables associated with gradation. Model validation showed high levels of accuracy using different methods (empirical, cross-classification, random sample and ROC analyses). In this paper, the best sets of predictor variables, as determined by logistic regression and linear discriminant analysis, are compared and the model constraints are discussed.

Introduction

Cereal aphids (Hemiptera: Aphididae) are the most important pests in winter wheat in central Europe (Basedow et al., 1994) and they were regularly treated in approx. 30% of cultivated winter wheat area (Rossberg et al., 2002; European agricultural statistics, 2008). However, population dynamics of cereal aphids depend on complex factor combinations; this leads occasionally to yield losses in years in which optimal conditions for population growth prevail (Freier et al., 2001). Since the Eighties, simulation models have been developed in order to forecast cereal aphid population dynamics and their impact on yield losses (Freier & Wetzel, 1980; Wetzel et al., 1980; Carter et al., 1982; Rossberg et al., 1986; Parry et al., 2006). To consider the population dynamics of cereal aphid species entirely, earlier models were enlarged and numerous influencing factors (e.g. meteorological parameters, antagonists, fertilisation, etc.) were incorporated (Rossberg et al., 1986; Friesland, 1994; Freier et al., 1996). Model validation studies comparing simulation results and field data have shown satisfactory agreement in some cases and major discrepancies in others (Carter et al., 1989; Kleinhenz, 1994; Gosselke et al., 2001). The practical implementation of most models failed ultimately, because hit rates of models were rather low. Furthermore, field advisers and farmers could hardly accomplish detailed field evaluations due to the tremendous time and effort needed to specify the input variables required for model runs (Kleinhenz & Jörg, 1998; Gosselke et al., 2001). Models will be only accepted and implemented in practice if they do not require intensive field observations. Moreover, the monitoring process must be easily feasible, reliable, quick and cheap (Kleinhenz & Jörg, 1998). Control measures suggested by models should preferably fit in the crop-working schedule of farmers.

Estimation of yield losses in relation to cereal aphid population levels at an early stage of winter wheat development was first attempted by Leather & Dixon (1981, 1984) and by Entwistle & Dixon (1986, 1987). Several cereal aphid management concepts using simple threshold levels have since been frequently developed and reviewed (Anderson, 1985; Lindqvist, 1985; Barbagallo & Suss, 1986; Basedow et al., 1989; Holz & Wetzel, 1989; Bromand, 1990; Basedow et al., 1994; Holz et al., 1994). Based on these fixed threshold levels, further research led to more complex and flexible threshold level concepts that consider the effects of antagonists and weather (MAFF, 1988; Holz & Wetzel, 1989; Rappaport & Freier, 2001). With growing scientific knowledge, very detailed and specialised concepts for insecticide decision support in integrated pest management have been developed. To date, plant protection services still recommend integrated aphid control strategies based on simple, inflexible threshold levels at the end of flowering (Basedow et al., 1994; F. Burghause, E. Jörg, G. Lauenstein, P. Matthes, pers. comm.). In spite of long-term scientific knowledge about threshold level concepts and specialised models for cereal aphids, acceptance of these strategies in practice is low. A reason for this lack of acceptance is the relatively high workload required to determine the population level for the subsequent comparison with the threshold level (Rappaport & Freier, 2001). A further drawback of most threshold levels for cereal aphids is the late time point for decision-making (i.e. at the end of flowering GS 69). In order to be economical, working schedules should not require multiple treatments and should ideally combine insecticide treatment with the final fungicide treatment, which is usually applied at the middle or end of ear emergence (GS 55/59). In practice, there is an obvious tendency to "insurance spraying", that is, the regular application of insecticides at an earlier crop developmental stage (e.g. GS 55/59) without verifying the presence of the pest beforehand (European agricultural statistics, 2008). This results in an overuse of insecticides with numerous undesired consequences, including increased costs and reduced profit per hectare, an increased risk of resistance development (as was recently reported for oilseed rape or potato pests; Parker et al., 2006), and an increased pesticide load on non-target organisms and in non-target areas, which is associated with well-known ecological consequences as well as the incidence of secondary pests and diseases (Dixon, 1998; Gurr et al., 2004).

The aim of our study was to develop advisory warning systems for cereal aphid control before the flowering stage of winter wheat (e.g. at GS 55). This was done by performing simple (e.g. simple logistic regression) and multiple statistical analyses (e.g. linear discriminant analyses) on cereal aphid datasets from field evaluations and suction trapping.

Logistic regression analyses can be used in epidemiological or population research, where the binary response usually is the presence or absence of a disease or a pest (Corkum et al., 2006; Graf et al., 2007). Linear discriminant analyses, which are widely used to identify variables contributing to the classification of binary response variables, have also been used in epidemiological and population research studies (Ahlers & Hindorf, 1987; Lawrence & Labus, 2003).

Materials and Methods

Field data evaluation

Thirty datasets on population dynamics of cereal aphids were collected in winter wheat fields in Germany from 2004 to 2006 (Fig. 1). Field evaluations were conducted in two-ha, insecticide-free “windows” at 10 locations ranging from maritime to continental climate. Evaluations were performed on a weekly basis from October to December and from March until the end of July (i.e. winter wheat harvest). Cereal aphids and their antagonists were collected by means of D-VAC suction sampling (Veenker & Ulber, 2004) or were counted visually and enumerated as the number of individuals per plant or per tiller. Sampling points were set up along transecting lines in order to avoid repetitive sampling of the same plants. The sample size per evaluation day varied according to aphid density and ranged from approx. 700 to 35,000 plants (i.e. 4 to 150 m² for D-VAC) in autumn and from 100 to approx. 8,000 tillers in spring and summer. The numbers of arthropods in the suction samples were converted to numbers per tiller or per square meter. Growth stages (GS) of winter wheat (Tottman & Broad, 1987; Meyer, 2008) were evaluated at each time using 20 tillers or 10 plants.

Twenty additional datasets collected in winter wheat fields near Fläming and Magdeburg were available for analysis (Freier et al., 1999; Gosselke et al., 2001; Fig. 1). H. Friesland, U. Heimbach and W. Rieckmann (pers. comm.) provided another 39 datasets taken in winter wheat fields near Braunschweig and Hannover (i.e. Elze, Langreder, and Poppenburg; Fig. 1). At those locations, the numbers of cereal aphid instars per tiller were visually counted from the end of May until the end of July (from 1994 to 2006); the numbers were then converted to square meter values according to the numbers of tillers in each field. Overall, 89 case studies (i.e. locations and years) were available for analysis (Fig. 1). All agronomic practices at each of the study locations were carried out according to the principles of good protection practice.

Suction trap samples

Datasets from fixed suction trap studies (Rothamsted-type, MaCaulay et al., 1988) performed in Germany were made available by the EXAMINE project (EXploitation of Aphid Monitoring systems IN Europe; Examine, 2008; P. Verrier, pers. comm.). This study includes the years from 1984 to 2006 and the locations Aschersleben, Göttingen, Hohenheim, Rostock, Braunschweig, Elze, Langreder, and Poppenburg (Fig. 1; Examine, 2008). Small fixed suction traps (height 2.0 m) were used at the last four locations. Datasets from only 69 case studies were suitable for our analysis because of the lack of suction trap for all years in some cases. The numbers of different cereal aphid species (alatae) were specified in daily catches from April to November in most of the case studies. In 2004 to 2006, some suction traps were checked only three times a week. In these cases, number of cereal aphids caught per day was calculated by dividing the total number trapped by the number of days in the trapping period. The suction traps continuously caught the aphids in all case studies and failed only briefly.

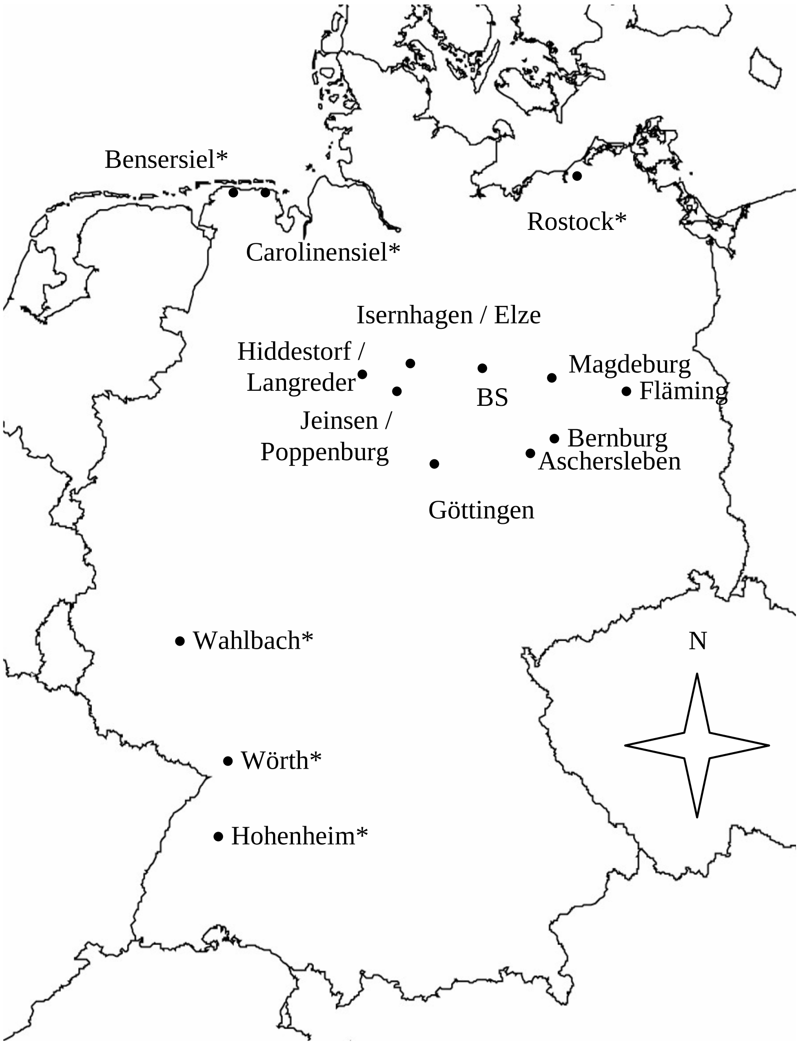


Fig. 1: Map of Germany sketching the collection sites (field evaluations and suction trap catches) where case studies were performed (BS = Braunschweig; north arrow is specified). *Asterisks indicate locations without typical continental climate (H. Friesland, pers. comm.)

Meteorological parameters

Meteorological data (hourly temperature, wind speed, precipitation, etc.) were obtained from weather station networks of the German Weather Service (DWD) and the Information System Integrated Plant Protection (ISIP) service. The distance between a field or suction trap and the next weather station never exceeded 20 km.

Definition of variables

The same binary response variable was defined for logistic regression analysis (log RA) and linear discriminant analysis (lin DA). Supported by cereal aphid thresholds (Holz & Wetzel, 1989; Holz, 1991; Basedow et al., 1994; Rappaport & Freier, 2001), available datasets were regrouped as follows. If, in a given case study, the population exceeded the threshold of three cereal aphids per ear and flag leaf at the end of flowering of winter wheat (GS 69) (Basedow et al., 1994), the dataset was referred to as “case study with gradation” (binary status 1); case studies below the threshold were defined as “case studies without gradation” (binary status 0). In this context, “gradation” means a cereal aphid outbreak, i.e. a heavy infestation, which causes yield losses (Ohnesorge, 1991).

Several predictor variables were defined to describe their influence on the response variable “gradation”. These influencing variables were arranged in two subsequent groups according to preliminary analyses. To describe “winter conditions” (i.e. conditions from November to May; first submodel), meteorological parameters (e.g. temperature, precipitation, snow, global radiation, etc.) and their transformations as positive or negative sum standards, numbers of days above certain critical values or as mean values over certain periods of time were defined as different predictor variables.

To characterise the population start (i.e. the early growth) and the first events of early immigration (“real migration”, second submodel) in spring and their subsequent influence on gradation, the numbers of cereal aphids (all stages) caught in fields or in suction traps (sum of individual aphids on certain days or over certain periods of time) were used as predictor variables.

Statistical analyses

Several statistical techniques (simple and multivariate methods) were applied to different datasets and variables. In all tests, significance levels were set at $\alpha = 5\%$. Square root ($\sqrt{(x+0.0001)}$) and arcsin-square root ($\arcsin \sqrt{x}$) transformations were performed to better meet the assumption of normal distribution in case of count and percentage values, respectively. Analysis of variance (ANOVA; proc glm, program SAS; SAS, 2008) was performed to test effects of further influencing variables (e.g. location, year) on cereal aphid gradation. In this context, the explanatory parts of a given predictor variable in combination with influencing variables like location or year were detected and estimated.

Logistic regression analyses (log RA)

Log RA were used to identify factors (predictor variables) significantly associated with cereal aphid gradation. In a given case study, the binary response variable *Y* was absence or presence of gradation of cereal aphids. The predictor variables are putative key factors and possible confounding variables (Armitage et al., 2002; Hosmer & Lemeshow, 2000). Common linear regression analysis with intercepts *a* and slopes *b* can be transformed to log RA in order to identify those predictor variables separating significantly between cereal aphid gradation, i.e. the best set of predictor variables,

$$\log\left(\frac{p}{1-p}\right) = a + bx \tag{1}$$

where *p* represents the probability that the response variable *Y* equals 1 and is constrained between 0 and 1 (Afifi & Clark, 1999). If *Y* represents possible formation of gradation in a case study, the probability of gradation occurrence can be modelled as follows:

$$p(Y = 1) = \frac{\exp(a + bx)}{(1 + \exp(a + bx))} \tag{2}$$

where *a* and *b* represents parameters to be estimated and *x* represents a covariate or a predictor. In generalisation, representative for several predictor variables x_i with the coefficients b_i may be entered (Mila et al., 2004). The response variable $p(Y = 1)$ is, as probability, constrained between 0 and 1 for any values of *x*. The coefficients b_i are similar to the regression coefficients in an ordinary multiple regression model. Their interpretations are somewhat different in logistic regression (Hosmer & Lemeshow, 2000), but they are used here to quantify the gradation risk factor.

Predictor variables were evaluated in two ways according to the likelihood ratio test (LRT). Firstly, the ability of a predictor variable alone to predict the risk of gradation was tested. This consists of testing the deviance reduction attributed to a predictor variable when it is first entered into the model. Secondly, removing it from a complete model with all explanatory variables tested the predictive ability of a predictor variable (Twengström et al., 1998). The latter LRT method, referred to as a Type 3 analysis in procedure genmod (program SAS; SAS, 2008), duplicates the analysis of deviance entry that a predictor variable would have if it would be the last predictor variable entered. If none of the independent predictor variables were correlated, the two LRT methods would be identical. Since the predictor variables are related here, any complete analysis of deviance tables would depend on the order of the predictor variables. This method (testing the significance of a variable if entered first and last) duplicates the essential portion of the analysis of deviance table in a manner that is not dependent on the order of the variables (Yuen et al., 1996).

The logistic procedure (stepwise forward method, program SAS; SAS, 2008) was subsequently used to select the best model, that is, the best set of predictor variables. Starting from an “empty” model, the procedure includes sequentially predictor variables that were significantly associated with the response variable. Predictor variables could also be eliminated from the model whenever they became non-significant. In the final model, all predictor variables were significantly associated with formation of the response variable (i.e. gradation). Goodness of fit was determined by the proportion of concordant and discordant pairs and by the values of Somers’ D, Gamma, Tau-a and c statistics for both submodels using log RA.

Linear discriminant analyses (Lin DA)

Lin DA is based on the Bayes’ theorem and refers to several different types of analyses (Fischer, 1936; Tatsuoka, 1971; Lachenbruch & Kupper, 1973). Classificatory discriminant analysis techniques are used to classify individuals into one of two or more alternative groups or populations based on a set of measurements. The populations are known to be distinct, and each individual belongs to one of them based on a selected dividing point *c*. The lin DA used in this study is based on Fischer (1936) and generates the linear discriminant function *z*:

$$z = c + a_1x_1 + a_2x_2 + .. + a_kx_k \tag{3}$$

where a_i are coefficients of predictor variables x_i and can be computed according to Fischer (1936), Cooley & Lohnes (1971), Lachenbruch & Kupper (1973), or Afifi & Azen (1979). The predictor variables x_i, used for classification, have a multivariate normal distribution, assuming that within-class covariance matrices are equal. However, the mean values for a given predictor variable may be different in the two populations. A further assumption was that random samples were taken from each of the populations.

Parametric lin DA (Roa, 1973) were performed in order to identify predictor variable combinations significantly associated with binary formation of cereal aphid gradation. The calculated discriminant function *z* is subsequently compared with zero:

case 0 (i.e. no gradation) occurs, if $z < 0$

case 1 (i.e. gradation) occurs, if $z \geq 0$

The option of prior probability p_p (on formation of gradation) was specified according to additional information gathered from the datasets. The stepwise forward method of lin DA (proc stepdisc, program SAS; SAS, 2008) was used to select predictor variables (details in section above). Predictor variables could be eliminated from this model whenever they became non-significant (and other predictor variable combinations became significant). In the final model, all predictor variables were significantly associated with the binary response variable. After the selection of significantly separating predictor variables, lin DA were further performed with those predictor variables for subsequent parameterisation and model calibration using another procedure from program SAS (i.e. proc discrim). Standardised discriminant coefficients were computed in order to directly compare the values of coefficients a_i and to judge the relative effect of each predictor variable on the discriminant function (Afifi & Clark, 1999; SAS, 2008). Correlations between predictor variables were performed in order to identify the degree of association between the influencing predictor variables.

Model validation

For model validation, empirical (procedures list and listerr, program SAS; SAS, 2008) and cross-classification methods (procedures crossvalidate, crosslist and crosslisterr; program SAS; SAS, 2008) were performed on datasets used for model selection according to lin DA. Since there is always a possibility of making the wrong classification, the probability (i.e. posterior probabilities) that a given individual came from one group or the other was computed as mean values for the empirical and the cross-classification methods in lin DA. Moreover, parameters from log RA and lin DA were graphically compared by using receiver operating characteristic (ROC) curves (Afifi & Clark, 1999; Pepe, 2000; Dewdney et al., 2007). ROC analysis is based on true positive (TP) and false positive (FP) decisions. The TP fraction is the number of correct classifications of gradation divided by the total number of case studies with gradation. The FP fraction is the number of incorrect classifications of gradation divided by total number of case studies without gradation. ROC curves plot TP as a function of FP at all possible decision thresholds (here: threshold levels ranged from 0.1 to 8 cereal aphids per ear and flag leaf). In an ROC curve, the origin of the graph represents the model result “no gradation” for all case studies. This classification yields no FP but captures no TP. The upper right corner would classify gradation of all case studies, thus detecting all case studies that truly showed cereal aphid gradation, but also classifying gradation for all case studies that do not show them. An efficient algorithm would yield a curve “pushed to the upper left corner” (Afifi & Clark, 1999).

Results

General results

Anholocyclical hibernation of cereal aphids was rarely observed in winter wheat fields, and cereal aphids were first detected in fields or in suction traps in approx. mid-May, with increasing numbers from spring to summer. Peak numbers of cereal aphids in continental locations appeared most frequently during the first week of July (i.e. at late milky or early dough stage of winter wheat, GS 77/83). Specific predators (i.e. Coccinellidae, Syrphidae, Chrysopidae) occurred earliest at the end of May or beginning of June. Their numbers were very variable within and between the case studies. Analyses of frequency distributions of important growth stages of winter wheat over several years showed that the end of tillering (GS 39/49), the beginning of ear emergence (GS 51/55), the beginning of flowering (GS 59/61) and the end of flowering (GS 65/69) most frequently occurred on May 26th (±0.7 days), June 3rd (±0.7 days), 10th (±0.6 days), and 17th (±0.6 days), respectively.

The case studies provided a total of 89 and 69 datasets for field populations and suction trap catches, respectively. Gradation was observed in 26 and 20 case studies, respectively, but only in regions with a continental climate. In preliminary analyses (ANOVA), it was shown that the influencing variables “location” and “year” affected population development in datasets from non-continental locations (i.e. from northern Lower Saxony and Rhineland Palatinate) significantly, which was not observed in case studies with a continental climate. Therefore, case studies from non-continental locations were excluded from the analyses. Among the included case studies from continental locations, 26 and 47 case studies with field data and 20 and 39 case studies with suction trap data were grouped as with (1) and without (0) gradation, respectively (i.e. prior probabilities of $p_{pf(1)} = 0.356$ and $p_{pf(0)} = 0.644$ for field data and of $p_{ps(1)} = 0.339$ and $p_{ps(0)} = 0.661$ for suction trap data, respectively). From the remaining continental case studies (73 field datasets and 59 suction trap datasets), 14 and 9 case studies with field data and suction trap data, respectively, were selected at random using the random number function in Microsoft Excel before data analysis. These case studies were used for independent validation of model results obtained from the basic dataset.

Logistic regression analyses (log RA)

Simple log RA were performed with field data taken at several growth stages of winter wheat (GS 39/49, 51/55, 59/61 and 65/69). For each growth stage, logistic regression functions (Fig. 2) were used to calculate the probability of gradation depending on the field counts of cereal aphids (sum of all aphid instars and species per m²). The subsequent event of gradation was more probable with significantly ($p < 0.05$) increasing numbers of cereal aphids (found at each of the growth stages in the field). In Fig. 2, datasets and regression functions, together with their classifications of gradation risks, are specified at two growth stages (GS 51/55 and 59/61). For GS 51/55 and GS 59/61, the probability of gradation is higher than 0.5 if the sums of all cereal aphids per m² are greater than 116 and 445, respectively. For the same datasets, ANOVA did not show significant effects of the influencing variables “location” and “year” on gradation.

Using simple log RA, gradation formation was estimated based on labour-intensive field counts at certain stages of crop development. However, this served to recheck the submodel performance (see below) and not for follow-up.

Results from simple log RA of diverse parameters defining the probability of risk of gradation showed that 13 of 56 predictor variables (e.g. positive and negative temperature sums from November 15th to May 1st with basis temperatures of 0° or 4°C, mean temperatures in different periods, and numbers of days with temperatures below 0°C between November 15th and May 1st) were significantly ($p < 0.05$) associated with cereal aphid gradation (Tab. 1). The probability of gradation decreased as temperatures decreased during the winter, as indicated by the slopes of the respective predictor variables (Tab. 1).

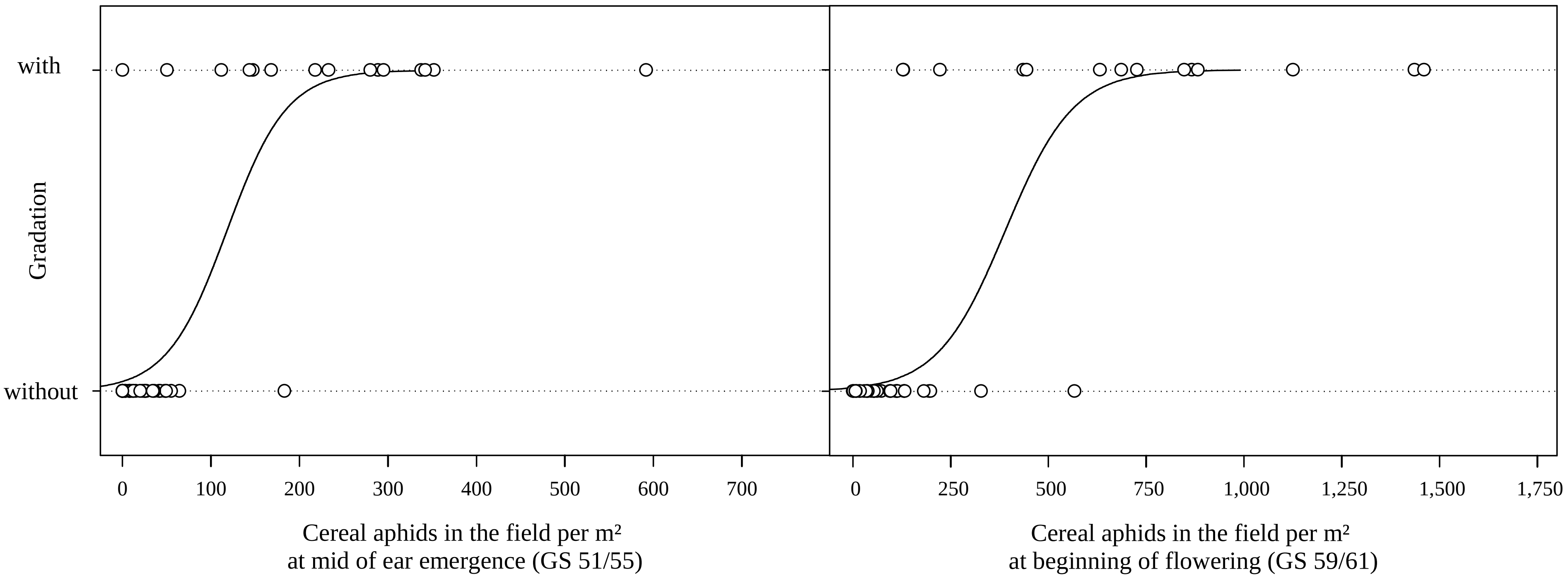


Fig. 2: Logistic regression analyses of field counts of cereal aphids (per m², sum of all instars and species) found in the field at the middle of ear emergence (left sketch: GS 51/55, June 2nd, *a*=-3.48, *b*=0.03) or beginning of flowering (right sketch: GS 59/61, June 9th, *a*=-4.49, *b*=0.01) and the subsequent formation of gradation (with and without gradation). In both sketches, scaling excludes the three highest values for case studies with gradation

Tab. 1a: Predictor variables significantly ($p < 0.05$) associated with gradation of cereal aphids according to each independent submodel. The estimates of slope *b* (± standard deviation, SD) from one-way logistic regression analyses (log RA) indicated the effects of each predictor variable. The likelihood ratio test (LRT) specified for a predictor variable entered into a model first (with one degree of freedom (df) for each variable) and last with the respective values for χ^2 and df (dd = degree day, # = number).

Submodel	**Predictor**	**Log RA**	**LRT: variable first**	**LRT: variable last**	
	variable	*b* (±SD)	χ^2	χ^2	df
Winter Conditions	Mean temperature in February [°C] based on daily mean values	0.71 ±0.22	42.48^{+++}	60.42^{+++}	2
	Mean temperature in February [°C] based on daily maximum values	0.63 ±0.19	42.45^{+++}	59.43^{+++}	2
	Mean temperature in February [°C] based on daily minimum values	0.73 ±0.24	12.97^{++}	58.59^{+++}	2
	Mean temperature in March [°C] based on daily mean values	0.84 ±0.35	9.13^{+}	59.85^{+++}	3
	Mean temperature in March [°C] based on daily maximum values	0.92 ±0.37	14.09^{++}	60.00^{+++}	3
	Numbers of days with mean daily temperatures < 0°C [#]	-0.17 ±0.06	19.86^{+++}	35.61^{++}	2
	Numbers of days with maximum daily temperatures < 0°C [#]	-0.16 ±0.06	26.33^{+++}	60.84^{+++}	3
	Numbers of days with minimum daily temperatures < 0°C [#]	-0.11 ±0.04	12.97^{++}	43.17^{++}	2
	Temperature sum > 0°C [dd] based on daily mean values	0.02 ±0.01	30.71^{+++}	59.43^{+++}	2
	Temperature sum > 0°C [dd] based on daily maximum values	0.01 ±0.01	38.60^{+++}	60.42^{+++}	2
	Temperature sum > 0°C [dd] based on daily minimum values	0.02 ±0.01	21.84^{+++}	65.09^{+++}	3
	Temperature sum < 0°C [dd] based on daily mean values	-0.02 ±0.01	13.66^{++}	62.09^{+++}	3
	Temperature sum < 0°C [dd] based on daily minimum values	-0.01 ±0.01	11.17^{++}	42.84^{++}	2

* Asterisks indicate association between time and entry of certain growth stages (see general results section).

$^{+++}$ Plus indicate significance level of $\alpha < 0.0001$

$^{++}$ Plus indicate significance level of $\alpha < 0.001$

$^{+}$ Plus indicate significance level of $\alpha < 0.01$

Tab. 1b: Predictor variables significantly ($p < 0.05$) associated with gradation of cereal aphids according to each independent submodel. The estimates of slope *b* (± standard deviation, SD) from one-way logistic regression analyses (log RA) indicated the effects of each predictor variable. The likelihood ratio test (LRT) specified for a predictor variable entered into a model first (with one degree of freedom (df) for each variable) and last with the respective values for χ^2 and df (dd = degree day, # = number).

Submodel	**Predictor variable**	**Log RA**	**LRT: variable first**	**LRT: variable last**	
		b (±SD)	χ^2	χ^2	df
Real Migration	1st catch of *S. avenae* in suction traps [Julian day]	-0,05 ±0,02	12.35^{++}	39.18^{++}	3
	5th catch of *S. avenae* in suction traps [Julian day]	-0,07 ±0,02	19.71^{++}	41.77^{+++}	3
	10th catch of *S. avenae* in suction traps [Julian day]	-0,08 ±0,02	21.19^{+++}	43.32^{+++}	3
	1st catch of *M. dirhodum* in suction traps [Julian day]	-0,06 ±0,01	14.41^{++}	36.29^{++}	2
	5th catch of *M. dirhodum* in suction traps [Julian day]	-0,04 ±0,01	8.33^{+}	40.90^{+++}	3
	10th catch of *M. dirhodum* in suction traps [Julian day]	-0,03 ±0,01	4.94	40.90^{+++}	3
	Sum of *S. avenae* in suction traps from April 15th to June 2nd [#]*	0.07 ±0.03	31.82^{+++}	39.14^{+++}	2
	Sum of *S. avenae* in suction traps from April 15th to June 9th [#]*	0.08 ±0.03	33.56^{+++}	40.24^{+++}	2
	Sum of *M. dirhodum* in suction traps from April 15th to June 2nd [#]*	0.11 ±0.05	26.89^{+++}	40.25^{+++}	2
	Sum of *M. dirhodum* in suction traps from April 15th to June 9th [#]*	0.06 ±0.03	19.99^{+++}	39.50^{+++}	3
	Sum of cereal aphids in suction traps from April 15th to May 25th [#]*	0,01 ±0,01	7.87^{+}	43.26^{+++}	3
	Sum of cereal aphids in suction traps from April 15th to June 2nd [#]*	0,01 ±0,01	13.32^{++}	42.63^{+++}	3
	Sum of cereal aphids in suction traps from April 15th to June 9th [#]*	0,01 ±0,01	15.07^{++}	41.68^{+++}	3

* Asterisks indicate association between time and entry of certain growth stages (see general results section).

$^{+++}$ Plus indicate significance level of $\alpha < 0.0001$

$^{++}$ Plus indicate significance level of $\alpha < 0.001$

$^{+}$ Plus indicate significance level of $\alpha < 0.01$

Tab. 2: Parameter estimates (± standard errors) according to logistic regression analyses (log RA) used to explain the gradation of cereal aphids for each submodel, i.e. "winter conditions" (November 15th to May 1st) and "real migration" (April 15th to June 2nd).

Submodel	**Predictor variable**	**Parameter Estimate (± SE)**
Winter Conditions	Constant	-21.38 ±7.38
	Mean temperature in February [°C] based on daily maximum values	1.71 ±0.67
	Temperature sum > 0°C [dd] based on daily mean values	0.03 ±0.01
Real Migration	Constant	-3.10 ±0.82
	Sum of *S. avenae* in suction traps from April 15th to June 2nd [#]*	0.15 ±0.07
	Sum of *M. dirhodum* in suction traps from April 15th to June 2nd [#]*	0.32 ±0.13

* Asterisks indicate association between time and entry of certain growth stages (see general results section)

13 of 36 predictor variables (e.g. 1st, 5th, and 10th catches in suction traps after winter and the sum of cereal aphids caught in suction traps up to certain days according to entry of GS) were significantly associated with gradation (Tab. 1). The slope *b* showed that, the later cereal aphids were caught in suction traps and the smaller the sums of aphids in suction traps on certain dates, the lower the probability of gradation (Tab. 1). ANOVA, applied separately on each of the temperature- or suction trap-derived predictor variables, showed that locations (influencing variable “locations”) never differed significantly with respect to the formation of gradation, whereas, in some cases, the influencing variable “years” significantly affected the possibility of cereal aphid gradation. All significant predictor variables (26) from simple log RA were highly inter-correlated ($R > +0.56$; $p < 0.01$). When the first predictor variables entered into the “winter conditions” submodel were tested by LRT, the highest Chi-square values were observed for the predictor variables “mean temperature in February based on daily maximum values” and “mean temperature in February” as well as for the predictor variable “temperature sum > 0°C based on daily maximum values” (Tab. 1). “Sum of *S. avenae* in suction traps from April 15th to June 9th”, “sum of *S. avenae* and *M. dirhodum* in suction traps from April 15th to June 2nd” and the “10th catch of *S. avenae* in suction traps” showed the highest Chi-square values for the predictor variables entering a model first according to the “real migration” submodel (Tab. 1). When the predictor variables were tested by excluding them one by one from a complete multiple model, the impact of the different predictor variables changed, and the importance of all significant predictor variables increased (Tab. 1). The order of the predictor variables affects their explanation potential, indicating that they are correlated. All significant predictor variables were of importance, regardless of which other predictor variables were included in the model (Tab. 1).

Multiple log RA was subsequently performed to select predictor variables most significantly associated with gradation for each of the submodels (Tab. 2). For the best model fit, “mean temperatures in February based on daily maximum values” and “temperature sum > 0°C based on daily mean values” were entered as predictor variables in the “winter conditions” submodel, whereas “sum of *S. avenae* in suction traps from April 15th to June 2nd” and “sum of *M. dirhodum* in suction traps from April 15th to June 2nd” were selected as predictor variables in the “real migration” submodel (Tab. 2). Fig. 3 (top) shows the distribution of case studies with and without gradation used in model parameterisation of the “real migration” submodel. Case studies above the straight line were classified as case studies with gradation (Fig. 3 top).

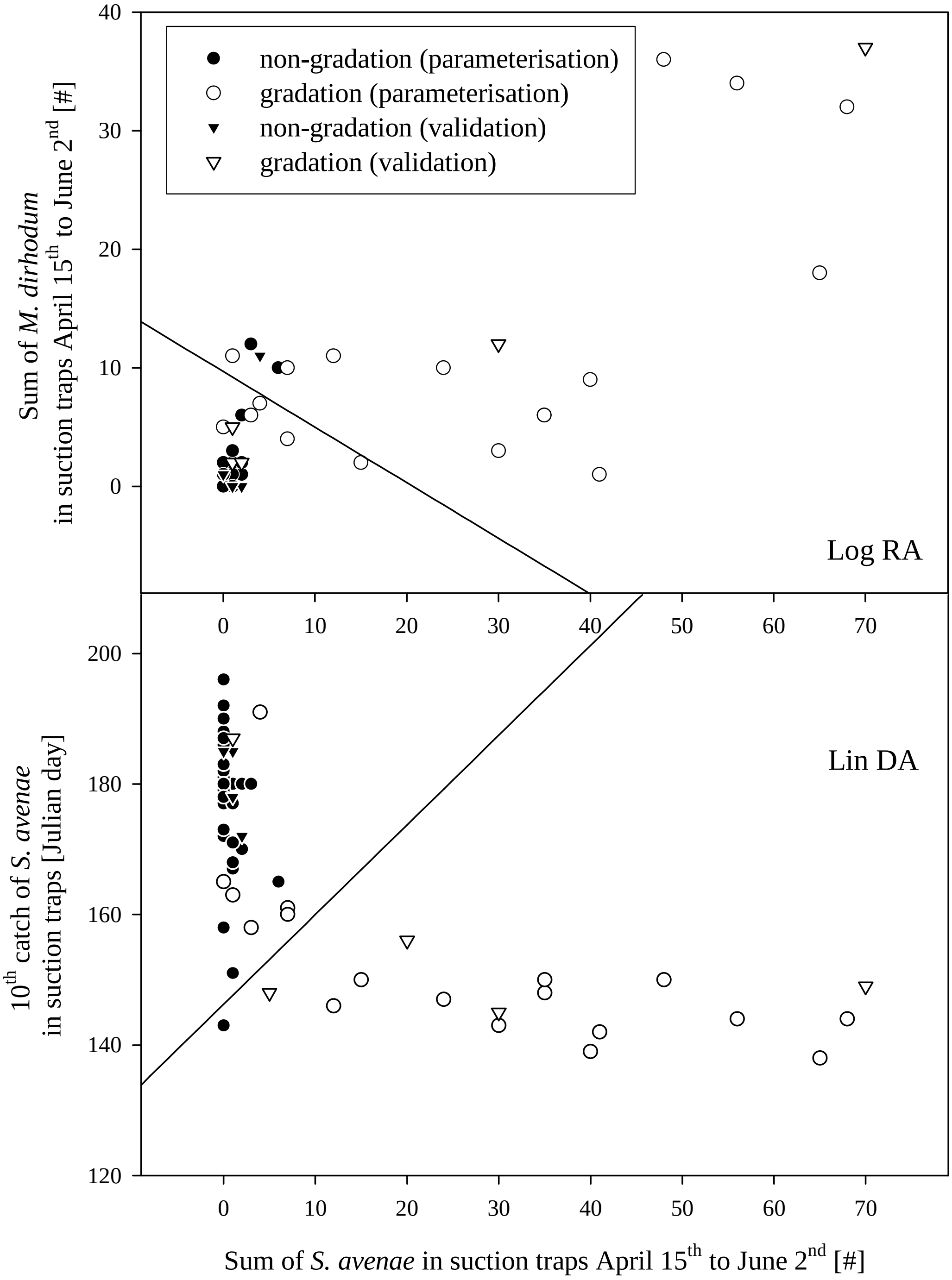


Fig. 3: Significant predictor variables for the “real migration” submodel, as determined by logistic regression analysis (log RA; predictor variables: “sum of *S. avenae* in suction traps from April 15th to June 2nd” and “sum of *M. dirhodum* in suction traps from April 15th to June 2nd”, Tab. 2) and linear discriminate analysis (lin DA; predictor variables: “sum of *S. avenae* in suction traps from April 15th to June 2nd” and “10th catch of *S. avenae* in suction traps”). White and black dots indicate case studies with and without gradation that were used for parameterisation, respectively. White and black triangles classify case studies with and, respectively, without gradation that were used for validation. The linear functions (straight lines) obtained from the logistic regression analyses (top) and linear discriminant analyses (bottom) separate case studies with and without gradation.

The number of concordant pairs was very high (97%), indicating that the submodels calculated high probabilities when gradation was truly observed, and low probabilities when gradation was not observed and when only a few probabilities were falsely predicted (as per the number of discordant pairs; Tab. 3). Other criteria (Somers' D, Gamma, Tau-a, and c) calculated from the number of concordant and discordant pairs were accordingly high. In particular, c was very high, indicating that the submodels had good predictive accuracy (Tab. 3).

Tab. 3: Goodness of fit criteria are specified for the "winter conditions" ($n = 59$) and "real migration" ($n = 50$) submodels according to the best predictor variable combinations from multiple logistic regression analyses in Tab. 2.

Criteria	**Winter conditions**	**Real migration**
Concordant (%)[a]	97.3	96.5
Discordant (%)[a]	2.7	3.5
Tied (%)[a]	0.0	0.0
Somers' D[b]	0.946	0.931
Gamma[b]	0.946	0.931
Tau-a[b]	0.462	0.438
c[b]	0.973	0.965

[a] Measurements assess the association of estimated probabilities and observed frequencies.
[b] Indices computed from the two first measurements. A model with higher values for these indices has better predictive ability than a model with lower values.

Linear discriminant analyses (lin DA)

In the lin DA, the following significant predictor variables (Tab. 4) were selected, leading to the best model fit: The "winter conditions" submodel included the predictor variables "mean temperatures in February based on daily maximum values", "temperature sum > 0°C based on daily mean values", and "number of days with minimum daily temperatures < 0°C" (Tab. 4).

Tab. 4: Parameterisation of predictor variables and further statistical results of linear discriminant analyses specified as the partial coefficient of determination (R^2) with test statistics (F-values) for the two independent submodels, “winter conditions” (November 15th to May 1st) and “real migration”. The ranking (i.e. “no. in”) of predictor variables specifies forward steps in cases in which significant predictor variables were entered. The significance level for F values is $\alpha = 5\%$ (dd = degree day, # = number).

Submodel	**Predictor Variable**	**Partial R^2 (no. in)**	**F-values**	**Coefficients**	**Standardised Coefficients**
Winter Conditions	Constant			-38.57	.
	Mean temperature in February [°C] based on daily maximum values	0.56 (1)	66.14	2.27	28.19
	Temperature sum > 0°C [dd] based on daily mean values	0.16 (2)	9.49	0.04	21.55
	Number of days with daily minimum temperatures < 0°C [#]	0.23 (3)	14.38	-0.17	-22.68
Real Migration	Constant			11.70	.
	Sum of *S. avenae* in suction traps from April 15th to June 2nd [#]*	0.46 (1)	41.69	0.11	10.58
	10th catch of *S. avenae* in suction traps [Julian day]	0.12 (2)	6.39	-0.08	-7.59

* Asterisk indicate association between time and entry of certain growth stages (see general results section)

In the “real migration” submodel, the significant predictor variables “sum of *S. avenae* in suction traps from April 15th to June 2nd” and “Julian days of 10th catch of *S. avenae* in suction traps” were entered (Tab. 4). Fig. 3 (bottom) shows the distribution of case studies with and without gradation used in the parameterisation and validation of lin DA. Case studies below and above the straight line of the discriminant function were classified as cases with and without gradation, respectively (Fig. 3 bottom). The partial coefficient of determination and the respective F-statistics (Tab. 4) indicate that the submodels correctly predicted high probabilities of gradation in cases in which gradation was truly observed. Selected predictor variables of the two final submodels (according to best model fit from lin DA) showed an average squared canonical correlation coefficient of 0.72 for “winter conditions” and 0.53 for “real migration”, indicating that the submodels had good predictive value.

Examples for lin DA and log RA

The following example uses the “winter conditions” at Braunschweig in 2006 to characterise this case study using the results of log RA and lin DA. In that case study, the mean temperature in February based on daily maximum values was 2.2°C, the mean temperature sum was 91.4 degree days > 0°C based on daily mean values between November 15th and May 1st, and 105 days were observed with minimum temperatures < 0°C between November 15th and May 1st. With these actual values for the predictor variables (values in italic) and coefficients for log RA (Tab. 2) and lin DA (Tab. 4), the following values were calculated:

$$\text{Logit}_{\text{log RA}}\ p(y = 1):\quad -21.38 + 1.71 \times \mathit{2.2} + 0.03 \times \mathit{91.4} = -14.88 \tag{4}$$

$$z_{\text{lin DA}}:\quad -38.57 + 2.27 \times \mathit{2.2} + 0.04 \times \mathit{91.4} - 0.17 \times \mathit{105} = -47.77 \tag{5}$$

Both functions (no. 4 and 5) result in values less than zero; hence, this case study was classified as a case study without gradation in both analyses.

The next example of “real migration” simulations uses suction trap data from Göttingen in 2004. The suction trap caught 35 individuals of *S. avenae* and 10 individuals of *M. dirhodum* between April 15th and June 2nd in 2004. The 10th catch of *S. avenae* was observed on May 28th in 2004, i.e. the 149th Julian day. These actual values for the predictor variables (in italic) and the respective coefficients according to log RA (Tab. 2) and lin DA (Tab. 4) yielded the following values:

$$\text{Logit}_{\text{log RA}}\ p(y = 1):\quad -3.10 + 0.15 \times \mathit{35} + 0.32 \times \mathit{10} = 5.35 \tag{6}$$

$$z_{\text{lin DA}}:\quad 11.70 + 0.11 \times \mathit{35} - 0.08 \times \mathit{149} = 3.63 \tag{7}$$

Since both functions (no. 6 and 7) yielded a value greater than zero, this case study was characterised as case study with gradation in both analyses.

Model validation

Validating the “winter conditions” submodel from lin DA, two and three gradation case studies (3.4% and 5.1%) were misclassified as non-gradation (false-negative classification) in both validation procedures (empirical and cross-classification methods). For empirical validation, three non-gradation case studies (5.1%) were additionally misclassified as gradation case studies (false-positive). Mean posterior probabilities (±SE), as determined by empirical and cross-classification, ranged from 0.393 (±0.06) to 0.607 (±0.06) for a given case study classified as a case study with and without gradation. ROC analyses showed high levels of sensitivity and specificity (Fig. 4), as shown by the parameter estimates in Tab. 2 and 4.

In 12 and 13 out of 14 case studies chosen at random before variable selection and parameterisation, the “winter conditions” submodel accurately predicted cereal aphid gradation as determined by log RA and lin DA (with two and one case studies, respectively, being determined as false-positive).

For validation of the “real migration” submodel from lin DA, six and seven gradation case studies (12% and 14%) were misclassified as non-gradation case studies (false negative) using empirical and cross-classification methods, respectively. Additionally in cross-classification, one non-gradation case study (2%) was classified as a gradation case study (false positive). Mean posterior probabilities (±SE) calculated from empirical and cross-classification methods ranged from 0.283 (±0.05) to 0.717 (±0.05) and from 0.279 (±0.05) to 0.721 (±0.05) for a given individual case study being classified as case study with and without gradation, respectively. ROC analyses showed moderately high levels of sensitivity and specificity (Fig. 4), as determined by the parameter estimates in Tab. 2 and 4.

In five and eight out of nine case studies chosen at random before variable selection and parameterisation, the “real migration” submodel accurately predicted cereal aphid gradation, as determined by log RA and lin DA. For the latter analysis, one case study was determined to be false negative, whereas one and three case studies were determined, according to the log RA, to be false positive and, respectively, false negative (Fig. 3).

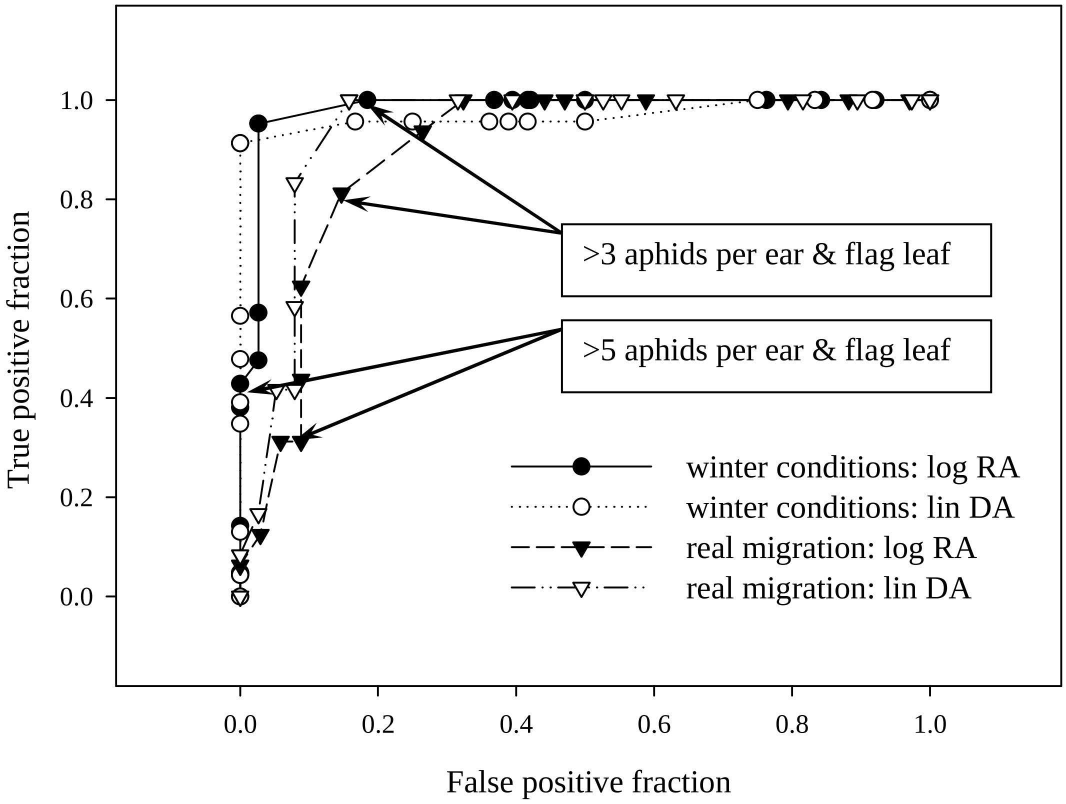


Fig. 4: Receiver operating characteristic (ROC) curves from multiple logistic regression analyses (log RA, black) and linear discriminant analyses (lin DA, white) for the “winter conditions” (circles) and “real migration” (triangles) submodels. Arrows indicate the relation between false positive (i.e. 1-specificity) and true positive fractions (i.e. sensitivity) obtained using control thresholds of 3 and 5 cereal aphids per ear and flag leaf, respectively.

Discussion

General discussion

Our primary aim was to develop a scientific model to forecast gradation in winter wheat at the time of ear emergence (i.e. in GS 55) that would be suitable for practical application. Cereal aphid gradation is not a frequent event (Borgemeister 1992; Volkmar et al., 1994; Rappaport & Freier, 2001; Freier et al., 2007), and safety concepts for well-targeted application of insecticides are needed (Pluschkell, 1997). However, problems associated with the effort of either starting values (e.g. input variables) or limited reliability of forecasting models have shown that implementation of very detailed population models describing the development of every single morph and species cannot be achieved (Carter et al., 1989; Gosselke et al., 2001). Field advisers and farmers cannot accomplish the immense amount of work required for very detailed specification of starting variables (Kleinhenz & Jörg, 1998).

We therefore established models based on suction trap catches and meteorological data, as both are not that labour-intensive compared to field evaluations. Meteorological data, for example, are frequently supplied by weather station networks (e.g. DWD, ISIP), and suction trap catches require a low workload, especially in the period between April 15th and June 2nd (Veenker & Ulber, 2004).

Establishment of "winter conditions" and "real migration" submodels

Winter strength seems to be a key event in the population development of cereal aphids in continental climate (Leather & Lethi, 1981; Lindqvist, 1985; Leather et al., 1989). When cereal aphid gradation occurred, the intercept and the slope of the regression line between evaluation dates and log numbers of cereal aphids in fields were significantly increased (data not shown). Thus, the initial population levels (i.e. the first occurring aphids) were significantly higher, and the population developed quicker in case studies with gradation compared to non-gradation situations (data not shown).

Several authors have shown that the winter exerts a strong influence on both holo- and anholocyclical cereal aphid populations (Dedryver & Gelle, 1982; Lindqvist, 1985; Leather et al., 1989). Leather & Lehti (1981) found that in holocyclical *R. padi* lineages, eggs died at constant rates throughout the winter (3% to 6% per week, depending on the latitude). These results are corroborated by Kleinhenz's work (1994) and our studies. Long and cold winters did not lead to gradation in the subsequent summer. Interestingly, gradation after winter was significantly associated only with the parameter temperature (Tab. 1), excluding other parameters like precipitation or wind speed. Precipitation does not play a major role, although this variable was involved in other models describing the effects of winter strength on population development (Kleinhenz, 1994; Leclercq-LeQuillec et al., 2000; Fabre et al., 2003). However, when plants are small (i.e. no tillers are formed) and temperatures are low (i.e. aphids are inert), it seems to be very unlikely that rainfall will strongly affect the cereal aphids hidden between developing leaves or near the roots, making them inaccessible by rain drops and washing solutions. Our findings confirm the importance of temperature within weather situations for the development of cereal aphids (Morgan, 1996; Zhou et al., 1996; Ma, 2000).

The simple log RA selected several predictor variables using counts of *S. avenae* and *M. dirhodum* (Tab. 1), which were also significantly involved in differentiating case studies with and without gradation according to multiple log RA and lin DA (Tab. 2 and 4). However, predictor variables solely based on counts of *R. padi* never showed significant influences on gradation, reflecting the fact that *R. padi* has never been the dominant species during cereal aphid outbreaks in Germany (Basedow et al., 1994; Freier et al., 2001). Moreover, these findings are in agreement with reports (Loxdale et al., 1993; Veenker et al., 1998) stating that *R. padi* is a constantly migrating aphid species that can be found regularly in suction traps in large numbers. To determine predictor variables for the "real migration" simulations, we used cut-off dates previously assigned to certain GS of winter wheat cultivars in accordance with the crop development model SIMONTO (Rossberg et al., 2005). This is important because pesticide treatments are commonly timed by crop GS. For example, the predictor variable "sum of *S. avenae* from April 15th to June 2nd" is determined just at the beginning of ear emergence (GS 51). This facilitates the decision whether or not to apply insecticides together with the last fungicide application (usually timed at the middle of ear emergence, GS 55).

The "real migration" submodel was developed using suction trap data. Over the past years in continental regions, the beginning of ear emergence started most frequently on June 3rd (±0.7 days). Suction trap data are available from continental regions, representing a catchment area of approx. 80-160 km radius (Loxdale et al., 1993). These data provided the most accurate estimates for comparison of aerial aphid populations with threshold levels in the field (Tab. 2 and 4; Malloch et al., 2006). A further advantage of suction traps is that they are able to fill the data gap between very early (i.e. irregularly aphid detection) and late (more regularly detection due to higher aphid counts after early population growth) population levels of cereal aphids in fields (Harrington et al., 1990; Jarosík et al., 2003). Hence, we regard suction traps the most important supporting tools to forecast cereal aphid field populations (Malloch et al., 2006).

Comparisons of methods

Using LRT for predictor variables entered into the model first, the highest Chi-square values (Tab. 1) were obtained just for predictor variables selected for the final model according to multiple log RA (Tab. 2) and lin DA (Tab. 4). This proofs the power of LRT and simple log RA for preliminary analysis of important predictor variables (Yuen et al., 1996; Twengström et al., 1998).

Comparison log RA and parametric lin DA were performed by Press & Wilson (1978). They concluded that log RA (simple or multiple) is preferable to parametric lin DA in cases for which the predictor variables do not have multivariate normal distributions within classes because, if normal within-class distributions fit data, log RA is less efficient than parametric lin DA (Roa, 1973). However, the majority of predictor variables in our study exhibited normal distributions (data not shown). Concerning the selection process, lin DA often did better in correctly selecting predictor variables than log RA when the data were log-normally distributed or when they were a mixture of dichotomous and log-normal predictor variables (Press & Wilson, 1978; Constanza & Afifi, 1979). Even with all dichotomous predictor variables, lin DA did as well as log RA simulations with sample sizes of 50 and 100, which is similar to our sample sizes (O'Gormann & Woolson, 1991). Efron (1975) showed that, with two normal populations having a common covariance matrix, log RA is one-half to two-thirds as effective as lin DA in achieving asymptotically the same error rates. As shown by our ROC curves (Fig. 4) and in the validation section, both methods exhibited comparable error rates, presumably, because no dichotomous predictor variables were used in our study. In general, the ROC curves are most frequently used in deciding which of several models (and their respective predictor variables) to use (Afifi & Clark, 1999; Pepe, 2000; Holmes et al., 2007). All else being equal, the one with greater area (closer to one) should be chosen (Swets, 1973; Metz, 1978). However, one might also choose the model with greatest height relative to the ROC curve at a desired cut-point (in our study: the control threshold level of > 3 aphids per ear and flag leaf). The closer the ROC curve is to the bisection line, the higher the probability that *other* (but not necessarily *more*) predictor variables will be needed in order to ameliorate the logistic regression or discriminative model (Metz, 1978; Afifi & Clark, 1999; Manzato, 2007). Therefore, a small advantage was found for lin DA (e.g. in datasets for "real migration"), which classified more case studies correctly. According to Afifi & Clark (1999), the method of choice is simply the one that, empirically, has the highest proportion of correctly classified cases. This led us to trust more the results of lin DA, particularly when taking the control threshold level of Basedow et al. (1994) into consideration (highest numbers of correctly classified case studies at the cut-off point of > 3 cereal aphids per ear and flag leaf; Fig. 4).

Interestingly, the F-test (together with the squared partial correlation criteria) and Chi-square test from lin DA and log RA, respectively, selected the same predictor variables in the same order for the "winter conditions" submodel. However, the variable "numbers of days with minimum temperatures < 0°C" was added additionally to the final model by the lin DA. All of these variables were significantly associated with gradation in previous simple log RA (Tab. 1). According to Roa (1973) and Press & Wilson (1978), increasing the sample size may tend to increase the number of predictor variables selected when using significance levels, but this is not necessarily true in every case. Since both analyses were calculated with the same datasets and the same sample size ($n = 59$), observed differences in selected predictor variables are due to the test statistics. The Chi-square test incorporated in log RA may have excluded the third predictor variable, because its statistic is more conservative compared to predictor variable selection with lin DA (Sachs, 1999; L.A. Hothorn, pers. comm.). The advantages of conducting the selection process according to lin DA compared to log RA was already discussed previously (Press & Wilson, 1978).

Concerning the "real migration" submodel, the same amount of predictor variables was selected from the corresponding datasets (n = 50) in those analyses, but the selected predictor variables differed between both analyses (Tab. 2 and 4). There is no doubt that *S. avenae* is the most frequent and dominant cereal aphid species responsible for most cases of cereal aphid gradation in the study area (Freier et al., 2001). Subsequently, the predictor variable "sum of *S. avenae* from April 15th to June 2nd" was first selected in both analyses. However, in some case studies with gradation, *M. dirhodum* was the most abundant species (Basedow et al., 1994), but *M. dirhodum* was only involved as the second predictor variable in the log RA. The explanation for this heterogeneity in predictor variable selection is not obvious. Possibly, both species have the same demands on factor combinations (i.e. abiotic and biotic factors) during the very early period of their development (e.g. during April and May), leading to similar suction trap counts by June 2nd. At later dates, they might be affected by different "weather conditions" (Sengonca et al., 1992), which favour either the one or the other species to form a gradation (Zhou & Carter, 1992; Ma, 2000). However, we conclude with regard to the ROC-curves and validation results (Fig. 4) that *M. dirhodum* is of minor importance for the majority of the case studies in predicting gradation as early as June 2nd.

Comparison of locations

Comparing datasets from different locations, the variable "location" was never significant in datasets from continental locations (i.e. Brandenburg, southern Lower Saxony, and Saxony-Anhalt; Fig. 1). Hence, the modelling results presented here refer only to continental locations of Germany. The major problem of the datasets without a typical continental climate (Fig. 1) was that cereal aphid populations rarely exceeded the threshold level at the flowering stage of winter wheat. Moreover, only 16 case studies were available from locations without continental climate compared to 73 case studies from continental regions. Possibly, datasets from non-continental regions were observed by chance, thereby overlooking years with gradation. On the other hand, the population development after winter and early immigration of cereal aphids might rely on other driving factors in maritime regions compared to continental regions (Lindqvist, 1985; Leather et al., 1989; Rappaport, 1998). In the latter regions, winter and summer seasons are longer, with notably more extreme temperatures than in maritime climate (H. Friesland, pers. comm.). Differences in density levels between maritime and continental regions were observed at the end of the flowering stage of winter wheat during the years 1994 to 1995. Only those fields situated in continental regions showed growth factors of 2 to 7 for cereal aphids until population peaks occurred, while more maritime regions (e.g. situated in Westphalia) showed growth factors of 1 to 1.2 for the same time (Rappaport, 1998). Moreover, several authors reported comparable population developments in continental regions (e.g. Saxony-Anhalt and southern Lower Saxony). There, the dominance structure of cereal aphid species differed substantially between years, but not between locations within a given year (Volkmar et al., 1994; Rappaport, 1998; Rappaport & Freier, 2001). Hansen (1999) found that his migration model worked well in regions in which *S. avenae* and *R. padi* were entirely holocyclic. Hence, differences in model reliability between climatic regions may also be linked to different overwintering conditions, with holocyclic hibernation being more frequent in continental regions (Kleinhenz, 1994) and more reliable to forecast (Hansen, 1999).

Model constraints

Both submodels are further constrained to case studies without large-scale insecticide treatments for virus vectors very early in the year (i.e. in March and April). Such large-scale virus calamities have been reported only twice in the past: In winter of 1988/1989 (Huth, 1990; Aßmann & Hamann, 1991) and of 2006/2007 (S. Krüssel, pers. comm.; own observations). Both vegetation periods were excluded from the datasets used for model construction. When winter conditions promoted such great quantities of anholocyclic clones that vector treatments in spring were legitimated, no further population outbreaks were observed in either vegetation period, because of natural and man-made aphid limitations (Aßmann & Hamann, 1991; Huth & Lauenstein, 1991; own observations). According to the “winter conditions” submodel, both years would be classified as years with gradation - indeed false positive cases. However, the base of data from two years is too small for more final conclusions on the importance of large-scale vector treatments. To overcome the problem of warm winters with a very large proportion of anholocyclical lineages, we refer to potent simulation models (e.g. SIMLAUS) that quantify accurately the amount of anholocyclic hibernating cereal aphids (Kleinhenz, 1994). For subsequent, all-embracing decision support of cereal aphid control in winter wheat, we suggest to combine such previously developed models with the present submodels for early decision-making concerning cereal aphid control measures before flowering of winter wheat (Kleinhenz, 1994; Leclercq-LeQuillec et al., 2000; Fabre et al., 2003).

Importance of threshold levels

In general, the simulation results indicated that the forecasting of population levels above or below the control threshold level (> 3 aphids per ear and flag leaf) at the ear emergence (i.e. June 3rd) was accurate. Nevertheless, most studies about control threshold levels highlighted that the most efficient cereal aphid control was achieved when insecticide treatments were applied at the end of the flowering stage (GS 69) of winter wheat (Basedow et al., 1994; Rappaport & Freier, 2001). We point out that our studies do not question the existing threshold level. In general, we support a late treatment strategy at GS 69. Depending on the degree of insecticide persistence and late immigration, cereal aphid populations may recover after early treatments and cause yield reductions (Basedow et al., 1994). For that reason, the submodels should be restricted to farms on which additional single late treatments against cereal aphids at the end of the flowering are not possible due to economic constraints. Our models give farmers the opportunity to decide whether or not to apply combined treatments of fungicides and insecticides as early as June 3rd. According to the validation method with independent datasets, the submodels accurately predicted cereal aphid gradation in 88.9% and 92.9% of case studies using suction trap and weather data, respectively. Past research on control threshold levels has led to more or less “static” spray thresholds, which are open to criticism (Mann & Wratten, 1991; Basedow et al., 1994). In particular, this strategy does not take into account economic considerations that will often vary from field to field and from year to year (e.g. crop values, crop yield, spray costs, etc.; Rappaport & Freier, 2001). However, our submodels for cereal aphid gradation in winter wheat can incorporate such demands. Gradation, defined as a population exceeding three cereal aphids per ear and flag leaf at the end of flowering, was used as the basis for all calculations to determine predictor variables (e.g. simple logistic regression analyses; Tab. 1). However, if wheat prices decrease, farmers would accept higher threshold levels (Rossberg et al., 2002). ROC analyses can be performed to compare the results of the decision support system in cases in which the control threshold level increases, e.g., from three to five cereal aphids per ear and flag leaf (Fig. 4). The FP fractions remain similar, whereas the TP fractions decrease strongly (i.e. cut in half). Each user can therefore judge the performance of the submodel (i.e. the numbers of FP fractions versus TP fractions; Fig. 4) and can therefore adjust the economical situations prevailing on a given farm. This is a great advantage in a wide range of situations in which the submodels may be applied. However, whenever the results of both submodels are contradictable or doubtful, users have the possibility to check and complete them using field counts at certain GS (e.g. GS 51/55, simple log RA; Fig. 2). The more cereal aphids found, the higher the probability of gradation. Knowledge about the types of different species is not necessary. However, large sample sizes are needed (up to 6,000 tillers per field; Jarosík et al., 2003).

Conclusions

This simplified data structure (gradation versus non-gradation) based on recommended control thresholds (Basedow et al., 1994) makes it possible to develop potent decision support systems (i.e. gradation models) for control of cereal aphids in winter wheat. This study established the first reliable models designed to predict the probability of gradation of cereal aphids in continental regions of Germany at an early time point (e.g. by June 3rd according to the “real migration” submodel) without the need for labour-intensive field counts.

Acknowledgements

We thank the farmers who allowed us to work in their fields, F. Schaarschmidt for assistance during data analyses, S. Wandrey for proofreading the manuscript, and T. Michel for assistance with fieldwork. We are especially grateful to plant protection services and several individuals for technical support. We thank H. Friesland, U. Heimbach, and W. Rieckmann for providing datasets on aphid populations. This work was financially supported by the Bundesministerium für Verbraucherschutz, Ernährung und Landwirtschaft, Germany (Federal Ministry of Food, Agriculture, and Consumer Protection; project code: 01HS083).

Chapter 3: Forecasting migration of cereal aphids (Hemiptera: Aphididae) in autumn and spring

A. Michael KLÜKEN, Bernhard HAU & Hans-Michael POEHLING

Institut für Pflanzenkrankheiten und Pflanzenschutz (IPP), Leibniz Universität Hannover, Herrenhäuser Str. 2, 30419 Hannover, Deutschland

Abstract

The migration of cereal aphids and the time of their arrival on winter cereals are of particular importance concerning plant health (e.g. Barley Yellow Dwarf Virus infection) and yield losses in autumn and spring. In order to identify days with migration potential in both seasons, suction trap catches of 29 and, respectively, 45 case studies (i.e. location-years) were set-off against meteorological parameters. For data analyses, we focused on days concerning the early immigration period during autumn (September 22nd to November 1st) and spring (May 1st to June 9th). In a first step, several statistical techniques were applied on meteorological parameters and suction trap data, in order to characterize important influences on migration in autumn and spring. With increasing temperature, global radiation, and duration of sunshine, the numbers of cereal aphids caught in suction traps increased, whereas lower numbers were found, when precipitation, relative humidity and wind speed increased. Concerning importance, the first two and the last parameters were most frequently significant associated with migration according to linear regression analyses. For model development, suction trap catches of case studies merged and were binary classified as days with and without a certain limit of migrating cereal aphids. Several predictor variables were created (focussing on the light hours of a given day) and were analysed with the binary response variables using linear discriminant analyses. Three different models in autumn forecast those days, where ≥ 1, ≥ 4, or ≥ 10 cereal aphids are migrating. Due to the predominance of *R. padi* individuals (99.3% of all cereal aphid catches) no distinction between the autumnal species (*R. padi* and *S. avenae*) were made. In spring, however, lower numbers of aphids were found in suction traps, and relations of dominance among species changed. Three further models were created on a species-specific level, i.e. for all cereal aphid species, for *R. padi* only, and one model for *M. dirhodum* and *S. avenae* together. The models were assessed for validation using empirical, cross-classification, and ROC-analyses and showed divers levels of accuracy. Moreover, additional datasets chosen at random before model construction and parameterisation showed 33% to 81% correct classifications for the six migration models. The

models help to assess the start of field evaluations. Further indications characterize the amount of migrating aphids and therefore the importance of immigration for early population development in cereal crops in a given season.

Introduction

Cereal aphids (Hemiptera: Aphididae) are the most important pests in winter wheat and winter barley in central Europe (Basedow et al., 1994). After immigration into fields, the population dynamics of cereal aphids depend on complex factor combinations and may occasionally lead to yield losses in years, when optimal conditions for population growth prevail (Freier et al., 2007). In autumn, migration of cereal aphids and the subsequent settlement of aphids on cereal crops are of particular importance for the dispersion of harmful viral diseases (e.g. Barley Yellow Dwarf Virus). Long periods with favourable conditions for development of cereal aphids can lead to intensive virus spread and severe damage of plants (Geissler et al., 1995). In spring, the time of first immigration and the subsequent population development of cereal aphids in fields are of particular importance for the formation of cereal aphid outbreaks (i.e. gradations), leading to substantial yield losses (Gosselke et al., 2001).

Since the eighties, simulation models have been developed in order to forecast cereal aphid population dynamics and their impact on yield losses (Carter et al., 1982; Rossberg et al., 1986; Friesland, 1994). To consider the population dynamics of cereal aphid species entirely, simple models considering mainly aphid developmental parameters have been extended, and numerous influencing factors (i.e. meteorological parameters, antagonists, fertilisation, etc.) were incorporated. But, so far, the factor migration (i.e. immigration) has not been successfully used to improve the quality of population models (Kleinhenz, 1994; Gosselke et al., 2001). However, the precise determination and evaluation of the migration of aphids, especially of the time scale of immigration phases into cereal crops, seem to be a crucial key factor controlling subsequent population development and risk to exceed the critical threshold level, which determine the initiation of insecticide treatments (Basedow et al., 1994; Fievet et al., 2007). The detailed knowledge about immigration of cereal aphids into winter cereals could therefore form a main parameter improving the population models and subsequent decision support systems (Gosselke et al., 2001).

Flight activities in cereal aphids are commonly divided into long-range migration (*sensu stricto*) and short-range “appetitive dispersal” (e.g. secondary dispersal; Irwin et al., 2007). The former rarely appeared before mid June in cereals (Loxdale et al., 1993), whereas the latter flight behaviour is most relevant for attacking winter cereals. In autumn, dispersal includes the shift between gramineous host plants (i.e. from surrounding habitats into autumn-sown cereals), and is especially important for virus spread (Geissler et al., 1995; Huth & Züchner, 1996; Dedryver et al., 2005). In early spring, the cereal aphid flight activities focus on the shift between winter and summer hosts (e.g. in *R. padi* and *M. dirhodum*), or between gramineous plants including cereals (e.g. in *S. avenae*). Therefore, the numbers of “suitable” host plants (e.g. areas with maize) and hence the overall amount of aestivating aphids may influence the flight activities in autumn, whereas the numbers of primary host plants as well as the strength of winter (affecting the different lifecycles of aphids) are of particular importance in spring (Leather et al., 1989; Dixon, 1998).

Several intrinsic and extrinsic factors leading to take-off of aphids have been described with host plant quality, “crowding” and the presence of natural enemies (e.g. on secondary host plants in autumn or on primary host plants in spring) as most important. Concerning the immigration into cereals, interactions between physiological and atmospheric influences are of major importance. For example, several temperature thresholds inhibiting aphid take-off have been discovered for cereal aphids. The lower limits were species- and morph- (i.e. season-) specific and ranged from 13 to 16°C (Berry, 1969; Wiktelius, 1981), while the upper threshold level is generally around 31°C (Walters & Dixon, 1984). However, factors other than temperature (e.g. day length, crop phenology, etc.) were additionally found to control flight phenology in certain regions of higher latitude (Clark et al., 1992). Moreover, landscape elements (such as hedgerows and small forests) and cropping systems consisting of patchwork like alternation of cereals with taller crops (such as maize or oil seed rape) may influence (and reduce) wind speeds above shorter cereals (Castro et al., 1991). This is most relevant for dispersal flight, but also for take-off and alighting in migration *sensu stricto*. Subsequently, cereal aphids, which prefer wind speeds close to their own flight speed of less than 1.5 m per sec (Robert, 1987; Kennedy, 1990), alight more readily in heterogeneous structures due to enhanced physical control over their flights (not being blown over; Bottenberg & Irwin, 1991). Moreover, temporal flight activity of aphids should be basically related to conditions stimulating “take-off” behaviour. Determination of take-off is not well studied in cereal aphids. In general, laboratory experiments have stated a range of possible conditions for take-off or landing behaviour of aphids, which, however, can’t be directly transferred into field conditions. One important factor affecting the likelihood of aphid take-off is light (i.e. intensity as well as daily or seasonal rhythmicity). In laboratory studies earliest take-off occurred at light intensities greater than 1,000 lux (approx. 3.85 W per m^2), without an apparently upper limit inhibiting aphid flight (Berry, 1969; Robert, 1987). However, the situation is much more complicated, because adverse atmospheric conditions were found to delay but not to cancel the flights of cereal aphids readily (Walters & Dixon, 1984). Still there are considerable gaps in knowledge for both, the autumn and spring seasons, with respect to the immigration of aphids in cereal fields and the relation of migration time and intensity to the early population build-up within the crop.

Accordingly, the aim of our investigations was to develop models for the immigration of aphids into winter wheat and winter barley in autumn and spring. For this, we employed several statistical analyses (including linear and simple logistic regression analyses, as well as linear discriminant analyses) on datasets from field or from suction traps. Linear discriminant analyses were widely used to identify predictor variables contributing to the classification between binary response variables, and have been proven in epidemiological and population research studies (Ahlers & Hindorf, 1987; Lawrence & Labus, 2003; Schmidtmann, 2006). The technique has shown to be superior compared to other analyses, e.g. multiple logistical regression analyses, especially concerning the process to select predictor variables (Efron 1975; Press & Wilson, 1978; Constanza & Afifi, 1979; O’Gorman & Woolson, 1991).

Materials and Methods

Field data evaluation

60 datasets on population dynamics of cereal aphids were collected in winter wheat and winter barley fields from 10 locations ranging from maritime to continental climate in central Europe from 2004 to 2006. Weekly evaluations were conducted in a two-ha large, insecticide-free “window” in fields from October to December and from March to end of July (i.e. harvest of crops). Cereal aphids and their antagonists were collected by means of D-VAC suction sampler (Veenker & Ulber, 2004) or counted visually per plant or per tiller (transect sampling). Thereby, we were sure to avoid sampling the same plants repeatedly. Sample size per evaluation day and field varied according to aphid density and ranged from approx. 700 to 35,000 plants (i.e. 4 to 150 m^2 for D-VAC) in autumn and from 100 to 8,000 tillers in spring and summer. The numbers of arthropods in the suction sampler were converted into numbers per tiller or per square meter. Growth stages (GS) of cereal crops (Tottman & Broad, 1987; Meyer, 2008) were evaluated at each time according to the mean of 20 tillers or 10 plants.

W. Rieckmann (pers. comm.) provided 12 additional datasets taken in winter wheat fields near Hannover (southern Lower Saxony). There, cereal aphid instars were visually counted per tiller from mid May to end of July (from 1999 to 2002) and numbers were converted to square meter values according to the number of tillers at each site (similar to descriptions above). Overall, 72 case studies (i.e. locations and years) were available for the calculations. All agronomic practices were carried out according to farmers' best practices in each of the case studies.

Suction trap samples

Datasets of fixed suction trap samples (12 m high, Rothamsted-type, MaCaulay et al., 1988) were made available by the EXAMINE project (EXploitation of Aphid Monitoring systems IN Europe; MaCaulay et al., 1988; Examine, 2008; P. Verrier, pers. comm.) at the locations Aschersleben, Göttingen, Hohenheim, Rostock, Braunschweig, Elze, Langreder, and Poppenburg for the years 1984 to 2006 (Examine, 2008). In the last four locations, small fixed suction traps (height 2.0 m) were used. Overall, datasets of 69 case studies were available, because not every suction trap was trapping in all years. Numbers of different cereal aphid species (alatae) from April to November were specified in daily catches for most of the case studies. In 2004 to 2006, some suction traps were controlled only three times a week. Subsequently, numbers of cereal aphids within each period of catch were divided by the numbers of days. Datasets from all case studies comprised a total of 795 and 1,273 daily catches in autumn and spring, respectively. Subsequently, 164 (autumn) and 226 (spring) days, respectively, from each season were chosen at random before data analyses (using the function of random number in Microsoft Excel) to be used for independent validation of model results from linear discriminant analyses. The remaining days were used for model development and parameterisation.

The suction traps caught the aphids continuously in all case studies between April and November. Only a few days were cancelled from the analyses, when suction traps failed briefly.

Meteorological parameters

Different meteorological parameters (e.g. hourly values of temperatures, wind speed, precipitation, etc.) were available from weather station networks of both, the German Weather Service (DWD) and the Information System Integrated Plant Protection (ISIP). The distance between a field or suction trap and the next weather station never exceeded 20 km.

Statistical analyses

The following statistical techniques (one-way and multivariate methods) were applied to different datasets and variables: correlation and linear regression analyses, simple logistic regression analyses, as well as linear discriminant analyses. In all tests, significance levels were set at $\alpha = 5\%$. Before statistical techniques are specified, the different variable types are presented.

Definition of variables

Binary response variables were defined on datasets from suction traps for simple logistic regression analyses and linear discriminant analyses. According to the numbers of aphids flying in autumn and spring, available datasets were regrouped as follows.

If, on a given day, the cereal aphids landing in the suction trap exceeded a certain threshold limit, the day was referred to as “day with migration” (binary status 1); below-threshold limit days were defined as “days without migration” (binary status 0). Focussing on the numbers of aphids in autumn and on the species composition in spring, several limits were worked out. In this context, “migration” referred to cereal aphids caught in fixed suction traps, without distinction between dispersal (e.g. secondary or appetitive dispersal) and migration (*sensu stricto*).

Several predictor variables were defined to describe their influence on the response variable “migration”. To characterise migration in autumn and spring, meteorological parameters were arranged according to the flight phenology of aphids, which is usually following the daylight. Aphids frequently leave plant canopy with increasing light intensities and alight (at least) with long wavelengths of 560 - 640 nm (Nottingham et al., 1991; Loxdale et al., 1993). Subsequently, numbers of cereal aphids found in daily suction trap catches (response variable) were assumed to arise primarily during light hours of a given day. Meteorological parameters and their transformations (e.g. positive and negative sum standards, numbers of hours above certain critical values, or mean values over certain periods of time) were defined as predictor variables according to daylight hours of one or several consecutive days. In autumn or in spring, five (i.e. using a small time window in the end of October) to 12 (i.e. large time window in mid June) daylight hours represent one day. Indications from literature review and systematic trial and error methods served to determine critical values for predictor variables (Nottingham et al., 1991; Loxdale et al., 1993; Dixon 1998; Malloch et al., 2006). Moreover, several combinations of predictor variables (e.g. weighted mean values) were allocated to new predictor variables.

Correlation and linear regression analyses

Correlation analyses (proc corr, program SAS; SAS, 2008) were calculated between several predictor and response variables (e.g. number of cereal aphids in suction traps or in the fields over certain periods of time).

Linear regression analyses (proc reg, program SAS; SAS, 2008) were performed between different predictor and response variables. In this context, the following models for distribution patterns of response variables (i.e. numbers of cereal aphids in suction traps) were assumed: Poisson, Quasi-Poisson, and Negative Binominal distribution. These model assumptions are commonly used in the study of rare events, when responses take the form of counts (Armitage et al., 2002). In suction traps, cereal aphids commonly occurred from mid April to mid of June on a few days and in low numbers. Thus, this kind of response variables (the occurrence of cereal aphids) was safely considered as a rare event using the model assumptions mentioned above (Armitage et al., 2002). Stepwise calculation of linear regression analyses (backward procedure, program SAS; SAS, 2008) detected those predictor variables (i.e. meteorological parameters), which significantly influence the number of migrating cereal aphids from May to end of July. In the final linear regression model, all predictor variables were significantly associated with the number of cereal aphids in suction trap catches (response variable).

Logistic regression analyses

The logistic regression analysis is frequently used in epidemiological and population research (Corkum et al., 2006; Graf et al., 2007). A comprehensive description of logistic regression would be difficult to give in this space. But generally stated, it calculates the probability of a given binary outcome (i.e. response variable) as a function of a set of predictor variables (Afifi & Clark, 1999). Denoting the true probability of the “outcome” as p, the model assumes that the logarithm of the odds $ln(p/(1-p))$ is a linear function of the predictor variables. Note that the logarithm of the odds of p is logit(p). In our study, simple logistic regression analyses were used (one-by-one) to test a given predictor variable (derived from meteorological parameters) being significantly associated with the binary response variable (i.e. days with and without migration).

Linear discriminant analyses

Linear discriminant analyses are widely used in epidemiological or population research, where the binary response usually is the presence or absence of a disease or a pest (Ahlers & Hindorf, 1987; Parsons & Jones, 2000; Wardiatno & Tamaki, 2001; Schmidtmann, 2006).

The predictor variables are putative risk factors and possible confounding variables (Hosmer & Lemeshow, 2000; Armitage et al., 2002).

Linear discriminant analysis is based on the Bayes' theorem and refers to several different types of analyses (Fischer, 1936; Tatsuoka, 1971; Lachenbruch & Kupper, 1973). Classificatory discriminant analysis techniques are used to classify individuals into one of two or more alternative groups or populations on the basis of a set of measurements. The populations are known to be distinct, and each individual belongs to one of them, based on a selected dividing point c. The linear discriminant analysis used in this study is based on Fischer (1936) and generates the linear discriminant function z:

$$z = c + a_1x_1 + a_2x_2 + .. + a_kx_k \tag{1}$$

where a_i are coefficients of predictor variables x_i, and can be computed according to Fischer (1936), Cooley & Lohnes (1971), Lachenbruch & Kupper (1973), or Afifi & Azen (1979). The predictor variables x_i, used for classification, are multivariate normal distributed, assuming that within-class covariance matrices are equal. However, the mean values for a given predictor variable may be different in the two populations. Further assumptions are random samples from each of the populations.

Parametric, linear discriminant analyses were preformed in order to identify predictor variable combinations significantly associated with binary occurrence of cereal aphid migration. Subsequently, the calculated discriminant function z was compared with zero:

case 0 (i.e. no migration) occurs, if $z < 0$
case 1 (i.e. migration) occurs, if $z \geq 0$

The option of prior probability p_p (on occurrence of days with (1) and without (0) migration) was specified according to additional information gathered from the datasets (Tab. 1).

The stepwise forward method of linear discriminant analysis (proc stepdisc; program SAS; SAS, 2008) was used to select predictor variables. Starting from an "empty" model, predictor variables were sequentially included that were significantly associated with the response variable. Within this process, predictor variables could also be eliminated from the model, whenever they became non-significant (and other predictor variable combinations became significant). In the final model, all predictor variables were significantly associated with the binary response variable. After the selection of significantly separating predictor variables, linear discriminant analyses were performed again with those predictor variables for subsequent parameterisation and model calibration using further procedure discrim from program SAS (SAS, 2008). Standardized discriminant coefficients were computed in order to directly compare the values of coefficients a_i and to judge the relative effect of each predictor variable x_i on the discriminant function (Afifi & Clark, 1999).

Tab. 1: Fraction of days with migration (i.e. prior probability $p_{p(1)}$) according to the different models in autumn (September 22nd to November 1st) and in spring (May 1st to June 9th).

Season	Model	Fraction of days with migration $p_{p(1)}$
Autumn	"≥ 1 aphid flies"	0.786
	"≥ 4 aphids fly"	0.439
	"≥ 10 aphids fly"	0.250
Spring	"≥ 1 species flies"	0.531
	"*S. avenae* and *M. dirhodum* fly"	0.177
	"*R. padi* flies"	0.419

Model validation

For model validation, empirical (procedures list and listerr, program SAS; SAS, 2008) and cross-classification (procedures crossvalidate, crosslist and crosslisterr, program SAS; SAS, 2008) methods were calculated on datasets used for model selection according to linear discriminant analyses. Since there is always a possibility of making the wrong classification, the probability (i.e. posterior probabilities p_{po}) that a given individual has come from one group or the other, was computed as mean values for the empirical and the cross-classification methods in linear discriminant analyses. Moreover, parameters from linear discriminant analyses were graphically compared by using receiver operating characteristic (ROC) curves (Afifi & Clark, 1999; Pepe, 2000; Dewdney et al., 2007). ROC analysis is based on true positive (TP) and false positive (FP) decisions. The TP fraction is the number of correctly classification of days with migration divided by the total number of days with migration. The FP fraction is the number of incorrect classification of days with migration divided by total number of days without migration. ROC curves plot TP fraction as a function of FP fraction at all possible threshold levels. The threshold levels ranged from 0 to 200 and from 0 to 90 migrating cereal aphids per day for autumn and spring, respectively. In a ROC curve, the origin of the graph represents the model result "no migration" for all days. This classification yields no FP but captures no TP. The upper right corner would classify days with migration, thus detecting all days when truly migrating cereal aphids were observed, but also classifying migrations for all days that do not show them. Therefore, an efficient algorithm would yield a curve "pushed to the upper left corner" (Afifi & Clark, 1999).

Results

General results

Among all case studies in autumn, *R. padi* was found in suction trap catches between September 22nd and November 1st in 78.2% of days, whereas *S. avenae* occurred only in 14.0% of days. Both species were detected together in suction traps in 13.6% of the sampling days. However, comparing the numbers of aphids caught, *R. padi* was the dominant species representing 99.3% of the cereal aphid catches. *S. avenae* was less abundant (0.6% of all cereal aphids) and *M. dirhodum* occurred only occasionally in very low numbers (< 0.1%). Because *S. avenae* and *M. dirhodum* were of minor importance in autumn, no distinction between cereal aphid species was made. According to the days with cereal aphids in suction traps (78.6%), the threshold level of one or more aphids being caught in suction traps was set for the first model. High numbers of more than 20 migrating cereal aphids were only found on few days and therefore, the threshold level was altered as follows. Increasing the threshold level to ≥ 4 and to ≥ 10 migrating cereal aphids per day, reduced the proportion of days with trapped aphids to 43.9% and 25.0%, respectively. Accordingly, the prior probabilities were specified in linear discriminant analyses (Tab. 1).

In general, the autumnal field counts of cereal aphids were low (especially winged morphs) and spatial distribution was strongly aggregated. Therefore, it was not possible to compare aerial (as derived from suction traps) directly with field populations. Winter conditions were harsh in most case studies, and anholocyclic hibernation was scarce (< 8%; i.e. only at one location in one year 2004). In general, the first cereal aphids occurred after holocyclic hibernation in the field or in suction traps at mid of May during the tiller elongation with increased numbers from spring to summer. In 2004, optimal development prevailed and led to extremely high population values for *S. avenae* (Fig. 1). In 2005 and 2006, no anholocyclic hibernation was detected at all in either location, and aphid populations reached only moderate peak levels (ca. 7,500 to 10,000 and 2,500 to 3,500 aphids per m^2, respectively). In those two years, *M. dirhodum* was the most abundant species.

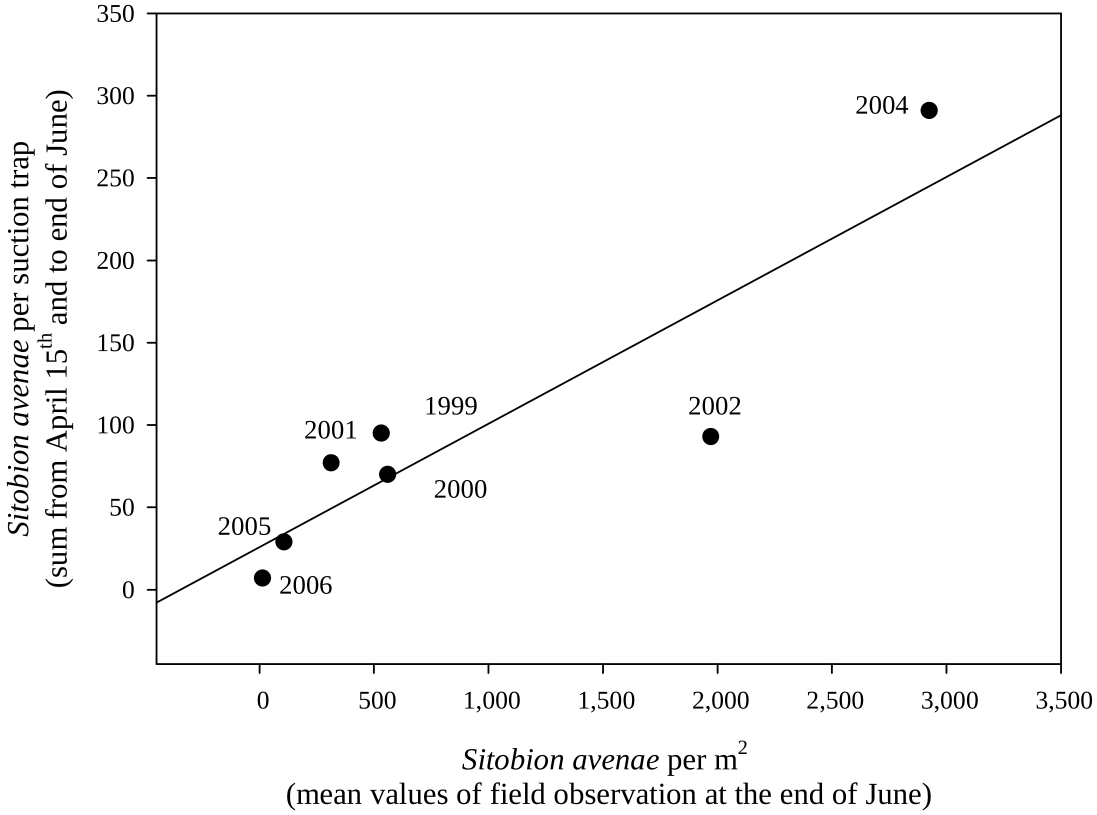


Fig. 1: Correlation analysis ($R = 0.89$; $p < 0.01$) between *S. avenae* caught in the field (i.e. per m² at the end of June) and in a suction trap (i.e. as sum from April 15th to June 30th). Data were collected in Poppenburg from 1999-2006 in all years, except in 2003.

In all case studies (all years), *R. padi* (75.8%), *M. dirhodum* (14.2%) and *S. avenae* (10.0%) were the most frequent cereal aphid species in spring suction trap catches. *R. padi* was found between May 1st and June 9th in 41.9% of daily suction trap catches, whereas *M. dirhodum* and *S. avenae* occurred only in 16.2% and in 13.6% of days, respectively. All species occurred together in suction traps in 5.0% of the sampling days and therefore, different forecasting models were developed for grouped species (i.e. "≥ 1 species flies", "*M. dirhodum* and *S. avenae* fly", and "*R. padi* flies"). The prior probabilities were specified in linear discriminant analyses (Tab. 1), based on the fraction of days with cereal aphid species in suction traps.

Comparisons of suction trap catches and field populations

To compare aerial and field populations in spring, correlation analyses between migratory events (i.e. calculated as sums of cereal aphids caught in suction traps from April 15th to the end of June) and numbers of cereal aphids in the field (i.e. numbers of cereal aphids per square meter by the end of June) were performed on datasets from several locations taken from 1999 to 2006 (no data available in 2003). In all comparisons with either species, results showed significant coefficients of correlation ranging from R = +0.87 to R = +0.99 (Fig. 1 specifies a representative case study for *S. avenae*; further data not shown).

Correlation analyses of suction trap catches and field counts were executed between autumn and spring populations of all cereal aphid species on both, datasets from within and between vegetation periods. The comparisons of suction trap catches between autumn and the following spring (i.e. within one vegetation period) showed a significant coefficient of correlation only for the species *R. padi* (R = +0.40). Comparisons between spring and the following autumn populations (i.e. between two vegetation periods) showed no significant correlations of suction trap catches at all. Similarly, coefficients of correlation, calculated from field data within and between vegetation periods for *R. padi* and *S. avenae,* were not significant. *M. dirhodum* did not occur in autumnal field crops and therefore was excluded from the latter analyses.

Importance of influencing parameters

Coefficients of correlation were calculated between mean counts of cereal aphids in the field at three growth stages of winter wheat (GS 51/55, 61, and 69; Tab. 2) and the sums of different meteorological parameters, calculated from May 1st until each GS was reached. Higher temperature sums led to significantly higher numbers of cereal aphids found at each GS. The aphid counts and the sums of precipitation were negatively correlated, but significantly only at the end of the flowering (GS 69), whereas the sums of relative humidity, of wind speed, and of global radiation were not significantly associated with the numbers of cereal aphids at any GS. Higher sums of predator units (Freier et al., 1997a) at GS 61 and at GS 69 significantly reduced the numbers of cereal aphids (Tab. 2).

Tab. 2: Coefficients of correlation (R) between mean number of cereal aphids in the field at each growth stage of winter wheat and the sums of different parameters, calculated from May 1st until the growth stages GS 51/55, 61, and 69 were reached.

	Growth stage		
Parameter	GS 51/55	GS 61	GS 69
Temperature sum	+0.37*	+0.39*	+0.45*
Precipitation sum	-0.22	-0.20	-0.48*
Predator units sum	-0.14	-0.30*	-0.55*

* Asterisks indicate significant coefficients of determination ($p < 0.05$).

Linear regression analyses were executed between 51 predictor variables (derived from meteorological parameters) and three response variables (three cereal aphid species caught in suction traps) under varying assumptions concerning the distribution patterns (i.e. Poisson-, Quasi-Poisson-, and Negative Binominal distributions). Among all predictor variables, 31 were significantly associated with suction trap catches. After nine calculations (three response variables and three assumptions concerning the distribution patters), 103 times predictor variables were entered into the final models, among which the temperature-based predictor variables (i.e. "numbers of hours ≥ 10°C in a period of eight consecutive days", "numbers of hours ≥ 7°C in a period of eight days") were most frequently (i.e. 18 and 15 times, respectively) significantly associated with numbers of cereal aphids caught in suction traps from mid April to mid June (Tab. 3).

Tab. 3: Frequency of significant predictor variables in linear regression analyses (between predictor variables and three different response variables) under different model assumptions: Poisson-, Quasi-Poisson-, or Negative Binominal distribution (total frequency, $n = 103$). Linear regression analyses were performed between sums of cereal aphid species (caught in suction traps from mid April to mid June) and 51 predictor variables derived from meteorological parameter sums (mid April to mid June).

Predictor variables	Frequency ($n = 103$)	Ranking
No. of hours ≥ 10°C in a period of 8 days	18	1st
No. of hours ≥ 7°C in a period of 8 days	15	2nd
No. of hours with sunshine within 1 day	11	3rd
No. of hours with wind speed < 1.5 m per sec in a period of 8 days	7	4th

Tab. 4: Predictor variables of linear discriminant analyses of the autumnal suction trap data, specified as partial coefficient of determination (R^2) with test statistics (F-values, all being significant at level $\alpha = 5\%$) according to independent models "≥ 1 aphid flies", "≥ 4 aphid fly", and "≥ 10 aphid fly" (between September 22nd and November 1st). The ranking (i.e. "no. in") of predictor variables specifies forward steps, when predictor variables were significantly entered (d = day, # = number).

		Linear discriminant analyses			
Model	**Predictor variable**	**Partial R^2 (no. in)**	**F-values**	**Coefficients**	**Standardised coefficients**
≥ 1 aphid flies	Intercept	.	.	-2.38	.
	Mean wind speed between 10 a.m. and 4 p.m. [m per s]	0.157 (1)	88.20	-0.57	-17.66
	No. of hours with temperatures ≥ 12°C within 1 d [#]*	0.065 (2)	32.95	0.21	13.69
	No. of hours with global radiation < 300 W per m^2 within 4 d [#]*	0.033 (3)	16.15	0.11	15.55
	No. of hours with global radiation ≥ 300 W per m^2 within 8 d [#]*	0.009 (4)	4.19	0.03	7.86
≥ 4 aphids fly	Intercept	.	.	-1.66	.
	No. of hours with wind speed < 1.7 m per sec within 1 d [#]*	0.157 (1)	88.46	0.23	19.01
	No. of hours with temperatures ≥ 12°C within 1 d [#]*	0.031 (2)	15.01	0.17	16.04
	No. of hours with relative humidity ≥ 70% within 1 d [#]*	0.028 (3)	13.69	0.13	10.85
	No. of hours with temperatures ≥ 15°C within 1 d [#]*	0.012 (4)	5.82	-0.05	-4.64
	No. of hours with wind speed ≥ 1.7 m per sec within 8 d [#]*	0.008 (5)	3.71	-0.01	-2.05
≥ 10 aphids fly	Intercept	.	.	-4.47	.
	No. of hours with wind speed < 1.7 m per sec within 1 d [#]*	0.121 (1)	65.14	0.22	17.96
	No. of hours with relative humidity ≥ 70% within 4 d [#]*	0.018 (2)	8.58	0.07	15.04
	No. of hours without precipitation within 2 d [#]*	0.014 (3)	6.45	0.12	9.54
	Mean precipitation between 10 a.m. and 4 p.m. [mm]	0.008 (4)	3.74	0.85	5.35

* Asterisks indicate predictor variables specified between 9 a.m. and 5 p.m.

Tab. 5: Predictor variables of linear discriminant analyses of the spring suction trap data, specified as partial coefficient of determination (R^2) with test statistics (F-values, all being significant at level $\alpha = 5\%$) according to independent models "≥ 1 species flies", "*S. avenae* and *M. dirhodum* fly", and "*R. padi* flies" (between May 1st and June 9th). The ranking (i.e. "no. in") of predictor variables specifies forward steps, when predictor variables were significantly entered. All predictor variables were calculated between 8 a.m. and 7 p.m. (d = day, # = number).

		Linear discriminant analyses			
Model	**Predictor variable**	**Partial R^2 (no. in)**	**F-values**	**Coefficients**	**Standardised coefficients**
"≥ 1 species flies"	Intercept	.	.	-1.650	.
	No. of hours with wind speed < 1.7 m per sec within 4 d [#]	0.051 (1)	50.37	0.113	15.88
	Duration of sunshine between 8 p.m. and 7 a.m. [#]	0.034 (2)	33.59	0.139	14.94
	No. of hours with wind speed < 1.7 m per sec within 1 d [#]	0.009 (3)	8.86	-0.053	-10.51
	No. of hours with wind speed < 1.7 m per sec within 8 d [#]	0.006 (4)	6.07	0.060	8.51
	No. of hours with global radiation ≥ 350W per m^2 within 4 d [#]	0.004 (5)	3.79	0.014	5.34
	No. of hours with mean temperatures ≥ 10°C within 1 d [#]	0.006 (6)	6.01	0.016	9.78
	No. of hours with mean temperatures ≥ 10°C within 2 d [#]	0.004 (7)	3.76	-0.019	-5.64
"*S. avenae* and *M. dirhodum* fly"	Intercept	.	.	-9.914	.
	No. of hours with wind speed < 1.7 m per sec within 3 d [#]	0.072 (1)	73.47	0.056	17.61
	No. of hours with mean temperatures ≥ 7°C within 8 d [#]	0.031 (2)	30.28	0.055	8.69
	No. of hours with wind speed < 1.7 m per sec within 1 d [#]	0.008 (3)	7.29	0.051	16.88
"*R. padi* flies"	Intercept	.	.	-1.037	.
	No. of hours without precipitation within 8 d [#]	0.015 (1)	14.47	0.096	13.56
	No. of hours with relative humidity > 70% within 4 d [#]	0.011 (2)	10.47	-0.003	-10.49
	No. of hours with mean temperatures > 7°C within 8 d [#]	0.009 (3)	8.59	0.026	9.46
	No. of hours with wind speed <1.7 m per sec within 1 d [#]	0.008 (4)	7.48	-0.048	-13.10
	Duration of sunshine between 8 p.m. and 7 a.m. [#]	0.008 (5)	7.29	0.046	15.88
	Mean global radiation between 8 p.m. and 7 a.m. [W per m^2]	0.010 (6)	9.19	-0.029	-12.30
	No. of hours with mean temperatures > 10°C within 4 d [#]	0.007 (7)	6.82	0.069	10.03

Simple logistic regression analysis between meteorological parameters and days with and without migratory events served to test predictor variables one-by-one. In autumn and spring, 58 out of 82 and, respectively, 31 out of 41 predictor variables were significantly associated with days, on which one or more cereal aphids (all species) were found in suction traps. In both seasons, predictor variables based on temperature, wind-speed, global radiation, and duration of sunshine were most frequently associated with the binary response variable, whereas only a few significant predictor variables belonged to parameters like precipitation (3 in autumn, 5 in spring) and relative humidity (0 and 4, respectively). However, significant predictor variables showed the same trend like linear regression analyses (see previous paragraph), i.e. migration became more likely if temperatures, global radiation, and hours with sunshine increased, or if precipitation, relative humidity, and wind speed decreased.

Development of models for migration

According to linear discriminant analyses, the two predictor variables “mean wind speed between 10 a.m. and 4 p.m.” and “numbers of hours with temperature ≥ 12°C between 9 a.m. and 5 p.m.” were most important to characterise a migration day (i.e. a day with one and more migrating aphids; model “≥ 1 aphid flies”) in autumn (from September 22nd to November 1st) as indicated with high partial R²- and F-values (Tab. 4). Concerning the model “≥ 4 aphids fly”, the predictor variable “number of hours with wind speed < 1.7 m per sec (between 9 a.m. and 5 p.m.)” provided the highest explanatory power. The partial R²- and F-value of other predictor variables were of minor importance (Tab. 4). Similarly, the first predictor variables (“number of hours with wind speed < 1.7 m per sec, measured between 9 a.m. and 5 p.m.”) implemented in the model “≥ 10 aphids fly” showed highest partial R²- and F-values, distinctly higher than the three subsequently entered predictor variables (Tab. 4). All selected predictor variables from each of the final models in Tab. 4 (according to best model fit from linear discriminant analyses) showed an average squared canonical correlation coefficient of 0.245, 0.222, and 0.155, respectively, indicating that the model had a moderately predictive value.

In spring (from May 1st to June 9th), the model “≥ 1 species flies” included the two predictor variables “number of hours with wind speed ≥ 1.7 m per sec within four days” and “duration of sunshine” (both measured between 8 a.m. and 7 p.m.), which were of major importance (highest partial R²- and F-values) as compared with subsequently entered predictor variables (Tab. 5). When only the migration events of *S. avenae* and *M. dirhodum* were considered together (model “*S. avenae* and *M. dirhodum* fly”), the predictor variable “number of hours with wind speed < 1.7 m per sec within three days (measured between 8 a.m. and 7 p.m.)” provided the highest explanatory power (Tab. 5). Concerning the migration events of *R. padi* solely (model “*R. padi* flies”), no clear pattern of important predictor variables resulted, because all entered variables showed similar partial R^2- and F-values (Tab. 5). Selected predictor variables from the three final models for spring migration (Tab. 5) showed an average squared canonical correlation coefficient of 0.097, 0.108, and 0.066, respectively. Therefore, the models had low predictive values.

Examples of forecasting models

The following example (independent datasets) specified the meteorological parameter values at Göttingen on October 28th 2004 (and, if needed, of the previous days) for the three models:

1. Mean precipitation between 10 a.m. and 4 p.m. [mm]	0
2. Mean wind speed between 10 a.m. and 4 p.m. [m per s]	2.1
3. No. of hours with temperatures ≥ 15°C within 1 d [#]	0
4. No. of hours with temperatures ≥ 12°C within 1 d [#]	5
5. No. of hours without precipitation within 2 d [#]	15
6. No. of hours with relative humidity ≥ 70% within 1 d [#]	8
7. No. of hours with relative humidity ≥ 70% within 4 d [#]	23
8. No. of hours with wind speed < 1.7 m per sec within 1 d [#]	3
9. No. of hours with wind speed ≥ 1.7 m per sec within 8 d [#]	50
10. No. of hours with global radiation < 300 W per m^2 within 4 d [#]	30
11. No. of hours with global radiation ≥ 300 W per m^2 within 8 d [#]	15

Using these values of predictor variables and the corresponding coefficients from Tab. 4, the linear discriminant functions of the three models resulted in the following values: $z_{\text{“}\geq\text{ 1 aphid flies”}} = +1.2$, $z_{\text{“}\geq\text{ 4 aphid fly”}} = +0.4$, and $z_{\text{“}\geq\text{ 10 aphid fly”}} = -0.4$, respectively. The positive values of z for the first two models indicated that both characterised October 28th, 2004 as “migration day”, while the last model “≥ 10 aphids fly” did not. However, 15 cereal aphids were caught in the suction trap at Göttingen on that day. Hence, the prediction of models “≥ 1 aphid flies” and “≥ 4 aphids fly” were true, but the model “≥ 10 aphids fly” failed.

Concerning the forecasting models in spring, data of June 5th 2006 (including information from the previous days) at Poppenburg was used as an example (independent datasets). On that day, the following parameter values were reported by the weather station of Poppenburg:

1. Duration of sunshine between 8 p.m. and 7 a.m. [#]	0
2. Mean global radiation between 8 p.m. and 7 a.m. [W per m²]	109.3
3. No. of hours with mean temperatures ≥ 10°C within 1 d [#]	8
4. No. of hours with mean temperatures ≥ 10°C within 2 d [#]	20
5. No. of hours with mean temperatures ≥ 10°C within 4 d [#]	48
6. No. of hours with mean temperatures ≥ 7°C within 8 d [#]	126
7. No. of hours without precipitation within 8 d [#]	112
8. No. of hours with relative humidity ≥ 70% within 4 d [#]	43
9. No. of hours with wind speed < 1.7 m per sec within 1 d [#]	13
10. No. of hours with wind speed < 1.7 m per sec within 3 d [#]	30
11. No. of hours with wind speed < 1.7 m per sec within 8 d [#]	66
12. No. of hours with global radiation ≥ 350 W per m² within 4 d [#]	12

Using these values of the predictor variables and the connected coefficients from Tab. 5, the linear discriminant functions of the three models resulted in the following values: $z_{\text{“}\geq 1\text{ species flies”}} = +6.8$, $z_{\text{“}\textit{S. avenae}\text{ and }\textit{M. dirhodum}\text{ fly”}} = -0.6$, and $z_{\text{“}\textit{R. padi}\text{ flies”}} = +12.4$, respectively. The positive values of *z* indicated that one or more aphid species as well as individuals of *R. padi* were predicted on that day, while for the model “*S. avenae* and *M. dirhodum* fly” the value is < 0. On June 5th 2006, only six individuals of *R. padi* were caught in the suction trap. Hence, the prediction of all models was true.

Validation of models

Tab. 6 specifies the validation results of different models according to the various validation methods. In contrast to the validation with independent datasets not included in the model parameterisation, the empirical and the cross classification methods showed similar fractions in all models. Using both methods, lower fractions of true compared with false classifications resulted in all models, indicating moderately low model performances. False positive and false negative fractions were similar in empirical and cross classification methods for the model “≥ 4 aphids fly”. For the same methods, the fractions of positive (i.e. true and false positive) classifications were near to one in the models “*S. avenae* and *M. dirhodum* fly” and “*R. padi* flies”. The validation of all models on datasets not used for the parameterisation (i.e. independent data) showed higher fractions of true compared with false classifications, indicating high model performance. According to this method, the models “*R. padi* flies” and “≥ 1 aphid flies” showed the highest predictive values (i.e. 81% and 76%

true classifications, respectively), whereas the lowest model performance was obtained from the model "*S. avenae* and *M. dirhodum* fly" (i.e. 33% true classifications).

Tab. 6: Validation results (i.e. numbers of true positive TP, false positive FP, false negative FN, and true negative TN cases) and mean posterior probabilities ($p_{po(1)}$; on occurrence of days with (1) migration) specified according to different validation methods (empirical, cross classification, and independent data methods) and the models ("≥ 1 aphid flies", "≥ 4 aphids fly", "≥ 10 aphids fly", "≥ 1 species flies", "*S. avenae* and *M. dirhodum* fly", and "*R. padi* flies").

Model	Validation method	*n*	TP	FN	FP	TN	$p_{po(1)}$
"≥ 1 aphid flies"	Empirical method	795	123	462	111	99	0.68 ±0.014
	Cross classification	795	99	486	118	92	0.63 ±0.012
	Independent data	164	51	28	11	74	.
"≥ 4 aphids fly"	Empirical method	795	116	247	272	160	0.47 ±0.009
	Cross classification	795	113	250	285	147	0.45 ±0.008
	Independent data	164	65	42	15	42	.
"≥ 10 aphids fly"	Empirical method	795	130	79	486	100	0.27 ±0.007
	Cross classification	795	130	79	498	88	0.27 ±0.006
	Independent data	164	84	17	28	35	.
"≥ 1 species flies"	Empirical method	1273	194	523	261	295	0.55 ±0.005
	Cross classification	1273	186	531	272	284	0.53 ±0.005
	Independent data	226	60	54	3	109	.
"*S. avenae* and *M. dirhodum* fly"	Empirical method	1273	222	9	1021	21	0.18 ±0.004
	Cross classification	1273	219	12	1021	21	0.17 ±0.004
	Independent data	226	40	0	151	35	.
"*R. padi* flies"	Empirical method	1273	465	46	701	61	0.38 ±0.006
	Cross classification	1273	460	51	709	53	0.37 ±0.003
	Independent data	226	124	44	0	58	.

n = basic sample size (i.e. numbers of day with and without migration)

The mean posterior probabilities ($p_{po(1)}$) on occurrence of days with migration were specified for empirical and cross classification methods. However, the values did not differ significantly from each other in both methods (Tab. 6).

The results from ROC analyses are given in Fig. 2 and 3 for the different models in autumn and spring, respectively. With an increasing threshold limit of migrating aphid species from 0 to 200 in autumn and from 0 to 90 in spring, the FP fractions (i.e. the model specificities) decreased as well as the TP fractions (i.e. the model sensitivities). However, the different models show a varying range of values, which form the ROC curves. Following the curves, the models "≥ 1 aphid flies" (in autumn) and "*S. avenae* and *M. dirhodum* fly" (in spring) showed the highest specificity and sensitivity, i.e. best model performances with the highest prediction potential (Fig. 2 and 3).

Discussion

Influencing variables

Our primary aim was to develop models with practical application to forecast migration events in autumn and spring. The different statistical techniques used to describe the influences of meteorological parameters on aphid flight behaviour in autumn and spring showed consistently that temperature, global radiation, and wind speed are of major significance (Tab. 2 to 5). This is in broad conformance with reports from literature (Haine, 1955; Robert, 1987; Kennedy, 1990; Bottenberg & Irwin, 1991; Nottingham et al., 1991; Malloch et al., 2006). It is noteworthy that precipitation and relative humidity are of lower importance compared to other the meteorological parameters mentioned above (Tab. 4 and 5). The precipitation-based predictor variables for example differ frequently and largely between neighbouring sites and measured mean values from weather stations do not readily reflect the very locally situation (data not shown). This is particularly true in the case for strong rain events, since they commonly last only a short time within a given day (Giesecke, 1983; Häckel, 2005; H. Friesland, pers. comm.). Subsequently, winged aphids may take-off before, or may arise from sites not affected by rain. However, studying the effect of precipitation on apterous *S. avenae* under controlled conditions, precipitation was more important than wind in determining distances travelled (Mann et al., 1995). Moreover, wingless aphids frequently fell off tillers, when drops pelted an aphid directly or hit the plant, jarring the aphid from that plant (Zuniga, 1985). The prevailing confusion about influences of relative humidity on flight activity (Rautapäa, 1979; Leather, 1985, Taylor, 1986) was corroborated by our results (Tab. 4 and 5).

The most striking results from modelling migration events in autumn and spring were the strong influence of *wind speed* on aphid flight behaviour. Predictor variables based on that meteorological parameter were always entered into the models in the first place, except for the model “*R. padi* flies” (Tab. 4 and 5). In general, with higher wind speeds fewer aphids occurred in suction traps. Moreover, the standardised coefficients of that first entered variable showed similar absolute values among the models (ranging from 15.88 to 19.01; Tab. 4 and 5). According to the linear discriminant analyses, the first variable included in a model always carried the highest weight of determination, which is therefore most significant concerning the model performances (Fischer, 1936; Afifi & Clark, 1999). In contrast the last predictor variable entered into a given model negligibly influences the response variable, and cannot always be interpreted logically, but reflects the best mathematical approximation (Afifi

& Clark, 1999). For example, the model "≥ 4 aphids fly" included in step number four (of five) the predictor variable "number of hours with temperatures ≥ 15°C (measured between 9 a.m. and 5 p.m.)" with a negative sign (Tab. 4). Therefore, the higher the numbers of hours with temperatures ≥ 15°C, the lower the number of cereal aphids caught in suction traps. This is in contradiction to the temperature-based predictor variable entered in step 2 in the same model (similar examples in Tab. 4 and 5) as well as to other studies (Harrington et al., 1990; Veenker et al., 1998). Cereal aphids are rather weakly flying insects, unable to control their flights when wind speeds rise up to more than 1.5 m per sec (Bottenberg & Irwin, 1992a, b). Many abiotic processes can account for deposition of aphids, including the subsidence of convection currents, turbulence, and precipitation (Isard & Gage, 2001). However, if meteorological conditions permit, a preference for alighting in agricultural fields has been observed (A'Brook, 1968; Fereres et al., 1999), clearly indicating that visual cues to land are not random (Fereres et al., 1999). Bailey et al. (1995) found that under controlled conditions, wind proved to be the major physical disturbance that significantly altered dispersal patterns of *R. padi*, which is supported by other studies (Friesland, 1994; Annan et al., 1999). Hence, the wind speed - based predictor variables were frequently involved in the different migration models.

Global radiation and duration of sunshine, two meteorological parameters highly correlated (data not shown), were frequently involved in the different models, too (Tab. 4 and 5). Light intensity was shown to affect the likelihood of aphid's take-off, with few species ever initiating flight in the absence of light (Robert, 1987). Light intensity, expressed e.g. in global radiation or duration of sunshine, is not only of major importance for the migration (*sensu stricto*), when the aphids are just flying to an UV light source (Loxdale et al., 1993), but it is also significant for orientation (seeking out contrasts or colours) and for host location during dispersal flights (Antignus et al., 1998; Fereres et al., 1999). Moreover, it is a further explanation, of why cereal aphids have been found to primarily fly during the light hours of a given day (Nottingham et al., 1991; Isard & Irwin, 1996).

Wiktelius (1981) defined *temperature* thresholds, which will inhibit aphid take-off, although these temperatures were found to vary species and morph specific. The lower threshold for most species varies between 13 and 16°C, while the upper threshold is generally around 31°C (Johnson & Taylor, 1957; Jensen & Wallin, 1965; Walters & Dixon 1984). Friesland (1994) characterised the combined conditions for cereal aphid flight as follows: On days with maximal temperatures lower than 14°C and strong winds (>1.5 m per sec), cereal aphids will not fly. On the contrary, conditions of high temperatures and windless represent optimal conditions for flight activity (Friesland, 1994). However, our studies indicate that the reality is much more complex, because winged cereal aphids were even caught in suction traps when wind speed was high (> 6 m per sec) and temperature low (< 8°C; data not shown). Therefore, a clear-cut distinction between passive physical-based drift and arbitrary or volitional take-off is not possible.

Performances of models

The model "≥ 1 aphid flies" gave best validation results (independent datasets) compared with other autumnal models. Forecasting relatively large amounts of migrating cereal aphids ("≥ 10 aphids fly") seems to be more difficult (than small amounts: "≥ 1 aphid flies"). Possibly the large amounts of flying aphids are not as directly dependent on meteorological conditions as compared to other models. One reason for this might be that even under best conditions for migration, the amount of aphids ready to fly must have been developed before (Dixon & Kindlmann, 1999). If local populations do not consist of high numbers of winged cereal aphids ready to fly, thresholds of more than 10 aphids cannot be exceeded in the suction traps. Generally, aphids are aggregated, but widely spread in the fields and show polymorphism and polyphenism (Dixon, 1998). Rappaport & Freier (2001) found that the age- and morph-structures of aphids are of minor importance for cereal aphid decision support systems, because a multitude of morphs (including alatae) are available at any time (in autumn and spring). Therefore, the likelihood (on a given day) is higher that at least one aphid will be in a behaviour mood to take-off and subsequently caught in suction trap (correctly classified with the model "≥ 1 aphid flies"), as compared to larger amounts (Walters & Dixon, 1984).

The spring model "*R. padi* flies" is different from all other models in several ways. All seven predictor variables contribute about similar coefficients of determination (partial R^2), and the standardised coefficients are equal (Tab. 5). Surprisingly, this was more or less independent from the calculation step, when a given predictor variable was entered into the model. Moreover, the algebraic sign changed with every predictor variable, as well as the logical sense of each predictor variable conforming with or adverse to knowledge from earlier analyses (Tab. 2 and 3) or studies (Nottingham et al., 1991; Loxdale et al., 1993; Isard & Irwin, 1996). However, the validation with independent datasets showed in 81% of all spring days, accurate prediction of cereal aphid migration. Therefore, the model "*R. padi* flies" is doubtless a superior model and the best one in a mathematical way. However, a convincing interpretation of all included predictor variables affecting the migration is not possible (Afifi & Clark, 1999).

Comparisons of statistical methods

The use of the appropriate statistical assumptions (i.e. distribution assumptions of response variables) is discussed, because cereal aphids appear highly aggregated in fields or suction traps (Feng & Nowierski; 1992; Sutherland, 2006). Some authors pointed out that the use of log-aphid counts and normal distribution of errors in statistical analyses is preferable to the use of generalized linear models with a Poisson or Negative Binomial distribution of errors in statistical analyses (McCullagh & Nelder, 1989). This is because cereal aphids may differ significantly not only from the Poisson or Quasi-Poisson distribution, but also from the Negative Binomial distribution (Ekbom, 1985, 1987; Krebs, 1989). The first distributions describe random distribution patterns, whereas the latter is commonly used to assess population densities, where the distributions are aggregated (Elliott & Kieckhefer, 1986; Elliott et al., 1990). Appropriate assumptions on aphid distributions are important to determine sample sizes for aphid density estimations in the field (Jarosík et al., 2003; Sutherland, 2006). The confusion about the appropriate assumption of distribution was the reason for the combined analyses in Tab. 2. However, the resulting predictor variables were similarly concerning the frequencies of entries (Tab. 2) and the significance levels (data not shown).

Using suction trap data, we have estimated the migration intensity, reflecting the potential immigration in cereals, for a given day in autumn and spring. Although the methodology is not direct, because field evaluations (e.g. visual counting) during the early time of immigration is much too laborious (due to the high sample sizes needed for reliable data; Jarosík et al., 2003; Sutherland, 2006), fixed suction trap catches reflect the infestation intensity and early phase of population build-up in the field (Fig. 1; Harrington et al., 1990; Veenker et al., 1998; Harrington et al., 2004). Moreover, suction trap catches can indicate reliably changes in abundances of aphid species between case studies.

Several predictor variables were found to be involved in the models contradictory to previous analyses (i.e. compare Tab. 2 and 3 with Tab. 4 and 5), or to other studies (Taylor, 1986; Loxdale et al., 1993; Isard & Gage, 2001). Explanation may be the statistical tests and constraints used. The models were constructed and analysed with multivariate techniques. As with any stepwise procedures, many significance tests are performed (each at a level of e.g. $\alpha = 5\%$), hence the overall probability of rejecting at least one true null hypothesis is much larger than 5%. To prevent the inclusion of any predictor variable that will not improve to the discriminatory power of the model, a very small significance level should be specified. In most applications, all predictor variables considered have some (but often only very small) discriminatory power (Tab. 4 and 5). To choose the model that provides the best discrimination, it is necessary to guard against estimating more parameters than can be reliably estimated with the given samples size (Afifi & Clark, 1999; Sachs, 1999; Binns et al., 2000). Therefore, Costanza & Afifi (1979) used Monte Carlo studies to compare alternative stopping rules that can be used with the forward selection methods in the two-group multivariate normal classification problem. They concluded that the use of a moderate significance level, in the range of 10 to 30%, often performs better than the use of a much larger or a much smaller significance level. In our studies, the significance level was set at $\alpha = 5\%$ for all statistical analyses, including the linear discriminant analysis. Subsequently, we have to point out that selected predictor variables are possibly error-prone according to that conservative puzzling significance level. Moreover, this process may also have contributed to the changing algebraic sign of the selected predictor variables in the model “*R. padi* flies” (Tab. 5), and it may be responsible for the inclusion of several predictor variables in last entry steps of linear discriminant analyses (all models), where we cannot give any convincing interpretation (Tab. 5 and 6; Afifi & Clark, 1999).

Density effects

The non-growing periods, when plant growth is not possible due to low temperatures (i.e. in winter) or, when winter wheat and winter barley have already been harvested (i.e. on large areas in late summer), have an outsized effect on the population of cereal aphids. Sequeira & Dixon (1997) argued that density-dependent processes acting within years regulate aphid population density, which is reflected in the year-to-year changes in overall abundances. Some results suggest curvilinear density dependence, with strong density-dependent regulation at low densities and weak at high densities (Jarosík & Dixon, 1999; Bommarco et al., 2007). Duration of wintertime and the cold temperatures in temperate climate have been frequently associated with reductions in cereal aphids, mainly for anholocyclic, but also for holocyclic lineages (Dean, 1974; Leather, 1980, 1983; Dedryver & Gelle, 1982). A further explanation of missing correlations between autumn and subsequent spring population densities may be based on a missing relation between autumnal flight activities and successful deposition of winter eggs (Leather, 1983; Veenker, 2000).

Concerning the situation in summer, mainly the absence of attractive host plants (e.g. large crop stands of winter wheat, winter barley, or maize) were associated with low population levels and low numbers of cereal aphids in suction trap catches (Taylor, 1986;

Agrawal et al., 2004; Vialatte et al., 2005; Bommarco et al., 2007). Although long time periods were considered in our study and data structure was simplified, only one significant positive dependency was directly detected (i.e. for *R. padi*). As rare as every sixth year, significant higher aerial populations of *R. padi* in spring have been reported, when a lot of *R. padi* individuals were also caught in the suction traps in the previous autumn. For other cereal aphid species and for all field data no such correlations were detected. Between the seasons, a lot of factors might be involved, affecting cereal aphid performance, which are not clearly defined or modelled (Leather, 1983; Bommarco et al., 2007). The effects of the non-growing periods (i.e. winter and summer) on the spring and autumnal population levels as well as the typical flight phenology pattern (Hullé et al., 1994) needed therefore further analyses in order to extend forecasting models concerning the amount of aphids available for immigration and early population development in autumn and spring.

Multitude of factors influencing migration

Recapitulating, presented results of suction traps and field evaluations showed that accurate and specific modelling of migration (immigration) during the early population development (before flowering of winter wheat) under the vagaries of weather and of physiological and historical aphid priming is still a challenge. The models were heterogeneous in validation results (Tab. 6; Fig. 2 and 3). Concerning the ROC curves in Fig. 1, the model "≥ 1 aphid flies" performed better as compared to the model "≥ 10 aphids fly". The closeness of the latter curve to the bisection line shows that we perhaps need other predictor variables (e.g. based on biotic factors) in order to obtain a better discriminative models. However, is not appropriate for interpretation to stick only to one of the several validation methods used. Therefore, we can state that the models showed overall poor to moderate predictive values (Tab. 6; Fig. 2 and 3). Insufficiency of migration models may be primarily based on the absence of important biotic factors incorporated. All classifications concerning the life history, the physical and behavioural state of aphids caught in suction traps might help to estimate, if individual cereal aphids would have the potential to establish in field crops and subsequently might build-up populations. However, they were not available in the datasets and therefore, we focused on abiotic factors for the model build-up. Moreover, it seems to be quite unrealistic that the user may ever obtain data in time, which are based on biotic factors (Loxdale et al., 1993; Hullé et al., 1994, 1996; Harrington et al., 2004).

In the following, several examples will elucidate that migration of aphids is a very complex subject and that the flight phenology of aphids results from a number of abiotic and biotic factors (e.g. development rate, natural enemies, quality and phenology of host plants, behavioural responses, readiness to take-off, maintaining the flight or physiological exhaustion (i.e. glycogen and fats reserve), and visual alighting cues.

Loxdale et al. (1993) found that after mean flight duration of 6.8 hours, the fat bodies were reduced by 50% in *A. fabae*. However, fecundity was not reduced, if a suitable pant was found and the aphids landed well before symptoms of fatigue decreased the control over its flight (Loxdale et al., 1993). The longer the flights lasted, the higher the readiness to settle down and to probe was observed (Dixon, 1998; Harrington et al., 2004).

However, the migration may depend on further information including the life history or the size of a given aphid. Cereal aphids landing in suction traps might therefore be further distinguished into migrants and “dispersers” (or “fliers”). The first usually fly before offspring is deposited whereas the latter ones fly also after offspring was deposited. These factors are of great concern, and it would be advantageous to attain this additional information, because aphids have only a “one-way ticket“, and the majority (e.g. 99.4% of autumnal, gymnoparae *R. padi*) will not reach a suitable host plant (i.e. the woody winter host; Ward et al., 1998). Although an aphid can be blown off its host plant and carried into the atmosphere, it rarely moves horizontally beyond the scale of neighbouring fields during a dispersal flight (Loxdale et al., 1993; Isard & Gage, 2001). The angle of aphid flight trajectories is physiologically regulated by the age of the aphid at take-off. Within a day of becoming adult, winged *R. padi* leave the plants at a mean angle of 34° above horizontal in spring, whereas the angle is only half after two to three days (Isard & Irwin, 1996; Isard & Gage, 2001). The authors further conclude that combined with the wind profile at the time of take-off, predictions can possibly be made about the success of alatae of different ages and of their trajectories in enabling ascent into the planetary boundary layer, which varies in depth from 0.3 (e.g. at night) to 3 km (e.g. during the day).

The genetic determination of the different lifecycle lineages has been reported (Simon et al., 1991; 1996a) as well as the possibility to detect infection potential of individual aphids charged with viral disease (e.g. BYDV; Foster et al., 2004; Dedryver et al., 2005). Infestation levels of winter cereals can be considered more detailed, taking this information into account. Moreover, enormous variability among and within aphid clones is partly responsible for frittered migration events (e.g. in *M. dirhodum*) observed with suction trap catches (Taylor, 1986; Nottingham et al., 1991).

The above mentioned biotic influences on migration are frequently not available e.g. from suction trap catches. Moreover, it seems to be relatively unrealistic from a practical point of view that they will be available for users at any time.

In summer, mono- or bi-phase flight activities per day prevail according to the actual light and temperature conditions. During autumn and early spring, however, mono flight activities were frequently found (data not shown). Therefore, focussing on the light hours of a given day was straightforward for the model construction. Previous results from linear regression analyses between numbers of aphids in suction traps and meteorological parameters yielded only low R^2-values (data not shown). Unfortunately, the minor coefficients for determination ($R^2<0.21$) are insufficient for very detailed prediction of migratory events based on abiotic factors. Therefore, we subsequently applied the technique of linear discriminant analyses to describe days with and without aphids caught in suction traps. Only this binary simplification was straightforward to clarify the influencing abiotic parameters and to build-up the models.

In general, the most important problems in modelling aphid and antagonist population dynamics have to do with describing the course of immigration and estimation of mortality rates (survival, which is influenced by several variables; Gosselke et al., 2001). In regard to immigration, detailed quantitative forecasts about the numbers of aphids migrating during a certain period of time, is not possible so far. However, using our forecasting models, suggestions about certain days can be made, if migration (e.g. immigration) and subsequent settlement of cereal aphids is possible. But by coupling our models with other existing models like SIMLAUS (Kleinhenz, 1994) and GETLAUS01 (Gosselke et al., 2001) or models forecasting the gradation of cereal aphids (chapter 2), more detailed suggestions about the amount of migration might be possible.

Warning schemes and decision support systems are based on several components, including monitoring. This involves sampling the pest either outside the crop (at overwintering sites or while they are dispersing) or on the crop. Field advisers or farmers can perform monitoring; however, to be successful, the pest to be monitored must prevail in the crop. Often, during the early development of winter wheat after wintertime, the number of cereal aphids is very low (Jarosík et al., 2003) and the timing of arrival of cereal aphids is of major importance (Harrington, et al., 1990). Our models may therefore help to identify days, on which cereal aphids have entered the fields. Subsequently, the monitoring may be more efficiently performed.

Conclusions

The allocation of case studies, the simplification of data structure (due to classification of days with and without a certain number of migrating aphids), and the consideration of light-hours of a day (hourly values) offered the possibility to develop models which identify days with migration potential. For the first time we have established models which predict the probability of migration events of cereal aphids without labour intensive counting of aphids or assessing of start values. Our developed models have shown that it is possible to identify days on which a certain number of species fly. These results are very valuable for extensions of detailed population models and for application in monitoring systems. The models for migration do not replace suction traps. However, they provide important support tools for estimations of aphid migration events, especially in those regions where no suction trap catches are available.

Acknowledgements

The authors are especially grateful to F.B. Boshold for proofreading the manuscript, to W. Rieckmann for access to datasets, to T. Michel for practical assistance with the assessment of suction trap caches, and to F. Schaarschmidt for discussions of data analyses.

Chapter 4: The importance of proximity between winter and summer hosts on immigration and early population development of host-alternating aphids in cereal fields

A. Michael KLÜKEN[1], Jean-Christophe SIMON[2], Peter HONDELMANN[1], Lucie MIEUZET[2], Aude GILABERT[2], Christine WARMKE[1], Hans-Michael POEHLING[1] & Bernhard HAU[1]

[1] Institut für Pflanzenkrankheiten und Pflanzenschutz (IPP), Leibniz Universität Hannover, Herrenhäuser Str. 2, 30419 Hannover, Deutschland.

[2] UMR INRA/Agrocampus Rennes, Biologie des Organismes et des Populations appliquée à la Protection des Plantes (BIO3P), BP 35327, 35653 Le Rheu Cedex, France.

Abstract

Host-alternating aphids regularly shift from winter to summer hosts in spring and from summer to winter hosts in autumn, and this shift is associated with a switch from parthenogenetic to sexual reproduction (holocyclic life cycle). However, many of these species show some populations that do not host-alternate and overwinter on summer hosts as parthenogenetic lineages (anholocyclic life cycle). Few studies are available concerning the importance (e.g. contribution) of proximity between winter and summer hosts for understanding immigration and early population development of host-alternating aphid species in winter cereals. Population density dependence on large- and small-scales may regulate population growth, which is particularly relevant for control of cereal aphids. In large-scale experiments in climatically different agro-ecosystems in Germany, numbers of winter hosts and counts of two host-alternating aphid species (*Rhopalosiphum padi* and *Metopolophium dirhodum*) in winter wheat and winter barley fields were analysed from 2004 to 2006 using different statistical techniques. Significant trends were observed with higher numbers of winter hosts in landscapes associated with higher counts of *R. padi* and *M. dirhodum* in the fields. For small-scale experiments, winter wheat fields adjacent to a large hedge with several winter hosts were used to investigate the direct influence of distances between winter and summer hosts. In the first of three subplots with different distances to the hedge (D_1: 0-8 m, D_2: 8-24 m, D_3: 24-60 m) significantly higher counts of *R. padi* were found in the wheat fields according to weekly evaluation from May to end of July each year. Unlike other cereal aphids (i.e. *M. dirhodum* or *S. avenae*), *R. padi* showed the strongest density dependence in the first 12 m next to its winter host. Movements of *R. padi* populations from winter to summer hosts were tracked by genotyping winged individuals at several

microsatellite markers. Adjacent winter hosts (*Prunus padus*) were a low source of *R. padi* colonizers of wheat fields across the whole colonization period. This was globally true whatever the distance between the *P. padus* trees and the subplots.

Introduction

Besides weather conditions, the extent of cereal aphid immigration and early population development in winter cereals such as wheat and barley can be influenced on the one hand by the availability, the amount, and the spatial distribution of host plants within a given landscape (Leather et al., 1989; Dixon, 1998; Bommarco et al., 2007). On the other hand, it is believed that landscape diversity plays a fundamental role in influencing aphid population dynamics by the impact of specialized and polyphagous aphid antagonists. Homogeneous, “cleared” landscapes with high proportions of arable monocultures (fields) frequently suffer from low bio-diversity (Pickett & Cadenasso, 1995; Polis et al., 1997; Thies & Tscharntke, 1999; Thies et al., 2003, 2005), especially from the lack of woody, winter host plants of cereal aphids. *Prunus padus* L. and *Rosa* species (e.g. *Rosa canina* L., *R. rugosa* L.) are winter hosts of *Rhopalosiphum padi* L. and *Metopolophium dirhodum* Walker, respectively. Both aphid species represent together with *Sitobion avenae* Fabricius, a species restricted to Poaceae, the most important pests of winter wheat and winter barley in central and western Europe (Rabbinge & Vereijken 1979; Basedow et al., 1994). All three aphid species can reproduce both asexually and sexually, with several parthenogenetic generations between each period of sexual reproduction. In host-alternating cereal aphid species such as *R. padi* and *M. dirhodum*, sexual reproduction and egg production occur on the specific winter hosts, whereas *S. avenae* reproduces asexually and sexually (winter eggs) on grasses. However, loss of sexual reproduction is achieved by specialized lineages of these three cereal aphid species that attempt to overwinter parthenogenetically on Poaceae hosts. This is regularly observed in regions with warm winter climate (e.g. maritime climate), whereas in winter cold areas (continental climate) the sexual overwintering is dominating, because of the higher frost resistance of the winter eggs. Parthenogenetic individuals have very short developmental times and potentially prodigious rates of increase, favouring fast population build-up especially after wintertime (Kindlmann & Dixon, 1989; Dixon, 1992). Both types of lineages (i.e. lineages with sexual overwintering as eggs or with asexual overwintering as parthenogenetic mobile individuals) have been shown to differ genetically (Simon et al., 1996a, b; Simon et al., 1999). However, little is known on the actual contribution of both forms to the population dynamics on the summer hosts (cereals). Important information such as the relation of the frequency of available winter host plants in different structured landscapes with the intensity of crop immigration processes and early population build-up is scarce. Individuals first colonising the crops could have come from local or remote origins, as winged cereal aphids are able to disperse over long distances (Robert, 1987; Loxdahle et al., 1993; Simon et al., 1999; Loxdale & Lushai, 2001; Llewellyn et al., 2003). Leather et al. (1989) first postulated that the abundance of *P. padus* is a substantial factor of the population dynamics of *R. padi* in Finland and Sweden, where *R. padi* is largely holocyclic. There, larger numbers of winter hosts coincide with a predominance of holocyclic *R. padi* populations. Rogerson (1947) and Basedow (1980) observed in northern Europe that cereal fields in the vicinity of *P. padus* trees supported larger *R. padi* populations than elsewhere. In central Germany, numbers of winter hosts are fewer and much more spatially scattered. Several anholocylic populations of *R. padi* were regularly observed to initiate the overwintering on gramineous host plants (Kleinhenz, 1994) but comparable data on the relation of winter hosts and summer development are missing. Concerning *M. dirhodum*, nothing is known about the contribution of winter host frequency to migration and early population development. Studies investigating the relative importance of distances between winter and summer hosts of cereal aphids should consider large-scale as well as small-scale influencing events (Winder et al., 2005). Furthermore, apart from distance to and density of winter hosts as a key factor for crop immigration in spring, the importance of regional landscape structure and diversity pattern was shown to influence cereal aphid dynamics, because of physical effects (such as wind exposure) or the control by natural enemies (A'Brook, 1968; Schultz et al., 1985; Kenney & Chapman, 1988; Bottenberg & Irwin, 1991, 1992a; Roschewitz et al., 2005; Tscharntke et al., 2005). Large populations of natural enemies of cereal aphid may therefore adversely affect the early population build-up in cereals. Predator units have been developed by Freier et al. (1997a) in order to consider a suitable approach for the evaluation of cereal aphid's predator community. Thereby, it is possible to study numerical response and aphid infestation-reducing effects of predators in winter wheat and winter barley (Freier & Triltsch, 1996; Freier et al., 1998; Freier et al., 2001).

Studying the importance of winter host pattern, the major drawback is that it is very difficult to trace the migration of aphids from winter to summer hosts. Suction traps (e.g. Rothamsted-type, MaCaulay et al., 1988) - on the one hand - do not provide insights detailed enough to relate the direct effects of winter hosts on immigration potential into summer hosts, because aphid catches in suction traps can neither be related to migration or dispersal modes nor to distinct sources (Taylor, 1986). On the other hand, the same problem is observed using field counts at small spatial scales, because they provide more or less static snapshots depending on frequency and amount of tillers evaluated. Molecular markers are very useful tools for examining insect movement along with other ecological parameters (Loxdale, 2001). They have been frequently applied as indirect measures of population divergence allowing assessment of gene flow, movement, and host plant sources (DeBarro et al., 1995a, b).

In this work, we examined the relative importance of proximity between winter and summer hosts of cereal aphids under large-scale (> 500 m; nine locations in Germany) and small-scale (< 500 m; one detailed field study) field conditions. We hypothesize that winter hosts adjacent to winter wheat and winter barley fields may favour the crop immigration of host-alternating aphid species and their early population build-up on the summer host (1). Moreover, we hypothesize that the density of winter hosts is related to immigration intensity on a landscape level and so we regarded the numbers of cereal aphid antagonists and discussed their possible influence on early population build-up (2). Finally, in order to assess the contribution of winter hosts as a source of cereal aphid colonizers, we analysed the genotypic composition of populations of *R. padi* on several *P. padus* and on an adjacent wheat field sampled at increasing distances from winter hosts (3).

Materials and Methods

Large-scale experiments

Field data on cereal aphid and antagonist densities were obtained from nine locations in Germany with considerably different agro-ecological zones (Fig. 1). All evaluations were performed in two-ha large, insecticide-free “windows” in fields of winter wheat and winter barley during the vegetation periods 2004 to 2006 (excluding wintertime from January to March), with special consideration of three sampling dates in June (beginning, mid, and end of June at growth stages (GS) 51, 65 and 73, respectively). On each evaluation date, the numbers of the three most important cereal aphids (i.e. *S. avenae*, *M. dirhodum* and *R. padi*) and their antagonists were counted visually (per tiller or plant) on 300 to 8,000 tillers (density dependent transects sampling) or by means of a mobile suction sampler (Veenker & Ulber, 2004). GS of the crops were evaluated at each time according to the mean of 20 tillers or 10 plants. The location of each field was chosen by regarding different landscape types and the closest proximity to next weather stations (< 20 km). Landscape structures and winter hosts of cereal aphids were mapped within a sector of three km radius around each field, comprising approximately 28 km² (Gutsche & Enzian, 2002). In this context, “sector” is not defined in the strict mathematically sense as part of a circle (*sensu stricto*), but it specifies a circularly landscape area. Due to crop rotation, the fields differed between the years, but fields from different years within each sector were located close to each other and to the centre of the sector. The distribution of the sectors was chosen at random without any north-south or east-west gradient to avoid possible correlations between landscape complexities. However, abiotic factors, e.g. microclimate (derived from meteorological parameters, see below) differed among the locations. In each sector, solitary *P. padus* trees (minimum three meters height) were counted during flowering (beginning of May), whereas smaller trees (i.e. new plantations along routes in East Germany) were merged according to their size. At the same time, the frequency of rosebushes per sector was estimated and grouped into five categories (< 100; 100 - 500; 500 - 1,000; 1,000 - 5,000; > 5,000 rosebushes per 28 km²; Garve, 1994; E. Garve, pers. comm.). Datasets of meteorological parameters were available by the German Weather Service (DWD) and the Information System Integrated Plant Protection (ISIP).

Small-scale experiments

Small-scale experiments were conducted in cereal fields near Hiddestorf (Fig. 1) separated by a large hedge (300×7×4 m; approx. 20 year old). Three subplots with different distances to the hedge (D_1: 0-8 m, D_2: 8-24 m, D_3: 24-60 m) situated in each winter wheat field on the west and east side of the hedge were evaluated in 2004. In 2005 (winter barley) and 2006 (winter wheat) only subplots eastward from the hedge were used. 100 to 300 tillers per subplot (with 10 or 15 sampling points along transects) were visually inspected per evaluation day. On two evaluation dates in 2005 and 2006, more detailed samples were taken along eight distances from the hedge (each with inspection of 150 tillers). Numbers of cereal aphids and their antagonists were recorded from May to July (based on weekly counts, converted into individuals per square meter with species determination as described in the previous section). All cereal aphid antagonists were summarised as predator units per m² according to Freier et al. (1997a). Additionally, sweep net catches (sub-sample of 100 sweeps) were taken in fields throughout June to estimate the abundances of antagonists. Inside the hedge, three out of nine *P. padus* trees and five out of 20 rosebushes were randomly selected. Overwintering eggs of *R. padi* were counted per bud at the end of March (all years) and the population development of *R. padi* and *M. dirhodum* on their respective winter hosts was evaluated.

Fig. 1: Map of Germany showing the collection sites where case studies were performed (north arrow is specified). The numbers behind location names specify the number of case studies per location (i.e. field evaluations in winter barley and winter wheat from 2004 to 2006).

Genotypic analysis of R. padi populations on winter hosts and wheat fields

During the emigration episode of *R. padi* that took place at the end of May-beginning of June, winged *R. padi* individuals were collected from three *P. padus* trees (trees no. 5, 6, and 9) within the hedge (see previous section) in Hiddestorf from different colonies (assuming that individuals more then 20 cm separated on twigs comprise offspring from different clonal colonies). These winged aphids correspond to emigrants of *R. padi* shifting from winter to summer hosts (Dixon, 1971). The tops of the trees (approx. four meters high) were excluded from sampling. On four evaluation dates in 2006 (June 20th and 27th, July 6th and 13th), several individuals of *R. padi* were collected by hand from winter wheat subplots D_1, D_2, and D_3 (see previous section). To compare field populations between locations, individuals of *R. padi* were also collected from a winter wheat field (i.e. as control plots) near Isernhagen (approx. 60 km north of Hiddestorf) on June 15th, 22nd, and 29th of the same year. In that location, winter hosts and hedges close to the field were missing. To reduce the risk of sampling individuals from the same colony repeatedly, aphids were collected from tillers separated by more than two meters. All samples were ice-cooled in cool boxes and later preserved at -20°C until further use.

DNA was extracted from individual winged aphids using the salting-out protocol described by Sunnucks & Hales (1996) and the DNA was resuspended in 25 µl HPLC grade water. Each aphid was genotyped at four microsatellite loci. The loci R5.10 and R5.50 were isolated from *R. padi* (Simon et al., 2001), while loci S16b and S17b were isolated from *Sitobion miscanthi* Takahashi (Sunnucks et al., 1996, 1997; Simon et al., 1999; Wilson et al., 1999).

PCR amplifications were carried out in a total volume of 7 µl using a DYAD Peltier® thermocycler with one cycle of 2 min at 94°C, 35 cycles of 30 sec at 94°C, 30 sec at 56°C, 60 sec at 72°C and one final elongation step of 2 min at 72°C. Reactions contained 1×$MgCl_2$-free reaction buffer (Promega), 3.2 mM $MgCl_2$, 100 µM of each dNTP, 1.5 pmol each of the forward and reverse primer, 0.25 µl of Taq polymerase (Promega), and ca. 50 ng of template DNA. Fragments were separated on ABI 3130 sequencer and data were visualized using Gene Mapper version 3.0 (ABI).

Statistical analyses

Data obtained from large-scale experiments were used to detect relationships between numbers of winter hosts within a location (28 km² sector) and population densities on the summer hosts of the corresponding cereal aphid species. Firstly, the exact Cochran-Armitage Trend test (Cochran, 1954; Armitage, 1955; Mehta et al., 1998; Cytel Cooperation, 2008) was applied to test for increasing (or positive) relation between number of winter hosts and cereals aphids on summer hosts among the different landscape sectors. The Cochran-Armitage Trend test is typically applicable to data of dose-response relationships, and tests whether the success rates of the two populations (i.e. numbers of winter hosts and counts of aphids) are the same, as against the alternative that they follow an increasing or decreasing trend (Mehta et al., 1998). Secondly, three-way analyses of covariance (ANCOVA; SAS, 2008) were used to simultaneously analyse the influences of summer host plants (i.e. either winter wheat or winter barley), percentage of arable land (i.e. above or below 63%), and microclimate during migration (i.e. mean temperatures in May above or below 12.5°C) on winter host and cereal aphid densities. As the summer host plant, the landscape structure, and the microclimate are expected to be of importance for aphid migration, these parameters were selected as covariates. Analyses were conducted separately for *R. padi* and *M. dirhodum* and for each evaluation date. In all locations and years, migration was terminated around mid of June (as checked when winter hosts were free of aphids). Hence, the last evaluation date (end of June) was not included in the analyses, because other effects (e.g. natural enemies) more than early immigration might have biased the direct migratory interactions between winter and summer hosts. The interactions between variables were tested, but they were not significant in any ANOVA analyses and therefore, not mentioned in the results below. Basically, we analyzed 54 case studies (Fig. 1), but due to missing values, only 51 and 50 case studies were used for evaluation on June 1st and 15th, respectively.

For small-scale experiments, differences between the three distance subplots were searched for each aphid species and predator units per evaluation date and year using Tukey-Kramer test (proc glm, all pairs; SAS, 2008). In order to quantify the influence of different distances from the hedge to the field plots, regression fits (SigmaPlot, 2007) were performed with data from evaluation dates with increased number of sampling transects (see above). Each two neighbouring lines of the eight distances were combined to reduce variability. To better meet the assumption of a normal distribution in case of count data and percentage values, the square root ($\sqrt{(x+0.0001)}$) and arcsin-square root (arcsin $\sqrt{x}$) transformations were performed, respectively.

Analyses of genetic data

Genetic differentiation between samples was calculated by F_{ST} values and pairwise tests of population differentiation using the program Fstat (version 2.9.3; Goudet, 2008) (using 1% as level of significance). This test uses the G-statistic to arrange tables after strict Bonferroni corrections, based on the indicative adjusted p-value for multiple testing. Gene diversity (heterozygosity) among individuals within samples was calculated using the software Genepop (version 3.4; Weir & Cockerham, 1984), genotypic diversity was simply determined by the ratio of the number of the genotypes per sample and total sample size. F_{is} values were calculated with the program Fstat (version 2.9.3; Goudet, 2008).

A Bayesian clustering method was also used to determine the number of optimal populations (genetic clusters or K) present in the dataset, to assess the level of differentiation among populations within and between winter and summer hosts and to quantify the contribution of winter hosts as a source of *R. padi* aphids colonizing wheat fields. The algorithm implemented in BAPS 4 (Corander et al., 2003) was used to identify the optimal number of K distinct populations among groups of samples. We run the program for K ranging from 1 to 29 with ten replicates for each K, to ensure that the algorithm had not ended up with different solutions in separate runs. We also performed an admixture analysis also implemented in BAPS for assessing individual coefficients of ancestry with regard to the inferred clusters of samples. 1,000 iterations were run to estimate admixture coefficients, with 50 reference individuals for each cluster and 50 replicates per individual.

Results

Large-scale experiments

In the majority of case studies, in 2004 no aphids (larvae or adults) could be found during wintertime, except in one winter barley field (location Wörth), where individuals of *S. avenae* were found very early in the year (8.3 adults per m^2 on April 8^{th}). In that year, *S. avenae* was the most abundant species in all locations. In 2005 and 2006, no anholocyclic overwintering could be detected at all in either locations, and *M. dirhodum* was the most abundant species. First individuals of *R. padi* were frequently found in the fields between mid (2004) and end of May (2005, 2006), whereas the first individuals of *M. dirhodum* arrived a few days later. Over all case studies, the numbers of *R. padi* found on June 1^{st} and 15^{th} showed mean values of 19.5 ±7.0 and 79.7 ±24.7 per m^2, respectively. *M. dirhodum* showed a similar abundance with mean values of 11.8 ±3.4 and 93.8 ±24.7 per m^2 on June 1^{st} and 15^{th}, respectively.

The studied locations were dominated by agricultural land use, i.e. arable land - grassland mosaics. The landscape sectors with a radius of three km were situated either in simple landscapes with high percentage of annual field crops (approx. 80%, i.e. at Bernburg) or in complex landscapes with a low percentage of arable land (approx. 50%) and with larger areas of non-crop habitats, such as grasslands, forests, fallows and hedgerows (i.e. at Wörth). Counts of *P. padus* trees were different between the locations, ranging from 2 to 141 trees per 28.3 km^2. The same applied for numbers of rosebushes (predominantly *R. canina* and *R. rugosa*), which were distributed over all five categories among the locations.

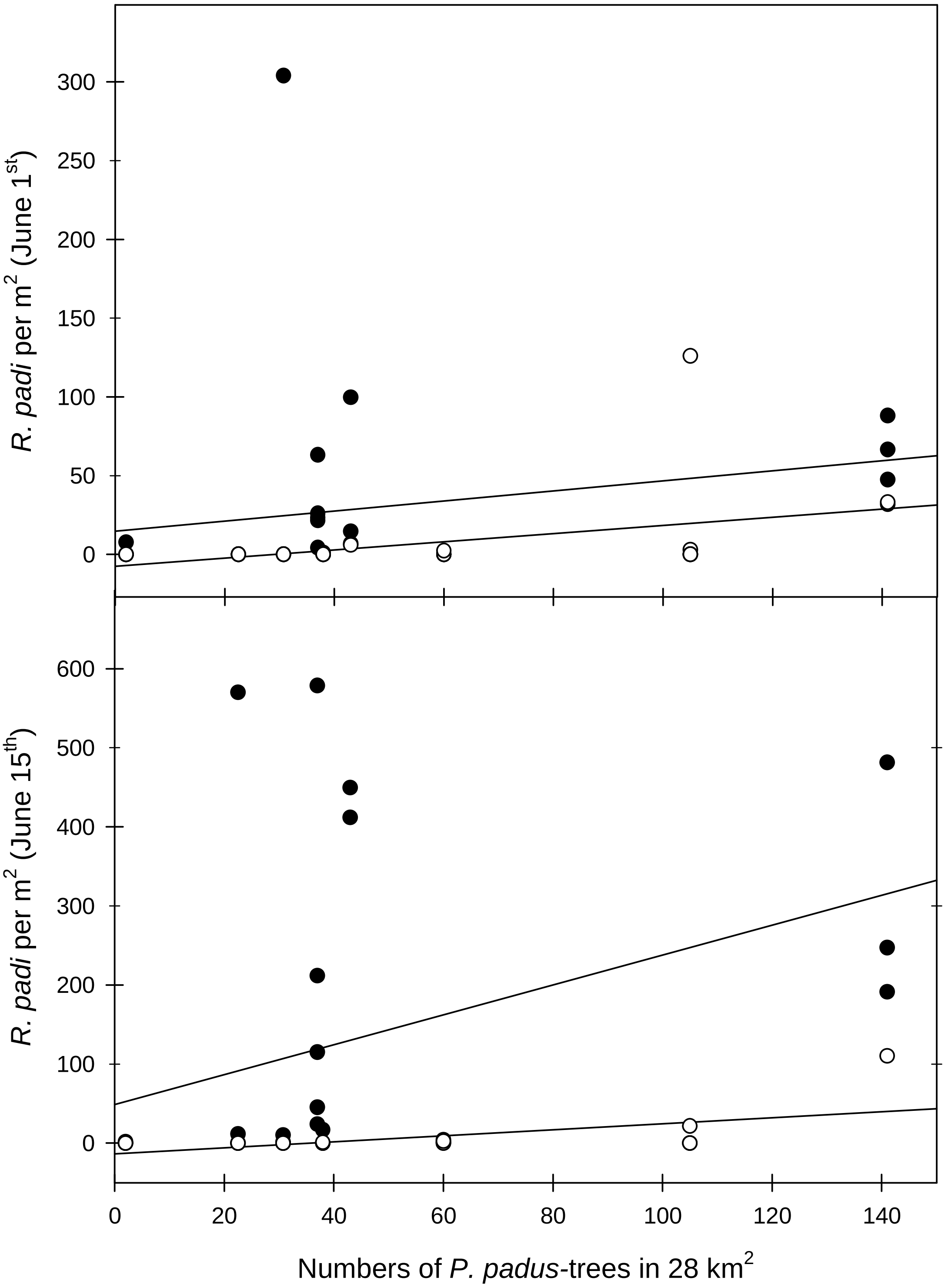


Fig. 2: Numbers of *P. padus* trees within a 28 km² landscape sector of nine locations and the mean numbers of *R. padi* per m² in cereal crops on June 1st (upper sketch) and on June 15th (lower sketch) specified according to the mean temperatures in May below (black circles, upper straight line) and above (white circles, lower straight line) 12.5 °C. The straight lines indicate significant trends ($p < 0.05$) according to Cochran-Armiatge Trend test for all situations.

Tab. 1: Results of analyses of covariance between numbers of aphids (*R. padi* and *M. dirhodum*) and the numbers of winter hosts. The type of summer hosts (winter barley and winter wheat), the percentage of arable land (above or below 63%), and the mean temperatures in May (above or below 12.5°C) are specified as qualitative variables.

	F-values (*R. padi*)		F-values (*M. dirhodum*)	
Variables	June 1st	June 15th	June 1st	June 15th
Numbers of winter host	1.85	2.32	5.18*	1.02
Type of summer host	3.30	1.41	0.21	0.92
Percentage of arable land	2.00	0.79	0.62	0.01
Mean temperature in May	5.27*	7.75*	0.58	0.90

* Asterisks indicate significance level of $\alpha < 5\%$.

For the nine locations, Cochran-Armitage Trend test showed a significantly increasing trend between the numbers of *P. padus* trees and the counts of *R. padi* in adjacent crops on June 1st ($p < 0.001$) and 15th ($p < 0.013$). However, ANCOVA did not detect a statistically significant ($p > 0.05$) relation between numbers of winter host and *R. padi* on either sampling date (Fig. 2; Tab. 1). Among the qualitative variables, only mean temperatures in May influenced significantly ($p < 0.05$) the regressions between numbers of winter hosts and counts of *R. padi* at both sampling dates. On June 1st and 15th, case studies with lower temperatures in May (< 12.5°C) were significantly associated with higher counts of *R. padi*, those with higher temperatures in May (> 12.5°C) with lower counts of *R. padi* (Fig. 2).

The Cochran-Armitage Trend test found also significant trends ($p < 0.001$) for *M. dirhodum* datasets. Higher numbers of rose bushes (categorical data) led to higher counts of *M. dirhodum* for both evaluation dates (June 1st and 15th). For the first sampling date, ANCOVA also revealed significantly higher counts of *M. dirhodum* on summer hosts in landscape sectors with higher numbers of rose bushes ($p < 0.05$, $R^2 = 0.12$, $a = -10.1$, $b = 7.25$, Tab. 1, Fig. 3). However, none of the qualitative variables did significantly ($p > 0.05$) influence the regression between numbers of winter hosts and numbers of *M. dirhodum* on either sampling dates (Tab. 1).

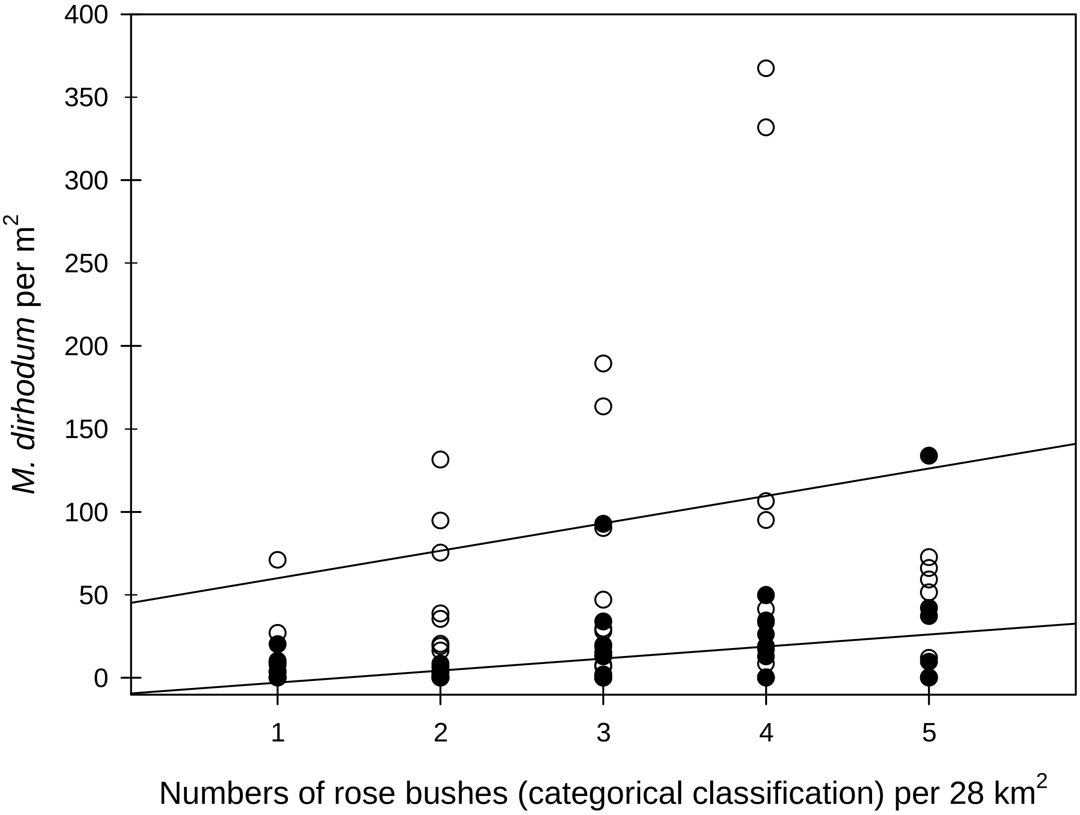


Fig. 3: Regression analyses between the numbers of rose bushes (*Rosaceae*, categorical classification: 1 = very rare, 5 = frequent) within a 28 km² landscape sector and the mean numbers of *M. dirhodum* per m² in cereal crops on June 1st (black circles, lower straight line: $R^2 = 0.12$, $p < 0.05$, $a = -10.1$, $b = +7.3$) and on June 15th (white circles, upper straight line: $R^2 = 0.10$, $p > 0.05$). The lines indicate significant trends ($p < 0.05$) according to Cochran-Armiatge Trend test for all situations.

Small-scale experiments

In small-scale experiments, significant differences in numbers of *R. padi* between subplots were rarely observed on both sides of the hedge (with *P. padus*) in 2004. In that year, counts of *R. padi* were equally distributed, among subplots as well as between the both sides of the hedge (Tab. 2). This was different in 2005 and 2006 (years characterised with higher population densities of *R. padi* on winter and summer hosts compared to 2004) for which significantly ($p < 0.05$) more aphids settled in cereal subplots nearest to the winter hosts. Comparing the three groups of distances on each of seven evaluation dates in 2004, only one and four times the counts of *R. padi* were significantly higher in the first subplot (D_1, closed to the hedge) than in D_2 or D_3 on the west and the east side of the hedge, respectively (Tab. 2). In 2005 and 2006, when comparisons were performed on fewer evaluation days (i.e. six and four times), significant higher counts of *R. padi* were more frequently observed in the first subplot (D_1; Tab. 2).

Tab. 2: Relative frequency (%) of comparisons with significantly greater counts of aphid or predator units found at three groups of distances from the hedge. Aphid species or predator units followed by the same letter do not differ significantly (Tukey-Kramer Test, p = 0.05).

Year and no. of evaluation days	Species	Relative frequency (%)		
		D_1vs. $D_{2/3}$	D_2vs. $D_{1/3}$	D_3vs. $D_{1/2}$
2004-West	*R. padi*	4.8	0	0
7	*S .avenae*	14.3	0	14.3
	M. dirhodum	14.3	0	4.8
	Predator units	9.5	9.5	0
2004-East	*R. padi*	19	0	4.8
7	*S. avenae*	14.3	4.8	19
	M. dirhodum	9.5	4.8	4.8
	Predator units	0	0	4.8
2005-East	*R. padi*	44.4	5.6	0
6	*S. avenae*	5.6	5.6	5.6
	M. dirhodum	0	0	5.6
	Predator units	5.6	0	0
2006-East	*R. padi*	66.7	0	0
4	*S. avenae*	25	8.3	8.3
	M. dirhodum	16.7	0	0
	Predator units	16.7	0	0
Mean	*R. padi*	33.7 ±13.7^a	1.4 ±1.4^b	1.2 ±1.2^b
relative	*S. avenae*	14.8 ±4.0^a	4.7 ±1.7^a	11.8 ±3.0^a
frequency	*M. dirhodum*	10.1 ±3.7^a	1.2 ±1.2^a	3.8 ±1.3^a
(N = 4)	Predator units	7.9 ±3.5^a	2.4 ±2.4^a	1.2 ±1.2^a

Likewise *R. padi, M. dirhodum* occurred on winter and summer hosts in larger numbers in 2005 and 2006, in contrast to 2004. Comparing the subplots in 2004, significant greater counts of *M. dirhodum* were most frequently observed in the first subplots (D_1). The same was observed for 2006, whereas in 2005 only on one evaluation day a significant focus of *M. dirhodum* was found in the subplot D_3 (Tab. 2).

The non-host-alternating species *S. avenae* was most evenly distributed over all subplots in all years. However, significantly greater counts were most frequently found in subplots D_1 and D_3 (Tab. 2).

Numbers of predator units, observed from counts per m² as well as from sweep net catches, were generally higher in 2005 and 2006 compared to 2004. In 2004, significantly higher predator units were found in D_1 and D_2 on two different evaluation days, whereas in D_3

only once (of seven evaluation days) significantly higher predator units were found. In 2005 and 2006, only the first subplot (D_1) showed significantly greater numbers of predator units (Tab. 2). The same distribution pattern was obvious from sweep net catches (data not shown).

Comparing for all years and subplots, the mean relative frequencies with highest values were found for *R. padi* in the subplot closest to the hedge (i.e. subplot D_1), followed by *S. avenae*, *M. dirhodum* and the predator units. Subsequently, the mean relative frequency of *R. padi* counts was significantly ($p < 0.05$; Tukey-Kramer test) higher in the first subplot compared to D_2 and D_3. This was in contrast to other cereal aphid species or predator units, where no significant differences were observed between the subplots concerning the mean relative frequency over all study years (Tab. 2).

Tab. 3: Results from regression analyses (coefficient of determination, intercept *a*, and slope *b*) between counts of *R. padi* in summer hosts and increasing distances ($n = 8$) from winter hosts at four evaluation days according to the formula (1): $y = a + b / x$.

Evaluation day	Coefficient of determination	Intercept *a*	Slope *b*
2005,06,08	0.93*	917 ±895$^+$	17,129 ±3,369*
2005,06,15	0.99*	2,289 ±228*	24,053 ±859*
2006,06,27	0.83$^+$	899 ±2,829	33,077 ±10,646$^+$
2006,07,13	0.99*	297 ±156$^+$	18,419 ±1,117*

*Asterisks indicate significance level of $\alpha < 5\%$.
$^+$Plus indicate significance level of $\alpha < 10\%$.

In 2005 and 2006, the more detailed field evaluations led to a precise description of the effects of the distance from the hedge into the winter cereals for counts of *R. padi* (Fig. 4). The regression analyses fitted the decrease of *R. padi* populations on its summer host best (i.e. with highest coefficients of determination; Tab. 3) using the following formula:

$$y = a + \frac{b}{x} \tag{1}$$

where the counts of aphids *y* found on the summer host are decreasing (slope *b*; Tab. 3) with increasing distance *x* (in m) from the winter host. The intercept *a* represents the mean population level (in a given study area) adjusted for a certain evaluation date (Fig. 4; Tab. 3). For *M. dirhodum*, no universal formula was found to describe precisely the small-scale effects of distance from its winter host into the winter cereals (Fig. 4).

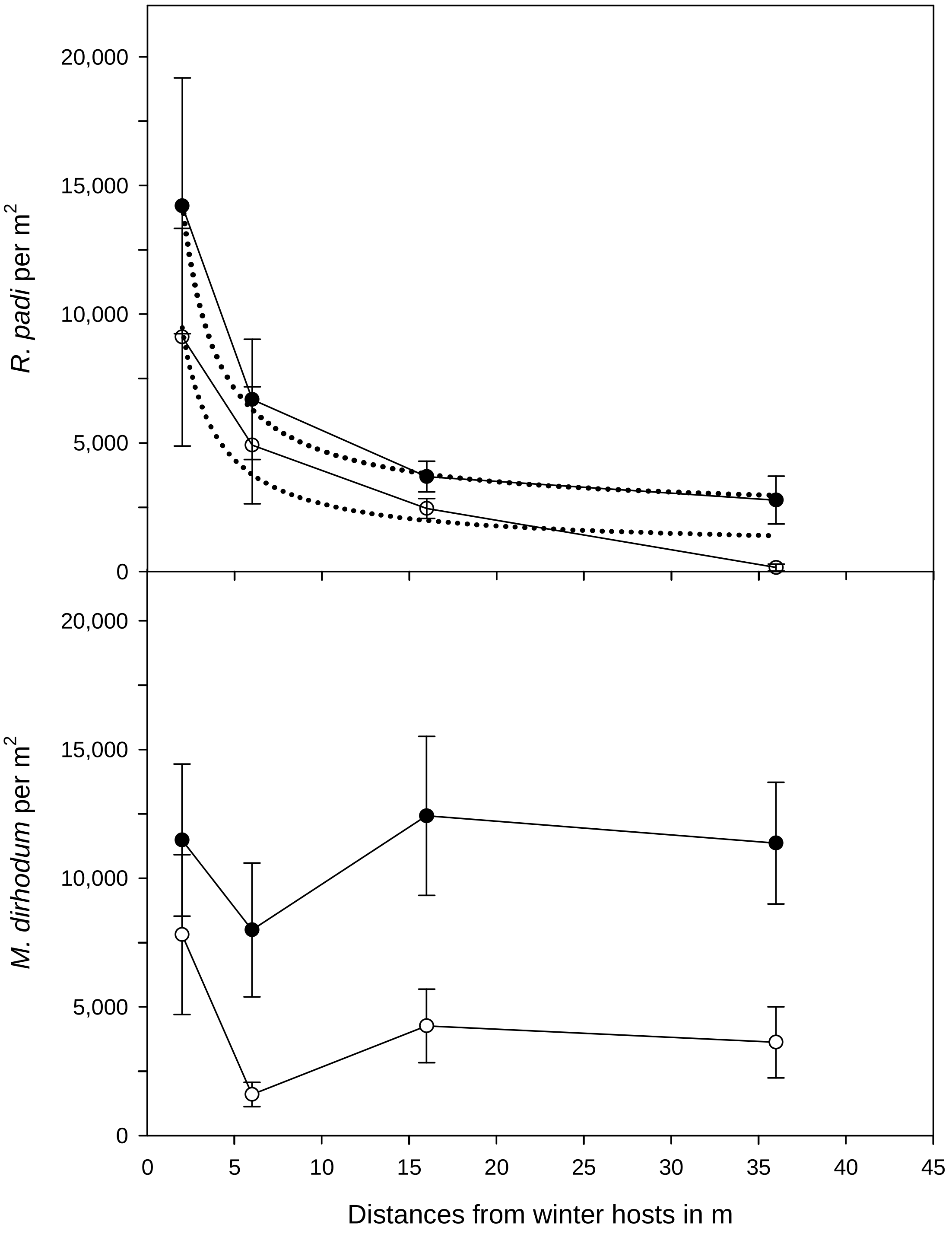


Fig. 4: Mean numbers (±SE) of *R. padi* (upper sketch) and *M. dirhodum* (lower sketch) per m² on winter wheat in relation to distances from winter hosts (in m) on June 8th (black circles) and on June 15th (white circles) in 2005. The formula specified in the text fits the decrease in numbers of *R. padi* with increasing distances from the winter hosts (dotted lines, upper sketch) for June 8th and June 15th (with coefficient of determination of $R^2 = 0.99$ and $R^2 = 0.93$, respectively).

Genotypic analysis of R. padi populations on winter hosts and wheat fields

A total of 466 individuals of *R. padi* were genotyped at the four microsatellite loci. Altogether 461 distinct genotypes were found, indicating high genetic diversity among populations of *R. padi* and high resolving power of genotypic composition of the four microsatellite loci. Hence, most multilocus genotypes were unique and only five genotypes with two copies each were detected (Tab. 4). Of the twice-occurring genotypes, two belonged to tree no. 5, one each to D_1 and D_3 (both July 13th), and one to the field of Isernhagen collected on June 29th. These few copies of 4-locus genotypes could represent either individuals belonging to the same aphid clone (since copies have been found on the same host and on the same date, this hypothesis is favored) or from random assortment of alleles following sexual reproduction and recombination. Substantial genetic variation was found, with loci R5.50 (51 alleles, mean per population: 12.5) and R5.10 (30 alleles, mean per population: 18.9) as most polymorphic ones (Tab. 4). In locus S16b, 19 alleles (mean per population: 4.1), and in locus S17b 18 alleles (mean per population: 7.9) were detected. It is notable that a large proportion of the genotypic variation resulted from rearrangements of identical alleles and not from rare alleles.

Tab. 4: Gene diversity, F_{is}-values, and allele composition specified for various *R. padi* populations genotyped with four microsatellite loci (Isern. = location Isernhagen).

Population (i.e. location & date)	Sample size (*n*)	Number of alleles per locus				No. of multilocus genotypes	F_{is}	Gene diversity / genotypic diversity (G/N)
		R5.10 (30)*	R5.50 (51)*	S16b (19)*	S17b (18)*			
D_1 June 20th	11	11	13	2	7	11	0.254	0.66 / 1.00
D_2 June 20th	18	10	8	4	6	18	0.107	0.65 / 1.00
D_1 June 27th	17	11	16	3	13	17	0.092	0.68 / 1.00
D_2 June 27th	28	13	11	1	8	28	-0.023	0.56 / 1.00
D_3 June 27th	20	15	15	5	9	20	0.159	0.73 / 1.00
D_1 July 6th	11	11	20	3	7	11	0.053	0.67 / 1.00
D_2 July 6th	20	14	19	4	9	20	0.018	0.72 / 1.00
D_3 July 6th	25	12	18	6	8	25	0.158	0.71 / 1.00
D_1 July 13th	11	13	20	4	4	10	0.182	0.72 / 0.91
D_2 July 13th	24	13	18	4	7	24	0.248	0.68 / 1.00
D_3 July 13th	20	11	15	4	8	19	0.203	0.75 / 0.95
Tree no. 5	45	11	31	2	7	43	0.118	0.63 / 0.96
Tree no. 6	47	13	27	5	9	47	0.219	0.73 / 1.00
Tree no. 9	58	16	28	5	10	58	0.129	0.73 / 1.00
Isern. June 15th	23	10	13	6	5	23	0.167	0.64 / 1.00
Isern. June 22nd	26	12	17	7	7	26	0.083	0.73 / 1.00
Isern. June 29th	62	16	33	5	11	61	0.059	0.68 / 0.90

* Asterisks indicate the total number of alleles per locus

Tab. 5: Results of pairwise tests of differentiation of 17 *R. padi* populations (D_1 to D_3 = collected in winter wheat subplots in location Hiddestorf; tree = collected from different *Prunus padus* trees; Isern. = collected in winter wheat in location Isernhagen) collected on several dates using microsatellite markers are specified above the diagonal (0): the values represent non-adjusted p-values of the G-test with bold values indicating significant differences at the $\alpha = 5\%$ level (see material and methods section for details). Below the diagonal (0), pairwise F_{ST} values (coefficient of differentiation between populations) for populations of *R. padi*. F_{ST} values > 0.10 are highlighted in bold.

	D_1 June 20th	D_2 June 20th	D_1 June 27th	D_2 June 27th	D_3 June 27th	D_1 July 6th	D_2 July 6th	D_3 July 6th	D_1 July 13th	D_2 July 13th	D_3 July 13th	tree no. 5	tree no. 6	tree no. 9	Isern. June 15th	Isern. June 22nd	Isern. June 29th
D_1 June 20th	0	0.22419	0.25074	0.09787	0.00779	0.05478	0.00140	**0.00015**	0.02044	**0.00007**	**0.00015**	**0.00022**	**0.00007**	**0.00015**	0.00103	0.00353	0.00074
D_2 June 20th	0.012	0	0.03478	0.20463	0.00110	**0.00022**	**0.00015**	**0.00015**	**0.00015**	**0.00007**	0.00029	**0.00007**	**0.00007**	**0.00007**	0.00074	0.00103	**0.00015**
D_1 June 27th	0.004	0.031	0	0.00574	0.10537	0.13551	0.00081	**0.00007**	0.20676	**0.00007**	**0.00007**	0.23324	**0.00007**	**0.00007**	0.00140	0.01794	0.66684
D_2 June 27th	0.007	-0.001	0.027	0	**0.00007**	**0.00007**	**0.00007**	**0.00007**	**0.00007**	**0.00007**	**0.00007**	**0.00007**	**0.00007**	**0.00007**	**0.00007**	**0.00015**	**0.00007**
D_3 June 27th	0.046	0.090	0.016	**0.100**	0	0.24919	0.36449	0.09919	0.85015	0.50000	0.11846	**0.00015**	**0.00007**	**0.00007**	0.00985	0.07051	**0.00015**
D_1 July 6th	0.037	0.096	0.024	**0.107**	0.006	0	0.43618	0.04132	0.70618	0.01691	0.01419	0.01662	**0.00007**	**0.00007**	0.00147	0.06882	**0.00037**
D_2 July 6th	0.047	**0.105**	0.034	**0.116**	-0.007	0.002	0	0.08735	0.31787	0.06463	0.61007	**0.00007**	**0.00007**	**0.00007**	0.00081	0.13860	**0.00007**
D_3 July 6th	0.062	**0.111**	0.058	**0.131**	0.014	0.013	0.005	0	0.01816	0.61007	0.20662	**0.00007**	**0.00007**	**0.00007**	0.07463	0.04544	**0.00007**
D_1 July 13th	0.051	**0.107**	0.024	**0.123**	-0.001	-0.010	-0.002	0.010	0	0.11287	0.00331	0.05691	**0.00007**	**0.00007**	0.00324	0.29993	0.00801
D_2 July 13th	0.070	**0.121**	0.059	**0.133**	0.017	0.019	0.013	-0.010	0.007	0	0.48191	**0.00007**	**0.00007**	**0.00007**	0.12456	0.56449	**0.00007**
D_3 July 13th	0.060	0.091	0.051	**0.126**	0.006	0.018	0.002	-0.004	0.013	0.003	0	**0.00007**	**0.00007**	**0.00007**	0.09000	0.04963	**0.00007**
Tree no. 5	0.057	**0.123**	0.029	**0.131**	0.036	0.011	0.043	0.061	0.009	0.053	0.059	0	**0.00007**	**0.00007**	**0.00007**	**0.00015**	0.29147
Tree no. 6	**0.181**	**0.199**	**0.159**	**0.230**	**0.134**	**0.138**	**0.133**	**0.127**	**0.127**	**0.134**	**0.118**	**0.161**	0	0.19963	**0.00007**	**0.00007**	**0.00007**
Tree no. 9	**0.204**	**0.215**	**0.182**	**0.247**	**0.155**	**0.161**	**0.157**	**0.150**	**0.150**	**0.153**	**0.135**	**0.182**	-0.003	0	**0.00007**	**0.00007**	**0.00007**
Isern. June 15th	0.088	**0.140**	0.068	**0.161**	0.036	0.030	0.027	0.008	0.016	-0.002	0.011	0.052	**0.126**	**0.148**	0	0.12022	**0.00007**
Isern. June 22nd	0.057	**0.104**	0.035	**0.115**	0.006	0.012	0.002	0.004	0.000	-0.003	0.002	0.034	**0.109**	**0.131**	0.010	0	**0.00015**
Isern. June 29th	0.066	**0.109**	0.023	**0.116**	0.026	0.013	0.034	0.054	0.006	0.045	0.052	-0.003	**0.149**	**0.168**	0.047	0.028	0

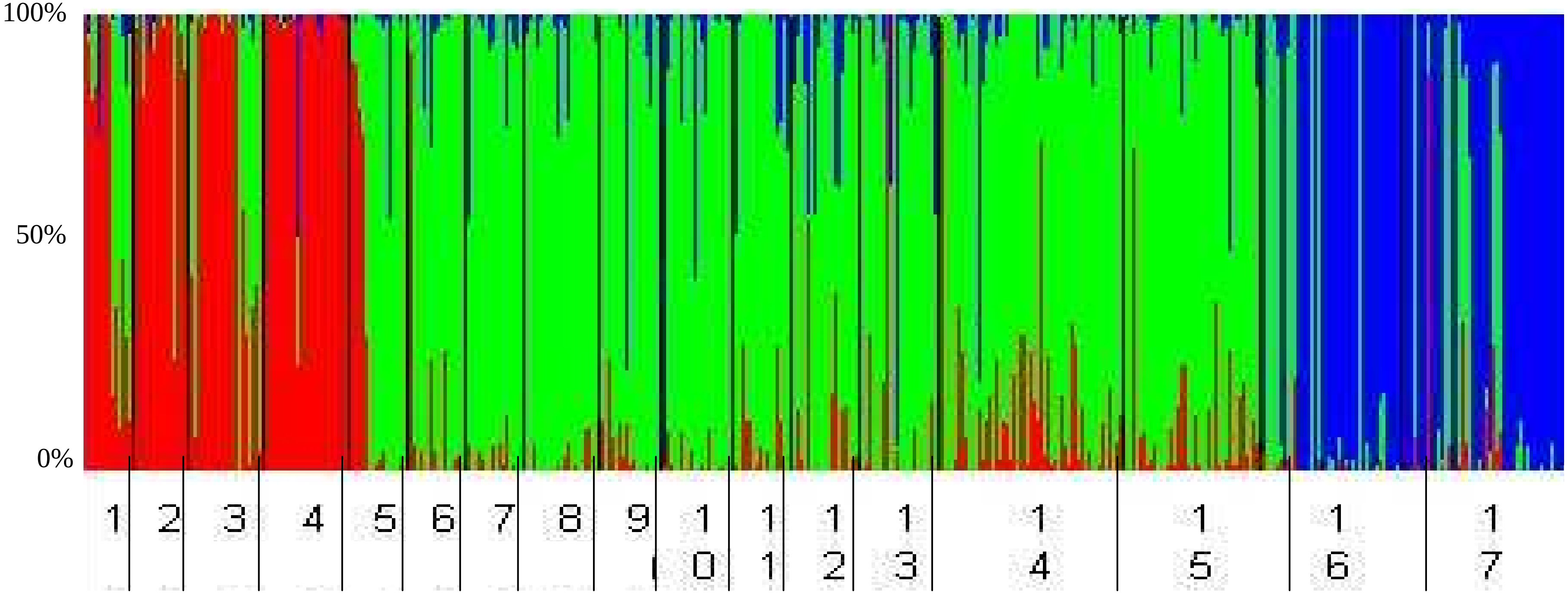


Fig. 5: The estimated genetic relationships between the *R. padi* individuals collected from three subplots (D_1: 0-8 m, D_2: 8-24 m, and D_3: 24-60 m) in location Hiddestorf (on June 20th, 27th, July 6th and 14th), from the winter hosts (tree no. 5, 6, and 9), and from a control field in Isernhagen (on June 15th, 22nd, and 29th). Each aphid is represented by a thin vertical line, which is partitioned into three major segments (red, green, and blue), representing the proportion of its genome derived from each genetic cluster. 1 = D_1 June 20th, 2 = D_2 June 20th, 3 = D_1 June 27th, 4 = D_2 June 27th, 5 = D_3 June 27th, 6 = D_1 July 6th, 7 = D_2 July 6th, 8 = D_3 July 6th, 9 = D_1 July 13th, 10 = D_2 July 13th, 11 = D_3 July 13th, 12 = Isernhagen June 15th, 13 = Isernhagen June 22nd, 14 = Isernhagen June 29th, 15 = tree no. 5, 16 = tree no. 6, and 17 = tree no. 9.

The pairwise test of population differentiation (Tab. 5) showed significant differences after 13,600 permutations (with an adjusted p-level for multiple comparisons of $p = 0.000368$) for various samples. The trees no. 6 and 9 were different from all other populations, whereas tree no. 5 was different from all populations except D_1 on June 27th, D_1 on July 6th, and D_1 on July 13th. Additionally, the samples from D_2 on June 20th, and June 27th, as well as from Isernhagen on June 29th showed various differences to other populations (Tab. 5).

The Bayesian clustering algorithm implemented in BAPS 4 supported three genetic clusters in the dataset (Fig. 5). The most abundant cluster corresponded to individuals found in the winter wheat fields (Hiddestorf and Isernhagen) and on *P. padus* three no. 5. The second cluster corresponded to individuals found early in the subplots in Hiddestorf (except for June 27th D_3), while the third cluster gathered mostly individuals found on the winter hosts trees no. 6 and 9. Using the admixture analysis, we found the lowest level of admixture in the first cluster and the highest in the second one (Fig. 5).

To summarise, population differentiation tests and Bayesian clustering analysis showed that *R. padi* populations on *P. padus* trees no. 6 and 9 did not contribute to the infestation of the adjacent and the remote winter wheat fields. This does not seem to be the case for *R. padi* on *P. padus* tree no. 5, which showed genetic proximity with several samples collected in the two wheat fields. Most early *R. padi* samples are genetically different from later colonizers. The distance between winter wheat subplots (D_1 to D_3) and the *P. padus* trees had low influence on the pattern of genetic structure of *R. padi* populations within the winter wheat field.

Discussion

Large-scale experiments

The most striking result from large-scale experiments was that higher counts of host-alternating cereal aphids (e.g. *R. padi* and *M. dirhodum*) were found in locations with higher numbers of winter hosts. However, this relationship was only significant according to Cochran-Armitage Trend test for both species. Using ANCOVA or correlation analyses (of pooled data; data not shown) a significant positive correlation between numbers of winter hosts and aphid densities could be only detected for *M. dirhodum* in the beginning of June.

Significant correlations between numbers of *R. padi* and *P. padus* have been reported from northern Europe (Finland; Leather et al., 1989). However, recently in similar locations (southern Sweden), weak or no indication at all of density dependence were found

(Bommarco et al., 2007). In Scandinavian countries, *R. padi* is strongly holocyclic (Leather et al., 1989), whereas anholocyclic overwintering has also been reported from countries of western or central Europe (e.g. France, U.K., Germany; Hand, 1980; Dedryver & Gelle, 1982; Kleinhenz, 1994). The relation of holocyclic and anholocyclic overwintering in different countries can be very important to determine density dependences between numbers of aphids on winter and summer hosts. However, anholocyclical hibernation was not observed for *R. padi* in any case study. This was also confirmed using the simulation model SIMLAUS (Kleinhenz, 1994; Klüken et al., unpublished data).

Both statistical techniques (the Cochran-Armitage Trend test and the ANCOVA) differ in their significance (Mehta et al., 1998; Afifi & Clark, 1999). Whereas the Cochran Armitage Trend test is frequently applied in dose-response data to show under the alternative hypothesis in- or decreasing trends (and so describing the kind of relationship; Cochran, 1954; Armitage, 1955), the regression analyses (e.g. ANCOVA) does not solely describe but - more importantly - predict the value of the dependent variable (based on the independent variable) according to the resulting equation (Mehta et al., 1998; Afifi & Clark, 1999). Moreover, detailed information from further influencing variables are available (e.g. influencing quality variables) using ANCOVA. Hence, differences between both statistical tests applied to the same datasets are frequently found (Cooley & Lohnes, 1971; Afifi & Clark, 1999). However, it is not clear (from biology background), why the relationship between winter hosts and host-alternating cereal aphids were not consistent in both statistical techniques. Therefore, it is difficult to provide specific suggestions on (early) immigration into winter cereals and on the early population development. Several studies have reported that *R. padi* has high dispersal and migration rates, and that it is - as “non-hedge-hopping” aphid species (H.D. Loxdahle, pers. comm.) - frequently occurring in suction traps (Taylor, 1986; Veenker & Ulber, 2004). Moreover, the winter hosts of *R. padi* were scattered and not very frequently distributed among the locations in our study compared to e.g. winter hosts of *M. dirhodum*. Nothing is known about distributions of *M. dirhodum* in dependence of winter host densities. However, our results showed somehow stronger density dependence for that species than for *R. padi*. Using catches from 12 m suction traps, Veenker & Ulber (2004) found that *M. dirhodum* were less frequently found as compared to *R. padi* (Taylor, 1986; Clark et al., 1992). The first species may predominantly fly relative short distances at lower altitudes. A further difference between both aphid species is that the dispersal of *M. dirhodum* from its winter hosts is scattered over a larger period. Therefore, these species seem to have a more limited dispersal power compared to *R. padi* (Reimer, 2004), and hence, higher dilution was indicated for migrating *R. padi* (Loxdale et al., 1993; Harrington et al., 2004).

It was somehow surprising that lower temperatures in May significantly influenced the regression between numbers of *P. padus* and counts of *R. padi* and led to higher counts of *R. padi* in the winter wheat. Other studies reported that with increasing temperatures in May, the aphids appeared earlier on the cereals and in higher numbers (Rautapäa, 1976; Dixon, 1998). Possibly, we have found a spurious correlation, because when certain (e.g. Isernhagen, Hiddestorf, Jeinsen, Wörth) or all locations of the year 2004 were excluded from the calculations, significant influence of the quality variable “temperatures in May” disappeared from ANCOVA ($p > 0.05$, data not shown). That means higher temperatures in May 2005 and 2006 tended to result in higher numbers of cereal aphids in the field corroborating results from trend tests in both host-alternating species (Leather et al., 1989; see paragraph above). Moreover, the temperatures in May never significantly influenced the relationship between the numbers of rosebushes and counts of *M. dirhodum*. Aphids occurred earlier in fields and in suction traps in 2004 as compared to 2005 or 2006 (data not shown). Possibly, the lower the temperatures in May the closer *R. padi* alighted to its winter host, so that dispersal and dilution was somehow restricted. An other reason may be that the time of major dispersal events is more different between the years than expected (Veenker & Ulber, 2004). Thus, we may have missed the first immigration phase with our field evaluation in 2004. Subsequently, the populations developed earlier and let to higher counts of *R. padi* in the beginning and mid June in 2004 than in other years (Dixon, 1998).

Dispersal distances largely depend on meteorological conditions, e.g. with periods of lower temperatures leading to lower population levels (Dixon, 1998; Bommarco et al., 2007). *R. padi* frequently leaves the winter host several days earlier than *M. dirhodum*. Thus, considering weather conditions during this study, it is unlikely that the latter species was inferior in migrating into the winter cereal fields, because the temperatures in May never influenced significantly the counts of *M. dirhodum*. Taking into account the high population levels of *M. dirhodum* observed in 2005 and 2006, it is unlikely that different migration intensities were affected by weather conditions.

The absence of distinct density effects in *R. padi* may be related to fluctuations of holocyclic winter eggs on winter hosts. In 2004, only very few eggs were counted on the trees, whereas mean numbers were significantly higher in 2005 (11.4 ±1.1 per 100 buds) and in 2006 (3.8 ±0.5 per 100 buds) in Hiddestorf (Klüken et al., unpublished data). Regarding the importance of winter host availability within regional sectors and landscape diversity, we could at first not consistently confirm the hypothesis of lower cereal aphid abundances in landscapes with fewer winter hosts than in landscapes with many winter hosts. This was predominantly due to higher density of overall spring populations per area and shorter distances to summer hosts favouring successful spring migration (Loxdale et al., 1993). According to our results, the landscape type did not seem to be an important factor determining the size of local sources of *R. padi* or *M. dirhodum* with respect to short distance spread (Tab. 1). This variable may be more important from mid June on, when predator and parasitoids influence (later) population dynamics of cereal aphids, as it was reported elsewhere (Pickett & Cadenasso, 1995; Polis et al., 1997; Thies & Tscharntke, 1999; Thies et al., 2003, 2005).

Small-scale experiments

In small-scale experiments, spring migration from the winter hosts into the crop was particularly evident for *R. padi*. This suggests that, in contrast to *M. dirhodum* (and *S. avenae*), *R. padi* benefited from a close proximity between its winter and summer hosts especially in those years, when high population levels occurred on *P. padus* (e.g. in 2005 and 2006). Density gradients levelled off at about 12 m distances to winter hosts (decreased abundances), and the population densities of *R. padi* were equal to the mean field densities. We have specified a function (equation no. 1) for the observed density dependences, which, however, needs to be adjusted to the overall population level of *R. padi* in a given year and location.

It has long been argued that migratory cereal aphids can be attracted to land predominantly on leeward sides of landscape elements (e.g. windbreaks, hedges, forested areas), due to turbulences or lower wind speeds (Kenny & Chapman, 1988; Bottenberg & Irwin, 1991, 1992a; Fereres et al., 1999; Isard & Gage, 2001). In 2004, however, significant differences between the population build-up were not detected, neither on the lee- (e.g. Hiddestorf East) nor on the windward side (Hiddestorf West). So, it seems unlikely that the major source for the observed high counts of *R. padi* settling close to the field edge was from long distance migration early in the years (June 1st and 15th; Loxdale et al., 1993). Therefore, detailed information about influences of winter hosts on the immigration and early population development in small-scale experiments are of major importance for small-scale distributions.

Interestingly, the small-scale influences of winter hosts were of minor importance for *M. dirhodum* as compared to *R. padi*. Indeed, higher counts of the former species were most frequently significant in the first subplot, too (as compared to D_2 or D_3; Tab. 2), but a mathematically dependency concerning distances between winter and summer hosts was not found at all (Fig. 4). These differences (as compared to *R. padi*) in density are not obvious, as both species have a very similar life cycle strategy and biology (Dixon, 1998). The counts of both species were comparable on the summer hosts, but highest standard errors were observed for *M. dirhodum*, indicating higher aggregation as compared to *R. padi*. Moreover, fewer *M. dirhodum* were observed on the winter hosts in the hedge. Possibly, a large amount of *M. dirhodum* cereal colonisers arrived from other surrounding structures than from the hedge under examination, where rosebushes were more frequent than *P. padus* trees (data not shown). Moreover, more rosebushes than *P. padus* trees were also frequently distributed in the study location and may therefore provide more aphids (Leather et al., 1989).

The hedge, which included also low numbers of grassy strips and patches, did not influence the distribution of the non-host-alternating species *S. avenae*, because it was most evenly distributed over the cereal subplots in different years. A corresponding relation similar to *R. padi* could not be found for *S. avenae*, which indicates the basically different hibernation and migration behaviour of this species (Basedow et al., 1994; Veenker & Ulber, 2004).

Interestingly, high numbers of predator units have also been found in subplots with higher counts of *R. padi* (e.g. in subplots D_1), but mean relative frequencies were not significant (Tab. 2). Moreover, within the guild of cereal aphid antagonists (i.e. predator units), counts of *Coccinella septempunctata* L. were significantly higher close to the hedge (e.g. in subplot D_1, data not shown), which can be explained in two possible ways: On the one hand, density dependencies have led to higher numbers in subplots with high abundances of *R. padi*. The functional and numerical responses of cereal aphid predators have frequently been described (Freier & Triltsch, 1996; Hemptinne & Dixon, 1997; Freier et al., 2001). However, aphid population dynamics may be either driven by predators (as predicted from theory; Freier & Triltsch, 1996; Kindlmann & Dixon, 1996, 1999), or, the predators are responding to aphid abundances (as self-regulated by aphid migration; Kindlmann et al., 2007). Concerning the confusion about density regulations of cereal aphid antagonists, detailed conclusions cannot be drawn here. On the other hand, many authors have demonstrated that diversified hedges, expanded and connected field margins promoted the abundance and diversity of predators and parasitoids in adjacent cereal fields (including a certain gradient; Storck-Weyhermüller, 1988; Rossing et al., 2006). The reason is that higher plant diversity supplies higher aphid antagonist diversity, e.g. by the availability of more diverse food resources or hibernation sites (Dennis et al., 1994; Nicolino et al., 1995; Thomas & Marshall, 1999; Ländis et al., 2000; Boller et al., 2004; Poehling et al., 2007). However, we cannot provide detailed information concerning the plant diversity and antagonist refuges in the hedge and we have to consider that observations may also be related to the sample size and the method used to estimate the predator units (Jarosík et al., 2003; Klüken et al., unpublished data).

Genotypic analysis of R. padi populations on winter hosts and wheat fields

Using Bayesian clustering, we detected three main genetic clusters among the populations. We refer to them as "early" and "late" colonisers, and "tree" populations (Fig. 5), as the early lineages only occurred in June 20th and July 27th (except D_3). Surprisingly, these early colonizers were only found in Hiddestorf and they largely disappeared later in the year. The late colonizers were found in Hiddestorf, Isernhagen, and on one of the trees (tree no. 5), but spread mainly later in the year. Therefore, the winter wheat field in Hiddestorf was most likely infested by two sources of colonizers: one was dominant ("late") and the other of minor ("early") importance (Fig. 5). One explanation of this phenomenon could be the two overwintering strategies of *R. padi* (Simon et al., 1991, 1996a, b), in which the early colonisers might have developed from anholocyclic and the later occurring colonisers from holocyclic lineages that originated at least partly from tree no. 5.

However, several topics contradict this hypothesis: Asexual lineages are assumed to be rare in northern Germany and the winter 2005/2006 was harsh (e.g. 105 frost days in Hiddestorf between November 15th and May 1st). Therefore, anholocyclic hibernation was not observed, neither during small-scale studies in Hiddestorf (almost continental climate) nor in other regions (i.e. during large-scale experiments; see section about large-scale experiment). Hence we assume that the harsh winter has erased most of the asexual lineages in the whole study region. Sample size, however, was restricted to 300 tillers per subplots, which is not always sufficient to detect population growth at low levels in anholocyclic lineages (Jarosík et al., 2003; Klüken et al., unpublished data). Additionally, the high genetic and genotypic diversity, the heterozygote deficit (data not shown), and the similar F_{ST}-values of the clusters make anholocyclic lineages very unlikely (Halkett et al., 2004, 2005). The positive F_{ST}-values indicate heterozygote deficit that is typical for sexually reproducing lineages (Papura et al., 2003). It may derive from a Wahlund effect arising from a temporal structuring of the population with various subpopulations differing in the timing of production of sexual forms (allochronic isolation; Delmotte et al., 2002). In case of individuals sampled from the trees, the sampling protocol and winter conditions prove that all individuals have developed from holocyclic lineages on the trees (heterozygote deficit, high genetic and genotypic diversity, etc.).

Alternatively, the early colonisers might have come from a differentiated source of holocyclic aphids, either locally or more distant. However, it is not very likely that the early colonisers came from a distant source as data from Loxdale et al. (1993) suggest that in early spring long-distance migration is uncommon in this species. Much more promising is the assumption that the early colonisers arrived from earlier developing *P. padus* trees with subsequent earlier *R. padi* colonies surrounding the wheat field and not involved in the study (only a few trees could be included into the study for examination). The development of individual *P. padus* trees is known to vary considerable, e.g. in time of bud breaking or flowering (Leather, 1996). The development of *R. padi* is very closely related to its host, and therefore *R. padi* individuals from different trees might differ in the development of winged forms (Sherlock et al., 1986; Archetti & Leather, 2005). However, it is likely that - at least - later in the year, migrants from greater distances may have added to the aphid population substantially as described by Hardie (1993) and Hardie & Campbell (1998). A further explanation concerning the apparently missing of spatial genetic structure at the field scale may be related to sampling. Our very detailed sampling protocol, avoiding the use of more than one individual per colony and focussing on the characterisation of winged adults, may have contributed to the low number of asexual clones, too. Subsequently, the individuals, taken in the subplots D_1 to D_3, may not entirely represent the small-scale immigration from the winter to the summer hosts. The genetically determined winged aphids may have come from more distant locations later in the year (neither from the winter host nor from the surrounding crops; Loxdale et al., 1993).

It is surprising that the early colonisers were apparently not persistent over time, which may be related to weak adaptation to winter wheat. In aphids, narrow adaptation to host plants has been frequently found using molecular markers (e.g. Weber, 1985; DeBarro, 1995a, b; Figueroa et al., 2005) and other methods (e.g. physiological-based interactions; Tsumuki et al., 1989; Kazemi & Van Emben, 1992; Riedell et al., 1999). Similarly, both, Haack et al. (2000) and Vialatte et al. (2005) revealed high genetic differentiation between *S. avenae* populations from wild Poaceae and those from cereal crops. Individuals from the latter host source showed low genetic differentiation among populations unlike those from wild Poaceae. Studies concerning this topic are missing for *R. padi* with one exception: Simon & Hebert (1995) studied allozymes of Canadian populations of *R. padi* and found little polymorphism, when three out of 51 loci were tested. Moreover, little geographic differentiation was reported between populations from a single host category. But differences in gene frequency were shown between subpopulations from the winter host (*Prunus virginiana* L.) and the summer host (e.g. gramineous plants), whereas the heterozygosity was substantially reduced on the summer hosts. The authors concluded a dilution effect concerning the genotypic diversity from the winter host, because “new” immigrants may have arrived from other sources (i.e. far from the south; Simon & Hebert, 1995). Related to *S. avenae, R. padi* may consist of more or less divergent groups with different host plant adaptations (i.e. one group may be largely restricted to cereals - as indicated by late colonisers; whereas the other group may be associated with wild grasses - as indicated by early colonisers). However, the mechanism behind is unknown (Simon & Hebert, 1995; Lushai et al., 2002).

The third main cluster (Fig. 5) consists of populations from *P. padus* trees no. 6 and 9, which differed significantly from all other samples (e.g. 16% of genetic differentiation between the trees no. 5 and 6) and therefore do not seem to contribute to the wheat colonisation in Hiddestorf and Isernhagen. The reason for that is not clear. Strong genetic heterogeneity in spring populations of *R. padi* individuals on *P. padus* trees was revealed at the local scale in the study area. However, this would be in contradiction to Delmotte et al. (2002), who found significant differentiation between spring populations of the same host - parasite complex on a scale of 500 to 1,000 km. A further explanation could be related to differences in development of the trees, which would be consistent to observations (as reported above; Leather, 1996). The *R. padi* individuals on tree no. 5 might have developed later than those on tree no. 6 and 9. We observed differences in the physiological development between the trees, which then influenced the development of winged *R. padi* (data not shown). Subsequently, we may have sampled individuals from populations at the end of their development of tree no. 6 and 9 (shortly before the total population crash on the trees), whereas individuals from tree no. 5 were sampled in the middle of population development (allowing more winged aphids to be produced some days later). Therefore, the earlier developing winged aphids (e.g. from tree no. 6 and 9) were replaced by later colonisers (e.g. originating from tree no. 5). Moreover, climatic influences (wind direction or washing-up by rain) may have changed between main periods of winged aphid development on the trees. Effect of natural forces such as rain and wind dislodge aphids to some degree, as do acts of mechanical brushing or raking (Bailey et al., 1995; Mann et al., 1995). Changes in wind direction from east to west winds, after the main bulk of winged aphids have left tree no. 6 and 9, might have favoured the contribution of individuals originating from tree no. 5 to settle into the wheat subplots. However, indications from analyses of meteorological parameters (data not shown) were not straightforward concerning wind or rain effects on tree populations. In small-scale field experiments, we have examined three trees for the numbers of *R. padi*.

Including larger numbers of trees from surroundings might have clarified the situation in a better way. Subsequently, more detailed information of dilution effects from winter to summer hosts might be possible. However, due to limited financial support, only a few individuals (i.e. from one vegetation period) were genetically assessed, possibly biasing the results.

Conclusions

Our study suggest that density dependence on large- and small-scales may regulate population growth, so that dispersal processes of host-alternating aphid species in the agro-ecosystem cannot be studied at small-scale field level alone, but have to be examined at the landscape scale as well. On small-scale levels, strong influences of *R. padi* were observed only in the first 12 meters from winter hosts. For other cereal aphid species or predator units, no such direct effects were found in small- or large-scale trials. The possible distribution patterns were lost in the noise of population fluctuations in the fields on each evaluation day. Unfortunately, the genotypic characterisation of individual *R. padi* could not completely highlight the locally contribution of the numbers of individual aphids originating from the winter hosts nearby and landing in closest proximity in the summer host for subsequent early population build-up. The genotypic composition of *R. padi* wheat colonizers did not differ between the edge and the more inside part of the field. There was apparently no spatial genetic structure at the field scale (which is in congruence to *S. avenae*, J.C. Simon, unpublished data). More follow-up studies in the study area are needed to clarify the contribution of primary hosts (after holocyclic hibernation) on the immigration and early population development in winter cereals.

Acknowledgements

We thank the farmers who allowed us to work in their fields, and T. Michel for help with the field evaluation. We are especially grateful to members of plant protection services for technical support. The study was financially supported by the Bundesministerium für Verbraucherschutz, Ernährung und Landwirtschaft, Germany (Federal Ministry of Food, Agriculture, and Consumer Protection; project code: 01HS083).

Chapter 5: Attractiveness and host suitability of winter wheat cultivars for cereal aphids (Hemiptera: Aphididae)

A. Michael KLÜKEN, Hans-Michael POEHLING & Bernhard HAU

Institut für Pflanzenkrankheiten und Pflanzenschutz (IPP), Leibniz Universität Hannover, Herrenhäuser Str. 2, 30419 Hannover, Deutschland

Abstract

Cereal aphids (Hemiptera: Aphididae) yearly infest winter wheat, occasionally leading to significant yield reduction when biotic and abiotic factors are optimal for rapid population growth. Within the host plant complex, influences of eight winter wheat cultivars on the development of cereal aphids were studied in a two-year project focussing on the most important species in terms of yield reduction. Therefore, antibiosis, aphid settlement behaviour, and the relation of infestation and yield loss were evaluated by observing the development of isolated aphids within clip cages, by estimating the natural infestation of alatae morphs, and by measuring yield parameters. The cultivar Hybnos I significantly reduced numbers of offspring of caged *M. dirhodum* and *S. avenae* at seedling stages (growth stage 13, in laboratory). During later stages such as shooting and flowering (in laboratory and fields, respectively), no significant differences in aphid development were observed among cultivars. During the period of immigration, alatae of *R. padi* and *S. avenae* preferred to settle on Batis (on May 25th) and Tommi (on June 10th), respectively. At other evaluations, no significant differences were found among the cultivars and aphid species. Crop yield (kg per ha) and hectolitre weight (g per ccm) were significantly reduced with increasing aphid density in all cultivars, with highest reductions in cultivar Dekan. In contrast, only some cultivars showed significant reductions in protein content with increasing aphid density, while others were tolerant and not reacting to aphid infestation with respect to protein content. In summary, no striking indications for different aphid susceptibility could be found in the set of cultivars tested, even though they differed strongly in attributes such as colour, height, yield potential and development pattern. The results are discussed in terms of cultivar selection to improve sustainability of integrated pest management and the importance of cultivar features for aphid migration and population models.

Introduction

Aphids annually infest winter wheat, *Triticum aestivum* L., in central Europe, but only occasionally densities leading to strong yield losses were reached (Basedow et al., 1994). Three to four aphid species usually occur in cereal crops in western Europe with increasing densities from late spring onwards, among which *Sitobion avenae* Fabr. and *Metopolophium dirhodum* Walk. are the most important in terms of yield losses (Basedow et al., 1994; Havlickova, 1997).

In central Europe, winter wheat is the most widely grown crop (FAO, 2008) and about 50% of the crops are annually treated with insecticides (European agricultural statistics, 2008). These regular treatments are often prophylactic, because farmers spray without considering economic thresholds for aphids. In the frame of a larger study aiming to forecast early season dynamics, important factors for aphid migration and early population build-up in winter wheat were analysed. In accordance with previous studies, pronounced fluctuations in aphid dynamics even between spatially related sampling sites occurred, which could not be linked to abiotic and/or biotic factors, when evaluated with the population model GETLAUS01 (Gosselke et al., 2001). This model described à posteriori the population dynamics of the three most important cereal aphids (including yield losses) based on several factors (e.g. weather data, aphid antagonists, etc.). We hypothesized that the different winter wheat varieties cultivated by farmers could be partly responsible for these observations. Thus, the main objective of our work was to assess possible differences in the attractiveness and host suitability of winter wheat cultivars. The idea to focus on aphid resistance and tolerance of cultivars was based on former observations that even low to moderately high levels of plant resistance can prevent cereal aphids from reaching economic damage levels (Caillaud et al., 1995; Weng et al., 2005). Antibiosis influencing development, survival or reproduction rates was found to be the most effective factor in reducing high population build-up (Kazemi & VanEmden, 1992; Escobar et al., 1999). Moreover, slowing down population development by antibiosis can improve efficiency of natural enemies, if no negative effects occur via the food chain (Hesler & Tharp, 2005).

Over the last 20 years, several research projects have dealt with resistance and tolerance in cereal cultivars. First experiments with ancestors of wheat and barley have shown promising results in terms of aphid reduction (Geissler et al., 1989; Moharramipour et al., 1997; Jimenez-Martinez et al., 2004) and, actually, some winter barley cultivars with partial resistance in seedlings and juvenile plants were developed and accepted by farmers (Friedt et al., 2003; Migui & Lamb, 2004). However, screening of winter wheat accessions for antibiosis, antixenosis, or tolerance to cereal aphids revealed low levels of resistance (Dedryver & di Pietro, 1986; Havlickova, 2001; Migui & Lamb, 2003). Most often, winter wheat cultivars showed effective levels of resistance, in particular not for typical central European cereal aphid species but more towards *Schizaphis graminum* Rondani and *Diuraphis noxia* Mordvilko (Havlickova, 1993; Gianoli & Niemeyer, 1998; Berzonsky et al., 2003). Yearly, several new winter wheat cultivars are licensed on the market but so far none of them was assessed for resistance characteristics towards most important cereal pests, i.e. *S. avenae* and *M. dirhodum* (Havlickova, 2001; Bundessortenamt, 2006).

Thus, we assessed the attractiveness and the host suitability of eight actually grown winter wheat cultivars for cereal aphids. Therefore we studied antibiosis effects in caging experiments at different growth stages of the cultivars, aphid settlement behaviour in field populations, and we calculated infestation loss relations. Finally, the importance of those suitability parameters was scrutinized in migration and population models.

Materials and Methods

Experimental design

Winter wheat cultivars were sown in plots at two locations: the experimental station of the Leibniz Universität Hannover in Ruthe in 2004 and at the campus fields of Hannover-Herrenhausen in 2004 and 2005. At both locations, each field was divided into two parts: untreated plots with the size of 6 × 10 m (2004) or 2 × 4 m (2005) and treated plots with the size of 4 × 10 m (2004) sprayed with Pirimor® (0.2 kg per ha) for aphid control at the end of flowering (growth stage (GS) 69, Tottman & Broad, 1987), in order to compare yield losses. The plots were arranged in a completely randomised block design with five replications per cultivar. All agronomic practices were uniformly carried out according to farmers’ practices in the study area, which, among others, implied two fungicide treatments. The plots in Ruthe were harvested by means of a small combined harvester on August 3rd 2005 at grain moisture content below 13%.

Winter wheat cultivars

Tab. 1 summarises the eight winter wheat cultivars used in the study. The cultivars chosen are actually important in practice, covering a broad range of genotypes and qualities (Bundessortenamt, 2006; F. Lenz, D. Rentel, F.-J. Strube, pers. comm.). Moreover, they were cultivated on those fields that we used to collect data for modelling migration and early population dynamics of cereal aphids. The “cultivar” Strube-type 93-11-21 (so-called ST-93), which has no official approval so far, was included in this study, because aphids showed a reduced performance on this cultivar in preliminary tests. This cultivar also differed by its numerous small hairs on leaves and ears from the other cultivars (J.-F. Strube, pers. comm.).

Tab. 1: Quality attributes of cultivars used in the experiments according to Bundessortenamt (2006; TGW = thousand grain weight).

No.	Cultivar	Leaf colour (visual grading)	TGW [g]	Germination [%]	Quality
1	Tommi	Yellow green	52.8	96	A
2	ST-93	Light green	45	96	B4/C
3	Hybnos I	Blue green	61	96	C
4	Akratos	Grey green	50	98	A
5	Dekan	Dark green	49	98	B
6	Batis	Yellow green	56	96	A
7	Certo	Blue green	52.5	96	C
8	Ritmo	Grey green	46.6	96	B

Cereal aphids

The two cereal aphid species used in clip cage experiments (antibiosis), *S. avenae* and *M. dirhodum*, were sampled in 2004 from fields within the region of Hannover and one clone of each species (*S. avenae* - “green-strain”, *M. dirhodum* - “white-strain”) was reared in climate chambers (20° ±1°C, 60-70% relative humidity, 10/14 hours l/d) until further use for antibiosis experiments. Cage experiments were started with synchronized adults. For evaluation of each experiment, aphids were grouped according to different instars and morphs: L1/L2-, L3- and L4-larvae, larvae with visible wing buds, adults without wings as apterae, and winged adults as alatae.

Antibiosis experiments

Two antibiosis experiments were carried out under laboratory conditions and one in untreated field plots using aphid in clip cages. For the first experiments, four young wheat plants of each cultivar grown in the field plots were transplanted after vernalisation stimulus into 12 cm pots (substrate: Fruhstorfer Erde, type P) at the end of November and in the middle of February. Plants were further cultivated in greenhouses under controlled conditions (20° ±1°C, 50 to 60% relative humidity, extra light during days < 25 k lux natural radiation: 10/14 l/d) until GS stages 13 and 30 were reached. At each of these stages, fifteen clip cages per cultivar and aphid species (one cage per pot), each containing two apterous adults, were caged for seven days. Moreover, cages with aphids were established in the untreated field plots at the middle of flowering (three cages per plot). Two apterous adults of *S. avenae* were caged onto the ears in tissue-bags (mesh-type: PA-132/40, Franz Eckert, Germany), whereas two apterous adults of *M. dirhodum* were caged onto the flag leaf, due to the different feeding behaviour (Niehoff & Stäblein, 1998). After seven days, cages together with leaves or ears were removed without opening, immediately frozen, and stored at -20°C until aphid counting and sorting took place in the laboratory.

Tab. 2: Plant growth stages and numbers of tillers evaluated per cultivar (five replications per cultivar) to determine aphid settlement behaviour (field trial Ruthe in 2005).

Date of evaluation	Growth stage	No. of sampling points per plots	No. of tillers per sampling point	Sum of tillers per plot evaluated
May 11th	30-32	4	15	300
May 25th	39-51	4	15	300
June 10th	55-61	3	15	225
June 16th	61-69	3	9	135
June 29th	73-78	4	6	120
July 7th	78-83	4	4	80
July 18th	81-85	4	5	100

Settlement experiments

Untreated plots were visually inspected to determine the settlement of cereal aphids (including *Rhopalosiphum padi* L.) in 2005 and 2006 (Tab. 2). Due to low natural aphid population level in the study area, 35 plants from laboratory rearing units, infested with approximately 50 winged *S. avenae* and *M. dirhodum*, were placed at least eight m away from field plot borders from the middle of May till beginning of June. Details of the sampling procedure are listed in Tab. 2. The data obtained were converted to number of aphids per square meter according to the number of tillers per square meter.

Infestation loss relation experiments

In 2005, infestation loss relationships were determined from field plots in Ruthe. For that purpose, different crop parameters (i.e. plant height [cm], crop density [numbers of plants per m²], crop growth stages) and yield parameters (i.e. crude protein content [% dry weight], crop yield [kg per ha], hectolitre weight [g per ccm], thousand grain weights [g]) were obtained from treated and untreated plots for comparison. The crude protein content was determined using the method of Kjeldahl (ICC, 2008). The factor 5.7 served to transform the nitrogen into the crude protein content in case of nutritional wheat (S. Seling, pers. comm.). Instead of visual counts in treated plots, the model GETLAUS01 (Gosselke et al., 2001) was used to determine the infestation level after the insecticide treatment. Therefore, the simulation of aphid population dynamics was adjusted according to the infestation level in the untreated plots separately for each cultivar (parameter optimisation). According to these datasets, the model was run again for each cultivar in the treated plots with basic efficiency data for insecticide treatment with Pirimor® on June 24th, available in the model's user interface. The aphid index (aphid days per m^2), which represents the area under the population curve, was used for subsequent calculations of infestation loss relation.

Statistical analyses

Data obtained from antibiosis experiments were used to detect differences among and within cultivars and locations using Tukey-Kramer test (proc glm, all pairs, program SAS) and T-test (lsmeans, program SAS), respectively (SAS, 2008). Repeated measurement analysis and Tukey-Kramer Test (proc glm, program SAS) were performed on datasets obtained from settlement behaviour experiments. If significant interactions between evaluation time (dates) and cultivars were detected, the comparison among cultivars was performed separately on each date. To better meet the assumption of a normal distribution in case of count data, the square root ($\sqrt{(x+0.0001)}$) transformation was performed. In case of datasets from infestation loss relation experiments, linear regression analyses (proc reg, program SAS) between aphid index and different yield parameters were calculated on pooled data per cultivar (i.e. treated and untreated plots) to estimate the tolerance level of a given cultivar.

Results

Antibiosis experiments

The first antibiosis experiment under controlled conditions in the greenhouse (at GS 13) showed no significant differences among cultivars (Fig. 1 and 2), except for cultivar Hybnos I. No reproduction of *S. avenae* occurred on cultivar Hybnos I, whereas on all other cultivars all instars were found (Fig. 1). Similarly, for *M. dirhodum*, comparatively low numbers of offspring (6 and 0.5 L1/L2- and L3-larvae, respectively) were obtained on cultivar Hybnos I

(Fig. 2). The numbers of L1/L2- and L3-larvae were significantly lower on Hybnos I compared to the other cultivars, which did not differ in the number of other aphid instars (Fig. 2).

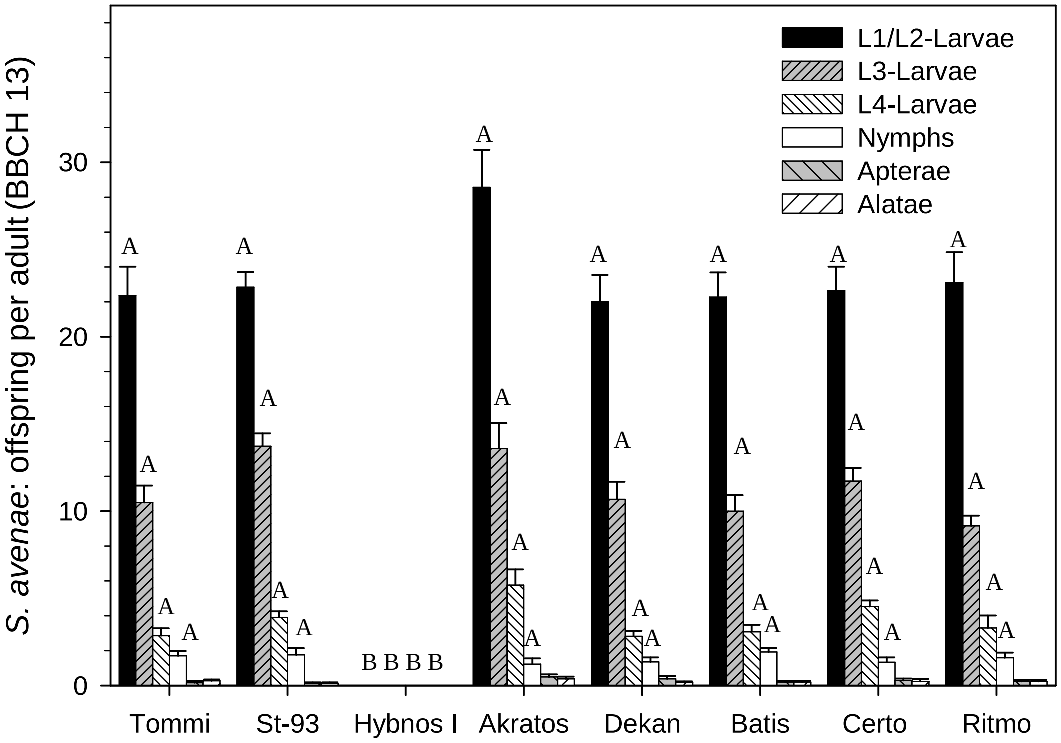


Fig. 1: Mean number (±SE) of offspring (grouped into developing instars) originated from single apterous adults of *Sitobion avenae* caged on eight winter wheat cultivars at growth-stage 13. Cultivars followed by the same letter do not differ significantly (significant differences only in larval-stages: Tukey-Kramer test, p=0.05, *n*=15).

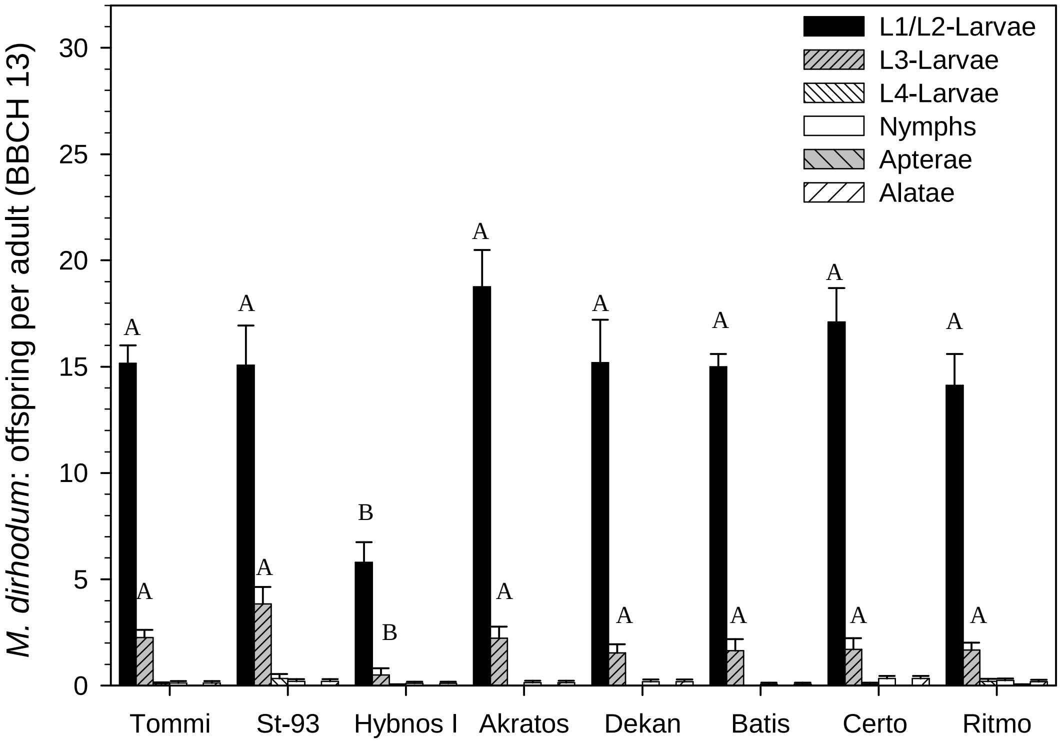


Fig. 2: Mean number (±SE) of offspring (grouped into developing instars) originated from single apterous adults of *Metopolophium dirhodum* caged on eight winter wheat cultivars at growth-stage 13. Cultivars followed by the same letter do not differ significantly (significant differences only in L1/L2- and L3-larvae: Tukey-Kramer test, p=0.05, *n*=15).

The second experiment at the shooting stage of the cultivars (GS 30-32) yielded higher overall mean aphid numbers (Fig. 3 and 4) than at GS 13. No significant differences in either instars of both cereal aphids were found among cultivars, except in L3-larvae of *M. dirhodum* (Fig. 3 and 4). Significantly more L3-larvae were found on cultivar Tommi compared to Ritmo.

Caged aphids in the field (GS 65-69) developed more slowly (mean daytime temperatures: 19.3°C) compared to laboratory conditions. Moreover, mean numbers of offspring varied more broadly and the standard errors were more pronounced. A whole population cycle of the offspring was rarely observed within the cages for either species. No significant differences among cultivars and aphid species were obtained (data not shown).

The caging experiments were repeated in 2006 and the results showed the same trend. Again, no significant differences in aphid populations were found among the cultivars tested (except at GS 13, no aphid developed on cultivar Hybnos I).

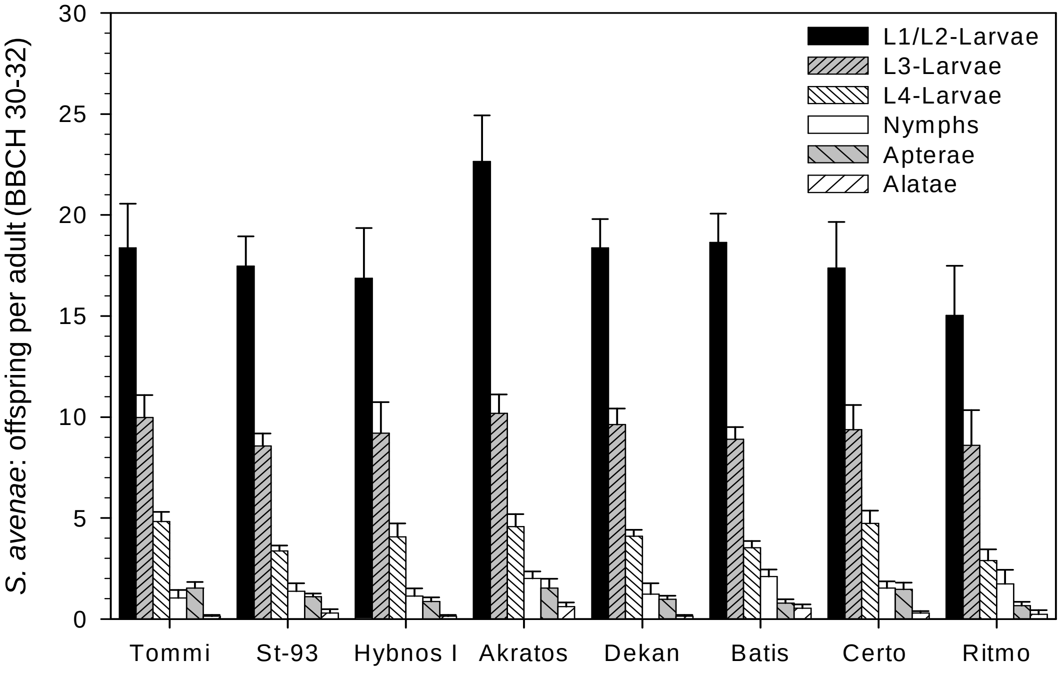


Fig. 3: Mean number (±SE) of offspring (grouped into developing instars) originated from single apterous adults of *Sitobion avenae* caged on eight winter wheat cultivars at growth-stage 30-32 (no significant differences: Tukey-Kramer test, p=0.05, *n*=15).

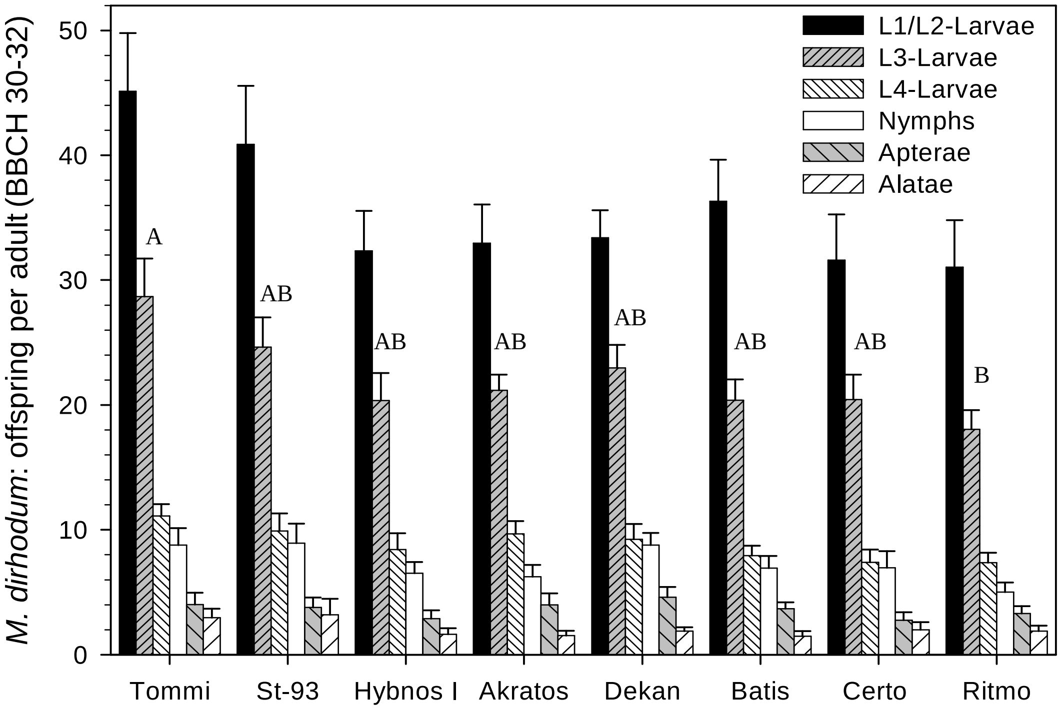


Fig. 4: Mean number (±SE) of offspring (grouped into developing instars) originated from single apterous adults of *Metopolophium dirhodum* caged on eight winter wheat cultivars at growth-stage 30-32. Cultivars followed by the same letter do not differ significantly (significant differences only in L3-larvae: Tukey-Kramer test, p=0.05, *n*=15).

Settlement experiments

The natural settlement of winged cereal aphids was evaluated in the untreated plots at Ruthe in 2005 (Tab. 2). The most frequent naturally immigrating species were *R. padi*, first found on May 25th, followed by *M. dirhodum* and *S. avenae* on the subsequent evaluation dates after the release of alatae of these species (data not shown). On most cultivars, aphid population peaked at early July (GS 77/83). The time of population crash differed among the cultivars according to their ripening stage. Cultivar Akratos entered the harvest stage first and cultivar Hybnos I last (data not shown).

For the analysis of the immigration period we focussed on aphid numbers on May 25th, June 10th and 16th. The mean number of all *M. dirhodum* and *S. avenae* did not differ significantly among the cultivars on any evaluation date (data not shown). However, for all *R. padi* several significant differences among the cultivars were found (data not shown).

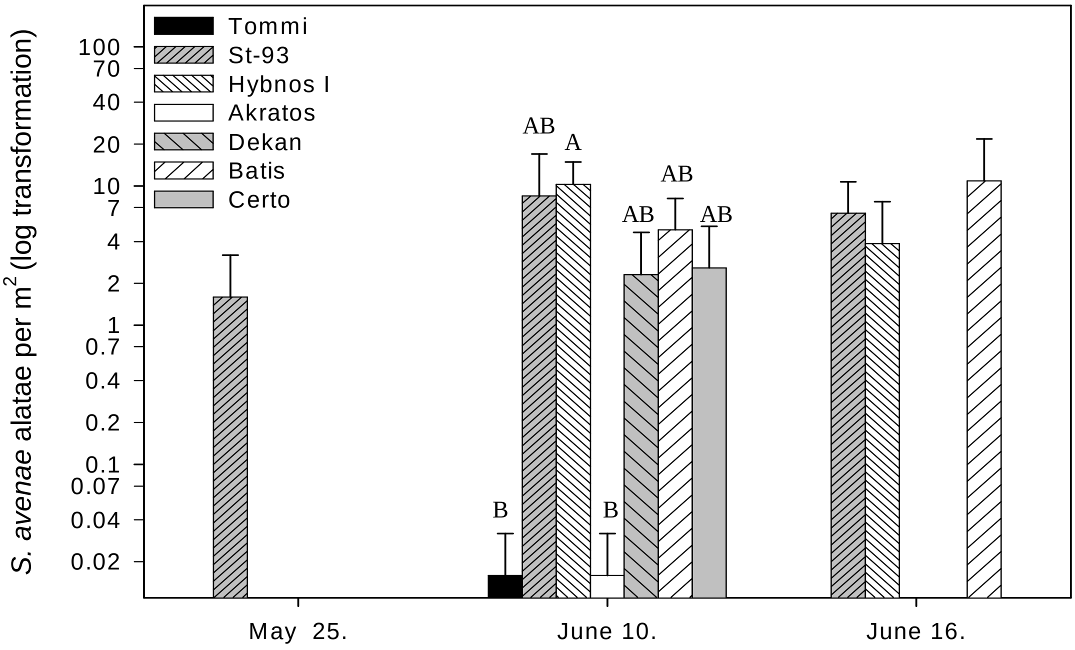


Fig. 5: Mean densities of winged *Sitobion avenae* (±SE) per m² on seven cultivars at three evaluation times. The count data (per tiller) were converted into individuals per m² according to the crop stands (tillers per m²). Cultivars followed by the same letter do not differ significantly (repeated measurement analysis and Tukey-test on each evaluation time, $p=0.05$).

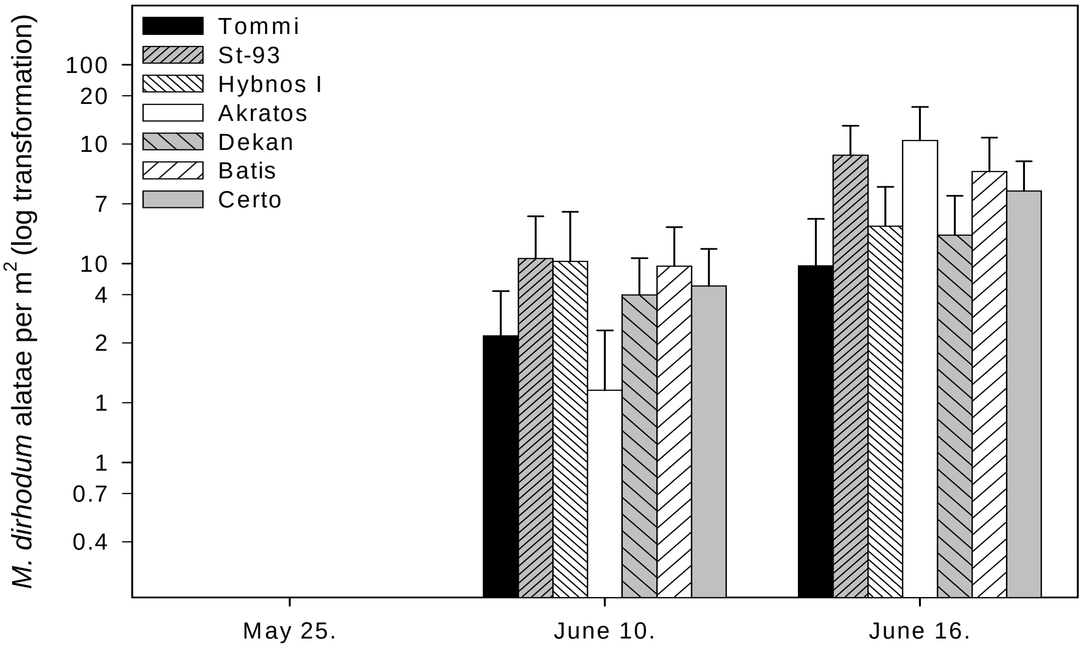


Fig. 6: Mean densities of winged *Metopolophium dirhodum* (±SE) per m² on seven cultivars at three evaluation times. The count data (per tiller) were converted into individuals per m² according to the crop stands (tillers per m²). No significant differences among cultivars were detected according to repeated measurement analysis and Tukey-test on each evaluation time (p=0.05).

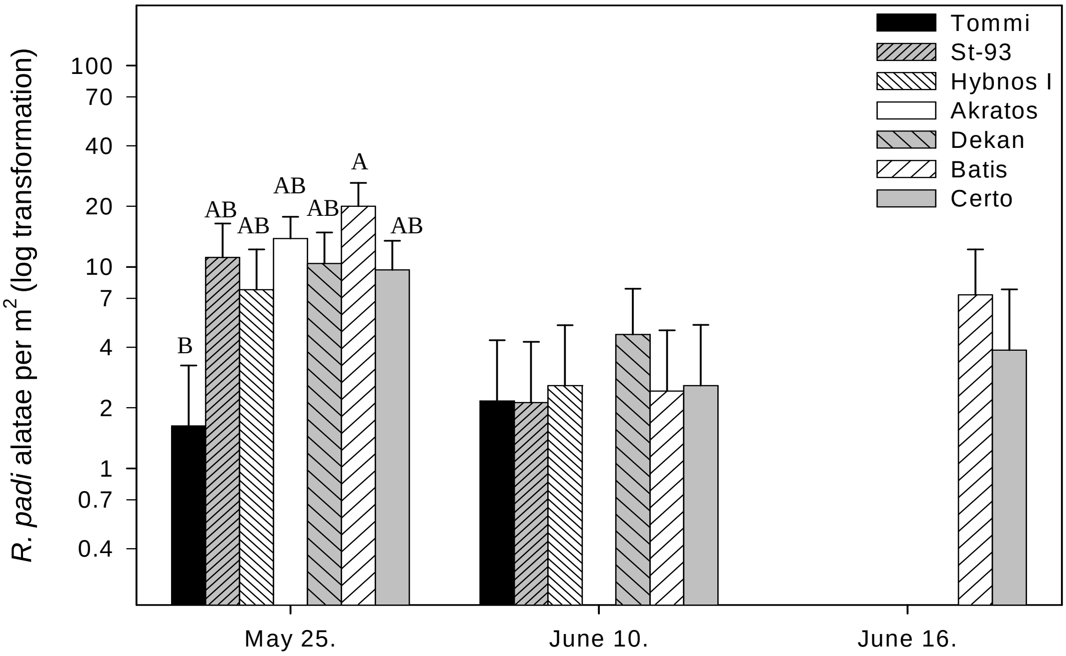


Fig. 7: Mean densities of winged *Rhopalosiphum padi* (±SE) per m² on seven cultivars at three evaluation times. The count data (per tiller) were converted into individuals per m² according to the crop stands (tillers per m²). Cultivars followed by the same letter do not differ significantly (repeated measurement analysis and Tukey-test on each evaluation time, p=0.05).

Since the pattern of aphid settlement during the immigration period should indicate cultivar-specific differences in attractiveness, we separately compared the different aphid instars. The most striking indicator for immigration intensity should be the number of alatae (Fig. 5 to 7). On May 25th, alatae of *S. avenae* were only found on St-93, but due to the overall low numbers that event was not statistically significant. On the following date, June 10th, significantly higher numbers of winged *S. avenae* settled on Hybnos I compared to cultivars Tommi and Akratos. No alatae of *M. dirhodum* were observed on the first evaluation date. On the following sampling dates, no significant differences in numbers of alatae were found among the cultivars (Fig. 6). On May 25th, significantly more winged *R. padi* were found on cultivar Batis than on cultivar Tommi (Fig. 7). Concerning the other evaluation times, no significant differences were found among the cultivars.

The observations of aphid immigration in field plots were repeated in 2006 focussing on *S. avenae* and *M. dirhodum*. The results showed the same trend and no significant differences in alatae numbers of either species were found among the cultivars.

Tab. 3: Coefficients of determination R² and slopes *b* of linear regression lines between aphid index (aphid days per m^2) and three yield parameters (i.e. crop yield [kg per ha], hectolitre weight [g per ccm] and protein content [% of dry weight]) of seven cultivars (calculated per cultivar on pooled data from treated and untreated plots). Sample size per yield parameter and cultivar is ten.

	Crop yield		Hectolitre weight		Protein content	
Cultivar	R²	*b*	R²	*b*	R²	*b*
Tommi	0.65	-1.0 ±0.04*	0.94	-10.4 ±1.3*	0.21	-0.4 ±0.4
St-93	0.83	-2.7 ±0.06*	0.92	-15.2 ±2.2*	0.13	-1.2 ±1.5
Hybnos I	0.72	-1.0 ±0.03*	0.78	-9.2 ±2.5*	0.50	-2.1 ±1.1*
Akratos	0.79	-1.2 ±0.03*	0.85	-12.0 ±2.5*	0.25	-0.9 ±0.8
Dekan	0.81	-3.5 ±0.08*	0.80	-31.6 ±8.0*	0.65	-4.1 ±1.5*
Batis	0.98	-0.8 ±0.01*	0.67	-12.8 ±2.6*	0.36	-1.3 ±0.8
Certo	0.86	-0.8 ±0.02*	0.73	-9.7 ±2.9*	0.63	-0.3 ±0.1*

* Asterisks indicate significant (p=0.05) differences from zero for the slope (*b*=0).

Infestation loss relation experiments

In 2005, different crop parameters were analysed to determine the effect of aphid infestation. The crop density (in tillers per m^2) and the length of tillers differed among cultivars but did not show any relation to aphid infestation when insecticide treated (low aphid density) and untreated (high aphid density) plots were compared. In contrast, several yield parameters significantly differed between treated and untreated plots for a given cultivar. Real crop yield and hectolitre weight losses of cultivars ranged from 2.1% in cultivar Akratos to 18.4% in cultivar Dekan and from 5.2% in cultivar Batis to 10.0% in cultivar Tommi, respectively (data not shown). The linear regression analyses between aphid index and yield parameters showed varying results for both, cultivars and yield parameters. With increasing aphid density, crop yields and hectolitre weights were significantly ($p = 0.05$) reduced in all cultivars, with strongest decrease in cultivar Dekan ($R^2 = 0.81$, $b = -3.5$ and $R^2 = 0.80$, $b = -31.6$, respectively; Tab. 3). The lowest protein contents were obtained in the untreated plots of all cultivars, but differences were not pronounced. Subsequently, protein contents were significantly reduced only in cultivars Hybnos I ($R^2 = 0.50$, $b = -2.1$), Dekan ($R^2 = 0.65$, $b = -4.1$), and Certo ($R^2 = 0.63$, $b = -0.3$; Tab. 3).

Discussion

Antibiosis experiments

The most striking results from our antibiosis studies with young seedlings were the strongly reduced performances of *S. avenae* and *M. dirhodum* on cultivar Hybnos I. However, these antibiosis effects were not consistent since in caging experiments at later growth stages, no significant differences among the cultivars were observed. The different relative performance of aphids on juvenile and adult plants has been reported before (Kuo-Sell, 1993; Migui & Lamb, 2004). Obviously, the cultivar Hybnos I is of very low host quality for cereal aphids only during its seedling stage with a main effect in preventing deposition of offspring. Possibly, morphological criteria and nutritional quality are responsible for that effect (Spiller & Llewellyn, 1987; Migui & Lamb, 2004). About the possible long term consequences of the much lower attractiveness of the cultivar Hybnos I during seedling stage in terms of offspring deposition of cereal aphids, we can only conjecture. The main effect of varieties (just like Hybnos I) can be a reduced establishment and growth of the initiated *S. avenae* population after immigration in autumn. The amount of autumn infestations of winter wheat strongly depends on the synchronisation of aphid autumn migration intensity and crop development. Due to the late sowing of wheat compared to barley in recent years in central Europe, the migration peak of *S. avenae* and *R. padi* has already passed when attractive winter wheat seedlings emerge, but this situation may change with more frequent periods of mild winters as predicted (H. Friesland, pers. comm.). Moreover, such a resistance effect, limited to the seedling stage, can help to slow down the population build-up - in particular - of *S. avenae* and to a limited extent of *M. dirhodum* after early immigration during the spring period. In several simulation models calculating the effects of wintertime on cereal aphid populations (Kleinhenz, 1994; own calculations, data not shown), it was found that the initial population level after winter is of major importance for the risk of cereal aphid outbreaks in summer. Nevertheless, in later growth stages of wheat plants, no resistant effects were observed in our experimental setups. Possibly, strong mass transfers of nutrients, which occur during the shooting and flowering, leading to the best nutritional status for aphids, may have compensated the resistance effects of younger growth stages. Moreover, the abiotic conditions (especially temperature) become more suitable to the aphid development. The findings are supported by Watt (1979), who found that a wheat plant's suitability for aphid growth and reproduction varies markedly with its growth stages and may affect the likelihood of outbreaks causing economic damage. Further experiments concerning the attractiveness and host plant suitability with the cultivar Hybnos I should focus on these circumstances.

Settlement experiments

Despite of a high sample size, no cereal aphids were found on the first evaluation day in 2005 (May 11th). After release of alatae of *M. dirhodum* and *S. avenae,* however, high numbers of alatae were recaptured in the field plots to compare distribution pattern of cultivars. With the evaluation of alatae as indicator for attractiveness - assuming that most of alatae during that early period were immigrants - significant differences in attractiveness of cultivars (Fig. 5, 6 and 7) were observed. About the mechanism behind, however, we can only speculate. Important signals triggering early host plant selection by aphids are colour (host plant and its contrast with environment), surface morphology of the target as well as odours emitted from plants. Particularly, we observed the variation in the greenish leaf colour of cultivars. In several studies, these differences were linked to different levels of aphid settlement and subsequent development (Tsumuki et al., 1989; Dixon, 1998). However, our visually achieved grading of leaf colour was not detailed enough to allow any correlation with the settlement data.

It has long been argued that variation in the morphology and chemistry of host species can act as an important selective agent for herbivores (Thompson, 1988). Hairs, epicuticular excrescences, waxes and colour attributes have often been perceived as important factors for aphid development (Dixon, 1998). Nevertheless, this relation is not compulsory (Fraser & Grime, 1999), because the cultivar St-93, for example, which exhibits high numbers of hairs, did not show a reduced aphid development in the antibiosis experiments. Furthermore, our settlement behaviour experiments did not indicate special preferences of colour or texture attributes for the cultivars tested, even though, the surface attributes differed among the cultivars while the immigrating aphids were choosing the best host plant for settlement. Whether a plant is accepted or rejected by a winged migrant, depends on the completion of a behavioural pattern, in which not only the plant's surface attributes but also the volatile organic compounds (VOC´s), intercellular compounds such as polysaccharides and phloem constituents are tested by the settling aphid in sequence (Blackman, 1990). The host plant quality in terms of nutritional compounds or plant secondary metabolites interfering with aphid feeding intensity of food conversion efficiency plays an important role for cereal aphid population development. Cultivar-specific levels of certain free amino acids (i.e. arginine, threonine, valine), enriched phenolics or higher Hydroxamin levels were found to interfere with aphid performance on cereals (Sandström, 2000). Concerning our results, we cannot provide sufficient data of cultivar-specific volatiles or intrinsic plant compounds relevant for aphid's decision process. However, early antibiotic or settlement behaviour effects played no significant role, since the differences in settlement intensity were later more or less completely compensated by propagation of the first established colonies (no significant differences in total numbers per m^2 on later growth stages of the winter wheat plants).

Following each single winged aphid, its settlement, and subsequent probing behaviour is not possible under field conditions. Thus, the results of settlement behaviour are more or less static "snap-shots" and cannot accurately distinguish antixenosis effects of cultivars. To comprehend the effects of antixenosis entirely, more detailed experiments are necessary, including choice experiments under laboratory conditions.

Infestation loss relation experiments

Both, the natural immigration and the release of winged aphids from rearing have led to high infestation levels in the field plots at very early stages of host plant development (starting in May). The resulting losses (crop and hectolitre yield losses) observed in the study agree with results of other studies in central Europe (Basedow et al., 1994; Niehoff & Stäblein, 1998). The regression analyses of pooled data (treated and untreated plots) indicated different tolerance levels of cultivar. With increasing aphid infestation, all cultivars showed significantly reduced crop yields and hectolitre weights (Tab. 3), but only cultivars Dekan and St-93 reacted more pronounced, i.e. not tolerant. Only a few significant protein content reductions were obtained with increasing aphid infestation. This means that several cultivars expressed pronounced levels of tolerance (concerning protein content), which is in accordance with Havlickova (1997) and Möwes et al. (1997). However, it is not obvious, why no stronger and consistent reactions of tested cultivars in all yield parameters were obtained with increasing aphid population levels, although the overall population level was very high.

According to our results, the cultivar Dekan reacted with strongest losses per aphid unit and can be ranked as the least tolerant cultivar. Interestingly, the cultivars reacted differently regarding the discriminative yield parameters with no continuous superiority of one cultivar within the collection (except cultivar Dekan). Tolerance seems to be a promising breeding aim with lower risk to be easily overcome by herbivore adaptation (selection) (Hesler & Tharp, 2005). Another variable that was found to be correlated with landscape structure was farming practice. However, we found no evidence for the impact of insecticides on genotypic diversity and within seasonal dynamics of genotypic composition at the field scale. Furthermore, no evidence was found for the presence of insecticide resistant strains as found in other aphids (*e.g.* the peach-potato aphid, *Myzus persicae* Sulzer, Foster et al., 2004). Resistant strains should lead to a lower genotypic diversity in intensive sprayed regions (structured population) although in fact the opposite was observed in the present study on *S. avenae*. On the other hand, we cannot exclude the possibility that ‘clonal copies’ have been reduced at the regional scale by frequent use of insecticides at different locations.

One explanation for the difference between genotypic diversity and homogenous aphid abundance between regions could have been the sampling method. To estimate abundance, all individuals on inspected tillers were counted, whereas for molecular analyses, single aphids were taken from different field plots independent to colony size on single plants. Therefore, frequently detected genotypes had already dispersed within and between fields, a behaviour which was earlier posited from field observations by Dean (1974).

The changes in genotypic diversity between years indicated that winter climate might outweigh the landscape effect in regions with frequent cold winters. If this is indeed so, the landscape effect might be best studied in regions with permanent mild winters to exclude this important variable.

Importance for population and migration models

According to our results, it seems that the attractiveness of wheat cultivars for winged aphids during spring immigration and following antibiosis reactions, are of minor importance as input variables for population and migration models, since they cannot explain the observed strong differences in aphid gradation between areas and years. Other factors like landscape structure, fertility of the soil and the ripening time of the host-plants (i.e. early or late maturing cultivars) may exert stronger effects on aphid population development and should be further checked as driving parameters for migration and populations models. Our study only showed certain differences in plant suitability, particularly in terms of offspring production intensity on young plants - a phenomenon that may influence aphid infestation levels in autumn and may be incorporated into models, which describe the population dynamics of cereal aphids before winter. Furthermore, environmental effects, such as plant nutrition or weather conditions that determine the growth pattern of the host plants, e.g. the duration of sensitive developmental phases, seem to be of major importance for aphid population dynamics and subsequent yield reactions. Differences among cultivars have been shown to be more or less marginal (Havlickova, 1997, 2001; Bundessortenamt, 2006). Thus, in accessing important factors in population and migration models, it seems that the factor cultivar is of minor importance.

Importance for integrated pest management

The future motivation to invest more in resistance or tolerance breeding in cereals is mainly influenced by economic circumstances. Winter wheat is the most widely grown crop in the study area, although the value per unit area (vegetation period) is low. If prices for wheat are decreasing (under a certain level) and more regionally narrow profit margins will be given, then farmers would rarely treat their crops, but risking yield losses (Rossberg et al., 2002; B. Freier, B. Hardeweg, H. Waibel, pers. comm.). As consequence, resistance and tolerance to aphids may become more interesting for plant breeders and farmers (Smith et al., 2004). Complementary strategies in an integrated pest management program against cereal aphids should ideally not only include more or less selective and well-timed chemical control, but also utilise plant resistance and tolerance. Combined with landscape management approaches to improve functional biodiversity, conservation biocontrol, etc., resistance and tolerance breeding could be an additional tool for a sustainable crop management in cereals, if no adverse impacts on aphid-specific predators or parasitoids will occur via the nutrition chain (Bosque-Perez et al., 2002).

In conclusion, the results clearly showed no superiority of any winter wheat cultivar concerning the attractiveness and host suitability for cereal aphids. No characteristic trait affecting the population level of cereal aphids was detected. Although the cultivars covered a broad range of genotypes and qualities, we assume that the genetic background of the prevailing material of currently winter wheat cultivars is rather narrow. Resistance effects of ancestors of wheat have been described (Hesler & Tharp, 2005; Migui & Lamb, 2004). Moreover, new resistant genes from *Aegilops neglecta* Req. ex Bertol. and *Triticum araraticum* Jakubz. expressing aphid antibiosis are available and can be used to develop multiple aphid resistance in winter wheat cultivars (Smith et al., 2004; Arzani et al., 2004).

We hope that future breeding lines will include new resources and enhance resistance and tolerance research as further key factor for sustainable wheat production.

Acknowledgements

The authors are especially grateful to T. Michel for practical assistance and S. Seling, Federal Research Institution for Alimentation and Food (Bundesforschungsanstalt für Ernährung und Lebensmittel, in Detmold), for the accurate determination of crude protein contents.

Chapter 6: Comparison of techniques to survey populations of cereal aphids (Hemiptera: Aphididae) in winter cereals during autumn and spring with special consideration of sample size

A. Michael KLÜKEN, Bernhard HAU, Inga KÖPKE & Hans-Michael POEHLING

Institute of Plant Diseases and Plant Protection (IPP), Leibniz Universität Hannover, Herrenhäuser Str. 2, 30419 Hannover, Germany;

Abstract

Cereal aphid populations (Hemiptera: Aphididae) in winter wheat and winter barley were evaluated in the autumn and early spring of two subsequent vegetation periods (2004/2005 and 2005/2006) by D-VAC mobile suction sampler, visual counts, and plant sampling in order to compare the efficiency of different cereal aphid survey techniques. Aerial populations of cereal aphids were additionally determined using yellow water traps and fixed suction traps at the field and regional scale over the course of several years. Plant sampling (i.e. collecting whole plants from fields for evaluation in laboratory) generally detected the highest numbers of instars per m² and enabled the most accurate aphid classifications while additionally permitting further laboratory analysis (e.g. immunosorbent assays). Visual counts (*in situ*) were most effective for producing quick, rough estimates of overall population density. D-VAC, which detected the lowest numbers of aphids/m^2, was the least effective technique and was determined to be unsuitable for cereal aphid monitoring in autumn crops. Coefficients of variation confirmed this trend for the three sampling techniques. In years with high population densities and/or small-scale (single-field) sampling, coefficients of variation were smallest with fixed suction traps. The minimum sample sizes required for estimation of aphid populations at different levels of precision (50%, 30%, 20%, and 5%) were determined using different calculation methods (Feng & Nowierski, 1992; Greenwood & Robinson, 2006) based on visual count data. The results of this study have important implications for the selection of appropriate techniques for surveying cereal aphid populations in winter wheat and winter barley in autumn and early spring.

Introduction

The aphids *Sitobion avenae* F. and *Rhopalosiphum padi* L. (Hemiptera: Aphididae) are the most abundant and devastating pests of winter wheat and winter barley in central Europe in autumn and early spring (Basedow et al., 1994). They cause direct damage to plants (as phloem feeders) and, more importantly, they are key vectors of viral diseases, such as barley yellow dwarf virus (BYDV). Mild winters can promote fast population growth and distribution of a large proportion of anholocyclic hibernating, virus-transmitting aphids. Yield losses in infested plants are determined by plant growth stage during aphid settlement (GS; Tottmann & Broad, 1987), plant resistance characteristics, virulence of virus strains and, in particular, by weather conditions controlling aphid survival, reproduction and intensity of secondary spread during autumn and early spring period (Huth & Lauenstein, 1991).

As chemical control is the only reliable way to minimise aphid damage in winter cereals, there is a high demand for adequate control thresholds. Proven and tested thresholds are available for late summer control (GS 69) of sucking damage (Rappaport & Freier, 2001). During this period in which aphids are less aggregated, visual counting to check for critical aphid densities is a simple, reliable, and well-accepted technique (Feng et al., 1993a, b). Nevertheless, economic injury levels used in autumn and early spring to reduce the risk of virus spread, that is, to estimate the aphid population levels necessitating intervention with insecticides, are very unreliable. Thresholds at these times are much lower than those used in late intervention situations. Considering the low thresholds during periods of overall low aphid densities, the choice of appropriate sampling techniques and sample sizes are issues of major importance (Binns & Bostanian, 1990; Feng et al., 1993a, b; Sutherland, 2006).

Since cereal aphid thresholds are derived from density-damage or density-yield loss relations, the efficacy of the sampling technique is a critical factor. An appropriate sampling technique must either detect all aphids on the plants or in a defined area, or it must have a known margin of relative estimation error (Sutherland, 2006). Ease of handling of the sampling technique is also critical: quick and simple determination of cereal aphid populations (and threshold levels) is important, especially if regional or decentralised decisions are to be taken at the field level by field advisers or farmers (Robert et al., 1988). In order to estimate the infection potential of virus vectors, the sampling technique must furthermore deliver live aphids from the fields, in high quantities, and suitable for laboratory analyses (e.g. immunosorbent assays).

Sample size is also important for the precision and validity of the sampling process (Mühlenberg, 1993; Jarosík et al., 2003; Sutherland, 2006). Sampling plans based on the estimated distribution of cereal aphids in the field are useful tools (Elliott et al., 2003). The level of precision of a method determines the required sample size. The greater the variability of results for a given sample size, the more subsamples needed. Fluctuation of measured values and hence of sample size is determined by the population density and distribution (aggregation) of a given species as well as by the accuracy of the sampling technique. The amount of samples needed is mainly determined by the distribution pattern (e.g. aggregation) and variation of aphid populations over time as well as by the target significance levels (Mühlenberg, 1993; Southwood & Henderson, 2000). However, sample size is always a compromise between technology and effort required in terms of tools, time, labour, and sensitivity. Several sequential sampling plans are available for cereal aphids in wheat from late spring or summer to harvest time (Boeve & Weiss, 1997; Elliott et al., 2003; Giles et al., 2003). In fields larger than 10 ha, 4×125 tillers are recommended as the minimum sample size to determine the infestation levels at the flowering stage of winter wheat (Freier et al., 1997b). The "counts per tiller" technique, i.e. careful visual evaluation of cereal aphids on a whole tiller, is widely accepted as the technique of choice during the vegetation period (from GS 31 on) in which the plants grow and the stems elongate (Dewar et al., 1982; Rappaport & Freier, 2001). In the vegetation period, this is a fast and effective technique of aphid population size estimation that also permits the collection of aphids for subsequent laboratory analysis. However, during the early growth stages in autumn and early spring, when aphids settle on the lower parts of the plant just above ground or in the heart of the plants, the choice of an appropriate sampling technique is much more difficult (U. Heimbach, P. Krüssel, P. Matthes, pers. comm.).

The main objective of the present study was therefore to compare the efficacy of three sampling techniques (visual counts, plant sampling, and D-VAC mobile vacuum sampling) used to estimate aphid populations in different cereal crops (winter wheat and winter barley) during different seasons (autumn and early spring). The efficiency of D-VAC sampling was additionally assessed in capture-recapture experiments (Southwood & Henderson, 2000). The efficacy of two techniques for estimation of winged aphid populations (fixed suction traps and yellow water traps) was also assessed. Moreover, different calculation methods and levels of precision were used to evaluate the importance of sample size with a focus on aphid populations developing on cereal crops in autumn and on winter wheat from spring to early milky stage.

Materials and Methods

Field sampling

These investigations were performed in winter wheat and winter barley fields in several regions of Germany over two subsequent vegetation periods (2004/2005 and 2005/2006; Tab. 1). Three techniques were used to estimate field populations of cereal aphids: (i) visual counts on plants (or tillers) in the field, (ii) plant sampling (whole plants were randomly selected, cut, and bagged in the field and examined for aphids in the laboratory), and (iii) D-VAC suction sampling: aphids were collected from plants using a modified Dietrich (D-VAC) vacuum suction sampler (Veenker & Ulber, 2004). One sampling unit (i.e. the smallest unit from which observations were taken) was defined as 50 to 60 plants (0.25 m^2) in autumn, and as 10 tillers in spring. Specified sample sizes therefore represent the number of sampling units. Sampling was performed weekly from crop emergence (GS 10) until the early milky stages (GS 71/73), except in winter (from January to the beginning of March). To minimise the effects of weather on sampling efficiency, all samples were taken simultaneously at each sampling date. 10 to 90 sampling units in the fields were randomly selected from a diagonal transect across the fields with margins of approx. 5 m to avoid repetitive sampling of the same plants in GS 11 to 29. In winter wheat, identical sampling methods were used after tiller elongation (GS 37/39), but the number of sampling units varied from 10 to 800 in order to analyse the effect of sample size on variability of aphid abundance.

Tab. 1: Datasets (i.e. case studies) from winter wheat and winter barley fields in different regions of Germany (sLS = southern Lower Saxony, RP = Rhineland Palatinate, nLS = northern Lower Saxony) used to compare sampling techniques.

Region	Location	Vegetation period	Crop
sLS	Isernhagen	2004/2005 2005/2006	Winter wheat & winter barley
sLS	Jeinsen	2004/2005 2005/2006	Winter wheat
sLS	Hiddestorf West	2004/2005 2005/2006	Winter barley & winter wheat
RP	Wörth	2004/2005	Winter barley & winter wheat
RP	Wahlbach	2004/2005	Winter wheat
nLS	Bensersiel	2004/2005 2005/2006	Winter barley & winter wheat
nLS	Carolinensiel	2004/2005 2005/2006	Winter barley & winter wheat

All arthropods (including cereal aphid antagonists) were identified to family or genus level, whereas aphids were identified to species level and classified as adult alatae, adult apterae, or larval instars. *R. padi* and the few *Rhopalosiphum maidis* L. found were not separated but pooled as the *R. padi* group. To convert sampled aphid numbers per square meter into numbers per plant or per tiller, the mean numbers of plants and tillers per square meter were determined for each field by counting the plants and tillers within a metal frame demarcating 0.25 m^2 (one sampling unit).

Visual counts

Cereal aphids on plants or tillers in each sampling unit were carefully counted, identified, and classified in the field (*in situ*). As long as no tillers were visible, whole plants (including hypocotyls and onsets of roots) in the sampling unit were visually inspected.

Plant sampling

Fifty or sixty winter wheat and winter barley plants, respectively, were randomly selected from each sampling unit, cut at root level, individually bagged, and stored in a cool bag. When they reached the laboratory, the plants were placed in cold storage at approx. 2°C until further analysis (counting, identification and classification of plant colonizing arthropods).

D-VAC sampling

The D-VAC device used in the present study is very similar in design and function to the mobile vacuum suction sampler described by Veenker (2000). The results of our study should therefore be comparable to those of other vacuum sampler studies (e.g. Dewar et al., 1982; Bothe & Heimbach, 1995; Holland, 1998). For sample collection, a 0.25 m^2 area (one sampling unit) was demarcated by a collection frame and vacuumed for 60 seconds with the D-VAC device (modified method of Southwood & Henderson, 2000; Veenker, 2000). All arthropods, soil and plant debris collected in the D-VAC net were transferred to a plastic bag and stored in a cool transport box. Upon arrival at the laboratory, they were deep frozen at -20°C until later analysis.

The efficacy of D-VAC sampling was evaluated in release-recapture experiments (five repetitions) in plots of winter wheat (cultivar: Tommi, GS 21-25) at the experimental station of Leibniz Universität Hannover in early spring 2005/2006. At each repetition, five collection frames were pressed three to five cm into the soil and vacuumed cleaned of any plant material or surface dwelling insects during a three-minute suction period. Afterwards, defined numbers of synchronised *S. avenae* (20 adults and 30 or 50 larvae) from the Institute’s stock culture were released 24 and 72 hours before resampling. To avoid migration of arthropods, the frames were covered with finely woven gauze (mesh-type: PA-132/40, Franz Eckert, Germany).

Sampling techniques for winged aphids

Several small suction traps (2 m - Rothamsted type; Taylor, 1955, 1986) from Examine projects (EXploitation of Aphid Monitoring systems IN Europe; MaCaulay et al., 1988; Examine, 2008; P. Verrier, pers. comm.) in southern Lower Saxony were available for use. Applicable datasets (from spring catches) were regrouped as follows: Case studies (i.e. location-years) with field and assigned suction trap catches exceeding three cereal aphids per ear and flag leaf at the end of flowering of winter wheat (GS 69; Basedow et al., 1994) were classified as “case studies with gradation”, whereas those with lower numbers were classified as “case studies without gradation”. Gradation was defined according to Ohnesorge (1991). In Braunschweig (in 1998, a case study with gradation), three suction traps were used for small-scale (single-field) efficiency tests, whereas suction traps in Elze, Langreder, and Poppenburg (1999 to 2006, with gradation in 2002 and 2004) were used for large-scale efficiency tests (between fields of one region, approx. 60 km). Suction traps were checked daily for cereal aphids from end of April to end of June and from beginning of September to mid-November.

Furthermore, yellow water traps (Moericke, 1951; DeBarro, 1991) were used to collect winged aphids. A total of 24 were set up near Braunschweig in 1998 (a case study with gradation), and 8 near Carolinensiel in 2005 (a case study without gradation). Traps were used from end of April to end of June, examined 2-3 times a week for arthropods, and adapted to crop development (i.e. crop high).

In autumn, yellow sticky traps were used. Sweep net catches were performed in autumnal crops; four repetitions at rates of 50 sweeps were conducted for better estimation of the proportion of winged cereal aphids and their antagonists.

Statistical analysis

Analyses of variance (ANOVA, proc glm, mixed model, program SAS; SAS, 2008) were performed on datasets for each sampling technique. To better meet the assumption of a normal distribution in case of count and percentage data, logistic (log(x+1)) and arcsin-square root (arcsin $\sqrt{x}$) transformations were performed, respectively.

The coefficient of variation (cv), which expresses the standard deviation (s) as a percentage of the mean (m), is appropriate to compare the variance of several samples with different mean values (Köhler et al., 1984). Variation coefficients for each sampling technique were calculated using the following formula:

$$cv = \frac{s}{m} \tag{1}$$

Methods and precision of sample size estimation

The number of random samples needed to attain fixed percentage relative precision (PRP) depends on the level of precision required (Sutherland, 2006). This may be expressed either in terms of achieving standard error of a predetermined size or, in terms of probability, by calculating confidence limits (*cl*) for a predetermined half-width ($d = cl / [2m]$), i.e. a percentage of the mean (Karandinos, 1976). A 5% standard error of the mean is often sufficient for research purposes. Such low error limits requiring large sample sizes are difficult to handle in practice because of limited time and resources. Rough estimates of cereal aphid populations are therefore a necessary compromise (Boeve & Weiss, 1997). The levels of precision (*d*) used for sample size estimation in the present study were 50%, 30%, and 20%. The sample size required to achieve 5% precision is 100 times the sample size necessary for 50% precision, irrespective of the calculation method used. The methods used to estimate the required sample size (*n*) with which there is a 95% chance of obtaining a fixed PRP of *d* or less based on the data from visual counts are described below.

1. Sample size with percentage relative precision (SPRP_{GR}):

This very simple method for rough estimation of sample sizes (*n*), which was introduced by Greenwood & Robinson (2006) and similarly reported by Mühlenberg (1993) and Southwood & Henderson (2000), is primarily based on true standard deviation values and mean values known from literature or experience. The approximation *n*' is first calculated using the formula:

$$n' = \left(\frac{2}{d}\right)^2 \left(\frac{s}{m}\right)^2 \tag{2}$$

where *m* represents the mean and *s* the standard deviation of the number of organisms per sampling unit and *d* is the required percentage (specified as a decimal number) of relative precision (i.e. level of precision), chosen according to the aim of the study. The sample size required (*n*) is then computed from *n'* as follows:

$n = n' + 2$ for $n' < 25$
$n = n' + 1$ for $50 > n' \geq 25$
$n = n'$ for $n' \geq 50$.

2. Sample size according to preliminary survey ($\mathrm{SPS_{GR}}$):

This method by Greenwood & Robinson (2006) is based on the $\mathrm{SPRP_{GR}}$, but requires a preliminary survey (*ps*) of organisms per sampling unit. The number of sampling units additionally required to have a 95% chance of obtaining a PRP of *d* or less (n^+) is calculated using the equation

$$n^+ = \left(\frac{2}{d}\right)^2 \left(\frac{s_{ps}}{m_{ps}}\right)^2 \left(1 + \frac{2}{n_{ps}}\right) \tag{3}$$

where m_{ps} represents the mean number and s_{ps} the standard deviation of the number of organisms estimated from the preliminary sample. The number of sampling units n_{ps} in the preliminary survey is specified as well as the required percentage of relative precision *d* (denoted as in $\mathrm{SPRP_{GR}}$). If ($n_{ps} + n^+$) is less than 50, it should be adjusted as specified in $\mathrm{SPRP_{GR}}$ for *n*'.

3. Sample size according to regression ($\mathrm{SR_{FN}}$):

This method of sample size estimation is based on the method of Feng & Nowierski (1992), who described the spatial distribution of cereal aphids and developed numerical sampling plans based on estimated distribution of cereal aphids in the field by Taylor’s power law (Taylor, 1961). Taylor’s power law defines the variance (i.e. the squared standard deviation, s^2) proportional to a fractional amount of the mean using the equation

$$s^2 = am^b \quad \text{or,} \quad \ln(s^2) = \ln(a) + b \times \ln(m) \tag{4}$$

where *a* refers to a specific constant (according to animal group) and depends on the sample size and on the estimation of variance. However, parameter *b* denotes an index of aggregation ($b < 1$ in regular distributions, $b = 1$ in random distributions and $b > 1$ in clustered distributions). To determine the sample size (*n*) required for numerical counts, the power law was incorporated into the formula as described by Karandinos (1976):

$$n = \left(\frac{z_{\alpha/2}}{d}\right)^2 \left(\frac{s}{m}\right)^2 \tag{5}$$

resulting in the equation:

$$n = \left(\frac{z_{\alpha/2}}{d}\right)^2 am^{b-2} \tag{6}$$

where *z* is a standard normal deviate such that $P\,(z > z_{\alpha/2}) = \alpha/2$ (for $\alpha = 0.05$; $z_{\alpha/2} = 1.96$), and *d* is the predetermined half-width of a confidence interval (*cl*) as a proportion of the mean. The parameters *a* and *b* were estimated by linear regression analysis (log-transformation) using SAS software (proc reg; SAS, 2008).

Results

General population development

S. avenae and *R. padi* were the predominant aphid species in autumn. The observed population densities permitted a comparison of sampling techniques. Winter barley and winter wheat reached GS 25-26 and 23-25, respectively, before the start of hibernation. Winter conditions were harsh in most locations (both vegetation periods), and holocyclic hibernation dominated (> 92%). First emergence of cereal aphids was observed in mid-May during tillering. The numbers of cereal aphids detected in early growth stages varied considerably between the different crops. The overall number of aphids per m² (mean ± SE; all species) in winter barley was 3.4 ±1.7 at GS 11-17 and 14.4 ±6.6 at GS 21-29; the corresponding numbers in winter wheat were 0.7 ±0.4 and 3.3 ±1.5 at GS 11-15 and 21-29, respectively. *R. padi* was always the dominant species in early growth stages, with up to 6 times more individuals per m^2 than *S. avenae*.

Comparison of sampling techniques

Fig. 1 shows the comparison between D-VAC sampling and visual counts in the early growth stages of winter wheat and winter barley. Visual counts revealed significantly more aphid instars per m², except for winged *S. avenae* in winter wheat. Accordingly, the D-VAC to visual count (D/V) ratios ranged from 0.10 to 0.63 for all winter wheat comparison groups except winged *S. avenae* in GS 11-15 (Tab. 2).

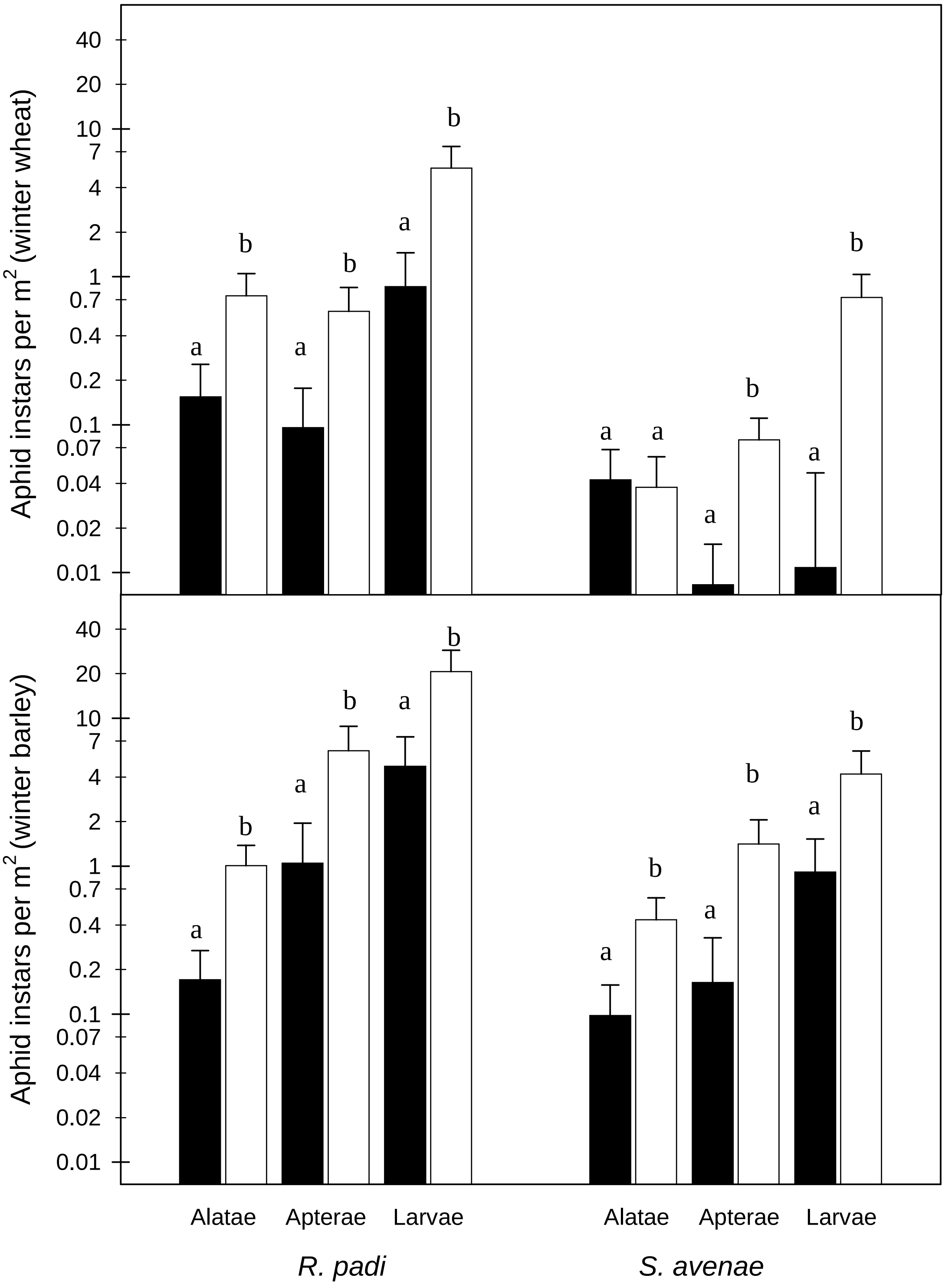


Fig. 1: Mean numbers of cereal aphid instars (±SE) per m² detected by D-VAC sampling (black) and visual counts (white) at growth stages 11 to 15 and 11 to 17 in winter wheat (upper part) and winter barley (lower part). Bars per aphid instars followed by the same letter do not differ significantly (ANOVA, $p < 0.05$).

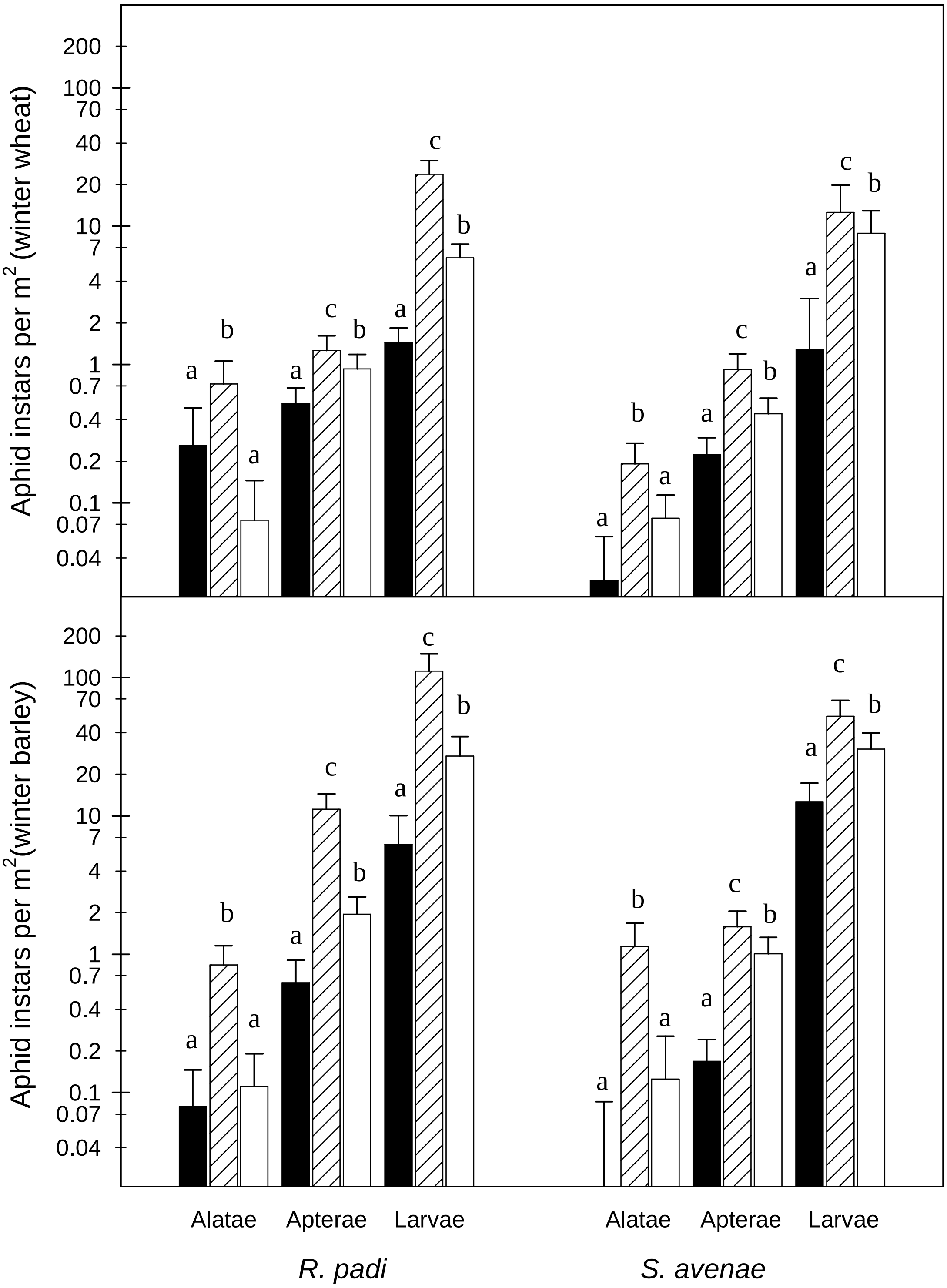


Fig. 2: Mean numbers of cereal aphid instars (±SE) per m² detected by D-VAC sampling (black), plant sampling (dashed) and visual counts (white) at growth stages 21 to 29 in winter wheat (upper part) and winter barley (lower part). Bars per aphid instars followed by the same letter do not differ significantly (ANOVA, p < 0.05).

The mean D-VAC to visual count ratio for all species and instars (excluding one non-significant value) was 0.17 ±0.01 for both crops in the early growth stages. D-VAC counts were also lower than visual counts in both crops at GS 21-29. Significant differences between the two sampling methods were detected in 7 out of 12 comparisons (Fig. 2). Only in the case of winged aphids were the D-VAC counts comparable ($p > 0.05$) to the visual counts. In cases with significantly different D-VAC and visual counts, the mean catch ratio (±SE) was 0.35 ±0.06 for both crops at GS 21-29. For all crops and developmental stages (excluding alatae and non-significant values), the mean catch ratio (±SE) was 0.25 ±0.04 (Tab. 2).

Tab. 2: Mean D-VAC to visual catch ratios (D/V) and mean plant sampling to visual catch (P/V) ratios for the evaluated cereal aphid instars (plant samples were only taken in growth stage 21 to 29).

Crop	Growth stage	Species	Instars	Catch ratio (D/V)	Catch ratio (P/V)
Winter barley	11-17	*R. padi*	alatae	0.37*	.
			apterae	0.17*	.
			larvae	0.23*	.
		S. avenae	alatae	0.63*	.
			apterae	0.12*	.
			larvae	0.22*	.
Winter wheat	11-15	*R. padi*	alatae	0.21*	.
			apterae	0.16*	.
			larvae	0.16*	.
		S. avenae	alatae	1.12	.
			apterae	0.10*	.
			larvae	0.11*	.
Winter barley	21-29	*R. padi*	alatae	0.72	7.55*
			apterae	0.32*	5.76*
			larvae	0.23*	4.11*
		S. avenae	alatae	0.20	9.06*
			apterae	0.17*	1.56*
			larvae	0.42*	1.73*
Winter wheat	21-29	*R. padi*	alatae	3.47	9.66*
			apterae	0.56*	1.36*
			larvae	0.24*	4.01*
		S. avenae	alatae	0.36	2.46
			apterae	0.51*	2.09*
			larvae	0.15	1.42

*Asterisks indicate significant ($p<0.05$) differences between sampling techniques (i.e. catch ratios).

Tab. 3: Mean coefficients of variation (±SE) of cereal aphid species calculated per week at three times (weeks of the year with corresponding growth stages) using different sampling techniques (field scale or overall population level).

Growth stage	Time (week no.)	Sampling techniques	Mean coefficients of variation (per week)		
			R. padi	*S. avenae*	*M. dirhodum*
0 - 13/15	36 - 45	Suction trap (regional scale, high population level)	1.12 ±0.22	1.83 ±0.42	2.21 ±0.72
0 - 13/15	36 - 45	Suction trap (regional scale, low population level)	1.26 ±0.31	2.28 ±0.34	2.34 ±0.73
13/15 - 21	44 - 49	D-VAC (field scale, low population level)	3.41 ±0.40	3.60 ±0.50	.
13/15 - 21	44 - 49	Visual counts (field scale, low population level)	2.93 ±0.28	3.01 ±0.30	.
13/15 - 21	44 - 49	Plant sampling (field scale, low population level)	2.57 ±0.17	2.72 ±0.18	.
31 - 65	18 - 24	Suction trap (field scale, gradation)	1.20 ±0.32	1.13 ±0.20	1.01 ±0.29
31 - 65	18 - 24	Suction trap (regional scale, gradation)	1.29 ±0.49	1.21 ±0.47	1.25 ±0.43
31 - 65	18 - 24	Suction trap (regional scale, no gradation)	1.25 ±0.40	1.84 ±0.57	1.72 ±0.57
31 - 65	18 - 24	Yellow water trap (field scale, gradation)	2.09 ±0.65	1.63 ±0.39	2.60 ±0.84
31 - 65	18 - 24	Yellow water trap (field scale, no gradation)	1.80 ±0.37	2.09 ±0.45	.

All three sampling techniques (plant sampling, D-VAC sampling and visual counts) were compared in later growth stages (GS 21-29). In most cases, the largest numbers of aphids were detected by plant sampling and the least by D-VAC (except alatae of *R. padi*, collected with D-VAC in winter wheat; Fig. 2). The mean plant sampling to D-VAC ratio ±SE at GS 21-29, excluding non-significant values, was 4.14 ±0.94 (Tab. 2).

Coefficient of variation

In autumn, the coefficients of variation for *R. padi* and *S. avenae* were highest with D-VAC sampling and lowest with plant sampling (Tab. 3). Coefficients of variation for *S. avenae* were higher than those for *R. padi* in autumn, but consistently smaller than those for *R. padi* in spring in case studies with gradation (Tab. 3). In spring, suction traps produced higher coefficients of variation at the regional scale than at the field scale, irrespective of species or population scale (e.g. case studies with or without gradation). *Metopolophium dirhodum* Walk. (Hemiptera: Aphididae) was only caught in fixed suction traps and yellow water traps. The corresponding coefficients of variation ranged between those of the two other species.

Overall, the coefficients of variation for suction traps and yellow water traps were smaller than those for D-VAC, visual counts, and plant sampling, as observed over several periods and evaluation times (Tab. 3). The coefficients of variation in case studies with gradation were smaller than those in case studies without gradation. This trend was generally observed for all species caught in suction traps and yellow water traps; the only exception was *R. padi* when collected in suction traps at a regional scale (weeks 18-24; Tab. 3).

Release and recapture experiments

In controlled release and recapture experiments with D-VAC sampling, recapture rates for *S. avenae* ranged from 10% to 56% (mean numbers (±SE) of 32.4 ±2.8%). Recapture rates for *S. avenae* larvae (31.3 ±3.1 %) and apterae (37.0 ±6.4 %) did not differ significantly ($p > 0.05$).

Tab. 4: Mean numbers (±SE) of sampling units needed to achieve the specified levels of precision (d = 0.5, d = 0.3, d = 0.2), as determined by the sample size with percentage relative precision ($\mathrm{SPRP}_{\mathrm{GR}}$) method (Greenwood & Robinson, 2006), the sample size according to preliminary survey ($\mathrm{SPS}_{\mathrm{GR}}$) method (Greenwood & Robinson, 2006), and the sample size according to regression ($\mathrm{SR}_{\mathrm{FN}}$) method (Feng & Nowierski, 1992). Up until growth stage (GS) 29, one sampling unit was defined as 60 winter barley plants or 50 winter wheat plants, respectively, equivalent to 0.25 m² in each case. In GS 39 - 69, one sampling unit of winter wheat was defined as 10 tillers. The main unit (*N*) expresses the number of fields and/or evaluation dates used for mean and standard error calculation. The sample size for 5% precision is 100 times larger than the sample size for 50% precision, irrespective of calculation methods used.

Crop	Growth stage	*N*	Calculation method	Number of sampling units at different levels of precision d = 0.5	d = 0.3	d = 0.2
Winter barley	11 - 17	10	$\mathrm{SPRP}_{\mathrm{GR}}$	17 ±7	44 ±21	97 ±47
			$\mathrm{SPS}_{\mathrm{GR}}$	31 ±8	63 ±24	126 ±56
			$\mathrm{SR}_{\mathrm{FN}}$	11 ±3	31 ±8	71 ±17
Winter wheat	11 - 15	8	$\mathrm{SPRP}_{\mathrm{GR}}$	21 ±3	55 ±8	124 ±18
			$\mathrm{SPS}_{\mathrm{GR}}$	35 ±2	76 ±9	156 ±22
			$\mathrm{SR}_{\mathrm{FN}}$	23 ±2	65 ±5	145 ±10
Winter barley	21 - 29	6	$\mathrm{SPRP}_{\mathrm{GR}}$	18 ±9	47 ±26	105 ±59
			$\mathrm{SPS}_{\mathrm{GR}}$	35 ±9	71 ±26	140 ±59
			$\mathrm{SR}_{\mathrm{FN}}$	7 ±1	19 ±3	44 ±7
Winter wheat	21 - 29	6	$\mathrm{SPRP}_{\mathrm{GR}}$	42 ±8	115 ±22	259 ±50
			$\mathrm{SPS}_{\mathrm{GR}}$	71 ±16	150 ±29	305 ±55
			$\mathrm{SR}_{\mathrm{FN}}$	20 ±3	56 ±7	125 ±17
Winter wheat	39 - 49	10	$\mathrm{SPRP}_{\mathrm{GR}}$	147 ±17	407 ±47	916 ±105
			$\mathrm{SPS}_{\mathrm{GR}}$	186 ±18	480 ±53	1053 ±121
			$\mathrm{SR}_{\mathrm{FN}}$	565 ±107	1569 ±298	3530 ±671
Winter wheat	51 - 55	9	$\mathrm{SPRP}_{\mathrm{GR}}$	143 ±35	396 ±96	891 ±216
			$\mathrm{SPS}_{\mathrm{GR}}$	179 ±38	463 ±104	1016 ±235
			$\mathrm{SR}_{\mathrm{FN}}$	121 ±15	336 ±41	756 ±92
Winter wheat	59 - 61	12	$\mathrm{SPRP}_{\mathrm{GR}}$	131 ±22	364 ±61	819 ±138
			$\mathrm{SPS}_{\mathrm{GR}}$	164 ±25	428 ±69	943 ±155
			$\mathrm{SR}_{\mathrm{FN}}$	113 ±17	313 ±46	705 ±103
Winter wheat	65 - 69	16	$\mathrm{SPRP}_{\mathrm{GR}}$	68 ±18	189 ±50	426 ±113
			$\mathrm{SPS}_{\mathrm{GR}}$	94 ±20	231 ±57	499 ±128
			$\mathrm{SR}_{\mathrm{FN}}$	57 ±17	158 ±48	355 ±108

Calculation of sample size

The basic sample size *N* (Tab. 4) for the different methods of sample size calculation ranged from 6 to 10 fields or evaluation dates in cereal crops in autumn, and from 9 to 16 fields or evaluation dates in winter wheat in early summer (Tab. 4). The mean number of sampling units per field or evaluation date was 32.1 in autumn and 71.8 in spring. The mean number of sampling units and the overall sample size are critical parameters for comparison of sampling techniques.

According to the SR_{FN} method, regression analyses performed for parameter estimation showed a mean coefficient of determination (±SE) of $R^2 = 0.91 \pm 0.03$. The mean intercept (±SE) was ln(1.81 ±0.36) in autumnal crops and ln(4.59 ±0.67) in winter wheat. The mean slope (±SE) was 1.87 ±0.08 in autumn and 1.62 ±0.06 in spring; all slope values were greater than one.

The estimated sample sizes varied between methods, plant growth stages and crops (Tab. 4). Generally, the SR_{FN} method estimated the smallest sample sizes, and the SPS_{GR} method the largest. The number of sampling units needed to accurately estimate aphid populations in winter wheat in early (GS 11-17) and late (GS 21-29) growth stages is higher than the number necessary in winter barley. In later growth stages, smaller numbers of sampling units were needed to achieve the minimum sample size. With increasing precision (i.e. smaller *d* values), the number of sampling units increased disproportionately (Tab. 4). According to the $SPRP_{GR}$ method, a minimum of 1,050 plants (21 (±3)×50 plants) is required to estimate cereal aphid populations in winter wheat at GS 11-15 with a precision of 50%. According to the SR_{FN} method, a minimum of 420 plants (7 (±1)×60 plants) is needed to estimate the aphid populations in winter barley at GS 21-29 with 50% precision.

In early summer, when the winter wheat development progressed from GS 39 to 69 and the population of cereal aphids increased (reaching a distribution closer to $b = 1$), the numbers of sampling units decreased (Tab. 4). At GS 39 to 49, the estimated number of sampling units needed to achieve a given level of precision varied among the different sampling methods (e.g. $SPRP_{GR}$ vs. SR_{FN}) by a factor of four to five. The estimated sample sizes for a given level of precision, as calculated by the different methods, were most similar at the flowering stage of winter wheat. According to the SR_{FN} method, at least 570 tillers (i.e. 57 (±17)×10 tillers) should be evaluated to achieve a precision level of 50%.

Discussion

Comparison of sampling techniques

The most striking finding of this comparison study was the disproportionately large number of cereal aphids per m² obtained with plant sampling (Fig. 2). The mean plant sampling to visual count (P/V) ratio of 4.14 ±0.94 showed that more than four times more aphids could be detected by plant sampling. The visual count technique was obviously less accurate, except for alatae and larvae of *S. avenae* in winter wheat (Tab. 2). However, it should be considered that the occurrence of consistently low densities of *S. avenae* in winter wheat resulted in high standard deviations, which made it difficult to prove differences statistically. Moreover, the visual count technique is not easy to manage in autumn, when plants are small and the ground is often wet. Crawling around on the ground is strenuous and, with time, the risk of overlooking small aphids (e.g. larvae) sticking to the soil or plant debris increases. With plant sampling, on the other hand, a precise evaluation of samples can be conducted under laboratory conditions. Another benefit of outdoor plant sampling with indoor evaluation is the possibility of carefully collecting unharmed aphids for further analysis, for example, for virus transmission tests (biotests). The major drawback of plant sampling is the time requirement: it proved to be the most time-consuming sampling technique (Tab. 5). Both plant sampling and D-VAC sampling require fieldwork plus intensive inspection of samples in the laboratory. The variability of evaluation time duration was most pronounced for D-VAC samples and was longest when a bulk of plant and soil debris was part of the inspection protocol. The total handling time for each technique (specified in Tab. 5) must be considered when comparing the suitability and costs of the different sampling technique.

Tab. 5: Time (in minutes) needed to evaluate cereal aphids and arthropods in one sampling unit, which consisted of 50 to 60 plants (0.25 m²) at growth stages 11-29 in visual counts, D-VAC, and plant sampling. One sampling unit from fixed suction or yellow water traps is based on one catch period, e.g. one day (between April 15th and November 1st).

Sampling Technique	Time [min.] to evaluate one sampling unit In the field	 In the laboratory	 Total
Visual counts	> 15	-	> 15
D-VAC	< 5	> 55 (10 - 240)	> 60
Plant sampling	> 5	> 160 (140 - 200)	> 165
Fixed suction trap	< 5	> 60 (10 - 180)	> 65
Yellow water trap	< 10	-	< 10

It seems unlikely that plant sampling overestimated the field population of cereal aphids, since plants were selected at random and a large sample size (> 600 plants) was used. Moreover, visual counts yielded similar numbers of *S. avenae* apterae or alatae in winter wheat (Fig. 2). The observed cereal aphid population levels were comparable to those measured in other studies done in southern Lower Saxony (Scholz, 1994; S. Krüssel, pers. comm.). Comparing the techniques used to follow the population development of cereal aphids in winter barley in autumn, the most aphids were detected by plant sampling and fewest by D-VAC sampling (Scholz, 1994). Plant sampling can therefore be regarded as the most accurate technique for evaluation of cereal aphids in winter wheat and winter barley in autumn.

D-VAC sampling was even less effective than visual counts and resulted in the lowest numbers of cereal aphids per m² (Figs. 1 and 2). Only about 25% of the visually counted cereal aphids were detected by D-VAC, and only for alatae was the efficacy of D-VAC nearly equal to that of visual counts (Figs. 1 and 2). These results are corroborated by Scholz (1994), who found a mean D-VAC to visual catch ratio of 0.31 during autumnal sampling in winter barley in southern Lower Saxony. Winged aphids are effortlessly caught by suction and can be easily recognised during the sorting procedure in the laboratory. Small larvae, however, may be hidden between developing leaves or near the roots, making them inaccessible to the D-VAC suction sampler (Scholz, 1994). Our results corroborate the findings of Dewar et al. (1982) that the D-VAC suction technique is less effective than visual counts for cereal aphids on tillers (GS > 31). Our release-recapture experiments produced similar results: After we released defined cereal aphid densities, D-VAC recaptured only 32.4% of the aphids under nearly optimal environmental conditions. Similar or moderately higher efficiencies were found in similar experiments monitoring insects (Homoptera: 32 - 76% efficiency) in grasslands from May to September (Henderson & Whitaker, 1977). Duffey (1980) reported lower efficiencies of D-VAC-sampled insects (Hemiptera) in grasslands in May (14 - 18%) than in August (33 - 58%). These findings contrast with the release-recapture rates reported by Dinter (1995) who, was able to recapture 84.2 ±5.4 of released spiders (males and females of *Erigone altra* Blackwall, and females of *Oedothorax apicatus* Blackwall) in later growth stages (end of July). However, vegetation structure and density has a considerable impact on the efficiency of D-VAC sampling (Henderson & Whitaker, 1977; Hand, 1986). Overall, D-VAC sampling may be more selective than the other techniques since active insects (e.g. predatory spiders at GS 85) are captured with much higher efficacy than those that withdraw in leaf sheaths or near the hypocotyls (e.g. larvae of cereal aphids at GS 21). Inversely, insects in leaf sheaths or near roots can be more easily detected with the plant sampling technique studied in the laboratory. Moreover, D-VAC is very unsuitable for efficiently collecting aphids when the crop or the soil is wet due to rain or dew; at these times, many aphids stuck to plant and soil debris are not picked up by suction (Henderson & Whitaker, 1977; Dinter, 1995; Veenker & Ulber, 2004). This is one of the greatest drawbacks of D-VAC sampling, and it reduces the performance of D-VAC sampling compared to visual counts or plant sampling, especially in autumn, winter and early spring.

Coefficient of variation

Coefficients of variation were calculated in order to compare the degree of variability of aphid population size estimates determined for numerous samples collected by the different sampling techniques (Tab. 3). The results are in accordance with the aforementioned statements regarding the comparison of sampling techniques. Plant sampling produced the smallest coefficients of variation and D-VAC the largest for *S. avenae* and *R. padi* in autumn. Coefficients of variation for *S. avenae* were generally higher than those for *R. padi*; this was possibly due to the higher overall population density of *R. padi* (Tab. 3). Dinter (1995), on the other hand, reported mean coefficients of variation of 0.28 or 0.59 for (predatory) spiders sampled with D-VAC in spring and summer. The spiders were caught more regularly and showed much smaller standard deviation (Dinter, 1995).

Coefficients of variation obtained using yellow water traps were convergent consistent with those found by DeBarro (1991), and the values ranged between those obtained using suction traps and other sampling techniques (plant sampling, visual counts and D-VAC; Tab. 3), in spite of colour attraction (DeBarro, 1991). Consequently, yellow water traps were not classified as inappropriate for surveying the activity density and flight phenology of cereal aphids (Kuroli & Lantos, 2006). The smallest coefficients of variation were observed using suction traps. The coefficients of variation for *R. padi* were small, independent of the catch scale or population level. *R. padi* seems to be a constantly migrating species that is caught regularly and in similar numbers (Geissler et al., 1995; Veenker & Ulber, 2004). Furthermore, *R. padi* is not strongly involved into outbreaks of cereal aphids in central Europe (Basedow et al., 1994). *S. avenae* and *M. dirhodum* exhibited higher coefficients of variation in large-scale datasets with lower overall population levels (years without gradation). This highlights the regional differences, with more suction traps used on smaller scales (< 160 km; Loxdale et al., 1993) being the more accurate technique of surveying (Veenker, 2000). In conclusion and in harmony with other authors (Dusi et al., 2000; Malloch et al., 2006), we found that suction traps provide the best output describing flight activity density and flight phenology of cereal aphids, which is most relevant in years with gradation.

The sampling techniques compared in our study may be robust with respect to minor differences in species composition of cereal aphid communities in different geographic regions, similar to other studies (Elliott et al., 1990, 1997). This may be primarily the outcome of similarity in variance-mean relations of the species, as summarised by coefficients of variation per week. It furthermore suggests that the species had similar spatial distribution patterns, at least at the spatial scale observable using our sampling protocol in autumnal crops. However, since aphid catches from yellow water traps and suction traps cannot be directly transformed into m² values, an unbiased comparison with other sampling techniques is not possible (Sutherland, 2006). Both types of traps provide useful information about the overall fight activity and phenology over the course of continuous trapping (DeBarro, 1991; Malloch et al., 2006). D-VAC, visual counts and plant sampling, on the other hand, provide snapshot views of the actual numbers of aphids per m² (Southwood & Henderson, 2000; Sutherland, 2006).

Other sampling techniques like yellow sticky traps, sweep net catches and washing-out did not provide satisfactory estimates of autumn populations of cereal aphids and were therefore discarded after a few trials. With the last two techniques, the cereal aphids were difficult to separate from the soil and plant debris. Furthermore, the sweep net draggled over small plants on the ground and was not effective at sampling winged aphids in autumnal crops. The labour required for washing-out techniques increased dramatically with small plants (GS 11-29) compared to tillers (GS 32-69). The results of Dewar et al. (1982), who found this technique less efficient than visual counts, are in agreement with our findings. Nevertheless, some authors (Bothe & Heimbach, 1995; G. Lauenstein, pers. comm.) have reported successful employment of the washing-out techniques, but their experiments and experiences were obtained using whole tillers (collected from GS 51 to 75) rather than small plants (GS 11 to 29).

Calculation of sample size

Appropriate sample size estimation is an everlasting dilemma in field inspection-based decision-making systems (Jarosík et al., 2003). Limitations include the time and effort required to collect and evaluate samples on the one hand and the necessary degree of certainty of the prognosis on the other. In all fields evaluated by us, cereal aphids commonly exhibited an aggregated, right-skewed distribution. In other words, numerous plants or tillers were not colonised, but few sheltered large cereal aphid colonies. Similar findings were reported by

Feng & Nowierski (1992) for *S. avenae* and *R. padi* and by Ekbom (1985) for *R. padi*, particularly during the time from population build-up (GS 32 to 39) to the end of flowering of winter wheat (GS 69). The appropriateness of sample sizes and sampling techniques in winter crops are most relevant from leaf emergence (GS 11) to the beginning of flowering (GS 61). The aggregated distribution, which was particularly observed from GS 11 to 61 in our study, is the most important reason for large minimum sample sizes being estimated by the different calculation methods for each level of precision (Tab. 4). Clumped or aggregated populations (e.g. when the variance is larger than the mean) can be analysed using adequate distributions (e.g. the Poisson or the Negative Binomial distribution). The methods used for estimating the minimum sample size in our study have different approaches to considering the aggregation of cereal aphids. For larger degrees of freedom or of sample sizes ($n > 500$), the test statistics of the standard Student's t-distribution z_α converged down to $z_\alpha = 1.96$ (Sachs, 1999). When sample size $n > 100$, the empirical value of 2.00 (specified as approximation n' according to the SPRP$_{GR}$ method; Greenwood & Robinson, 2006) is therefore an appropriate standard, and no further transformation of the approximation n' is needed (i.e. $n' = n$; Greenwood & Robinson, 2006). This (conservative) standard value has been proven in several calculation methods for estimating the minimum sample sizes required for invertebrate studies (Karandinos, 1976; Mühlenberg, 1993; Southwood & Henderson, 2000; Sutherland, 2006). However, if the sample sizes are small ($n < 50$), increased z_α values > 2.00 must be considered (Karandinos, 1976; Sachs, 1999). Therefore, the approximation n' is transformed to n according to SPRP$_{GR}$ and SPS$_{GR}$ (Greenwood & Robinson, 2006). The use of this transformation is meaningful and easy to handle even for field advisers unfamiliar with sample size estimation formulae. Moreover, it fitted well in the case of small sample sizes ($n < 50$) with $z_\alpha = 2.20$ in the numerator of equations (2) and (3) according to Greenwood & Robinson (2006; data not shown).

Early infestation of plants at GS 11 to 29 has a stronger impact on yield than later infestation of several tillers. This is mainly due to the compensatory potential of plants in later growth stages (Hansen, 1999; Fabre et al., 2003, 2005). Younger plants are generally more susceptible to yield loss from aphids than older plants. Moreover, the spread of viral diseases by cereal aphids can reduce yield substantially (Leclercq-LeQuillec et al., 2000). Doodson & Saunders (1970) found that new infections of barley yellow dwarf virus did not damage small-grain cereal crops once they had reached GS 31. Since threshold levels for cereal aphids are much lower in early growth stages of winter wheat and winter barley (GS 11 to 21), larger sample sizes are then required for accurate estimation of cereal aphid populations (Fabre et al., 2003; Jarosík et al., 2003).

Compared to the other methods for minimum sample size calculation, the SR_{FN} method differed from the others fundamentally due, perhaps, to the use of the regression approach. SR_{FN} most frequently estimated the lowest minimum sample sizes (Tab. 4). However, the calculation results were largely dependent on the coefficients of determination, with lower R^2 values resulting in larger sample sizes (e.g., at GS 39-49, as described in Tab. 4; other data not shown). According to other sample size estimates at GS 21-29 (Feng & Nowierski, 1992), 19 and 56 sampling units are necessary to reach a precision level of 0.3 for winter barley and winter wheat, respectively. Accordingly, three field advisers must count visually aphids in the field for about 1.5 hours in winter barley and 5 hours in winter wheat. With plant sampling, however, the sampling procedure would take two and six days, respectively (Tab. 5).

In winter wheat at ear emergence, according to the method of Feng & Nowierski (1992), aphids on a minimum of 3,360 tillers (i.e. 336×10 tillers) must be counted visually in order to reach of level of precision of 0.3. Samples sizes of 3,000 to 8,000 tillers can be easily managed by two or three samplers, as demonstrated by Freier et al. (2002). Our calculated sample sizes and time specifications in winter wheat at the end of the flowering are in conformity with the findings of Pluschkell (1997) and Rappaport & Freier (2001). Both studies reported that a conventional transect evaluation to collect cereal aphids in winter wheat fields at the end of the flowering stage takes approx. 20 and 30 minutes in approx. 60 and 100 tillers, respectively. Moreover, several studies have shown that, instead of counting aphids on whole tillers, cereal aphid population estimates can be performed considering only present / absent data (Elliott et al., 1990, 2003). However, significant correlations between the severity of population density and decay incidence were relevant only at GS > 69 (Basedow et al., 1994). Unfortunately, the correlations failed at early growth stages (i.e. when our study was performed), because of more aggregated distribution of fewer cereal aphids (Southwood & Henderson, 2000; Sutherland, 2006). This is the centre of the problem and the ongoing challenge in autumnal cereals. Future research should develop control threshold levels with the use of appropriate survey techniques and appropriate sample sizes (Pluschkell, 1997; Rappaport & Freier, 2001; Jarosík et al., 2003).

According to all sampling methods, sampling time decreased with increasing aphid densities (Tab. 5; Karandinos, 1976; Mühlenberg, 1993; Southwood & Henderson, 2000; Sutherland, 2006). However, the sampling time spent visually counting aphids on tillers in winter wheat did not change as dramatically as the number of aphid instars increased on the tillers. This is attributed to the fact that, when the number of tillers sampled i.e. the minimum sample size was lower, the relative amount of time needed to count the aphid instars (including different morphs and cereal aphids' antagonists) on a single tiller was longer.

Despite the smaller differences between sampling methods and techniques at each growth stage, the minimum sample sizes required were justifiable and manageable (if several field advisers evaluate a few fields each), and it was possible to achieve precision levels equal to or greater than 20%. This level of precision is appropriate to estimate the much lower thresholds given at early growth stages (e.g. GS 21), but not for late stages (e.g. GS 69). The 5% precision level, which is frequently used in scientific work (e.g. for the development of detailed population models), is relatively unrealistic and impossible to achieve with a few field advisers in fields with at very low aphid densities (Kleinhenz, 1994; Gosselke et al., 2001).

After the introduction of control threshold level in winter wheat (Basedow et al., 1994), advisory services and practitioners started counting 10 tillers on 10 sampling units (i.e. 100 tillers per field) at the end of the flowering stage, irrespective of the field size, the overall aphid population density, or the landscape structuring. This empirical formula was often assigned to the whole vegetation period of winter wheat. In autumn, 10 plants were frequently sampled on 10 sampling units (Kleinhenz, 1994; P. Matthes, pers. comm.). The use of such marginal sample sizes in early growth stages of winter crops may result in frequent calculation error due to masking of the actual number of cereal aphids in fields. Cereal aphids have an aggregated distribution and a high reproductive potential (Dixon, 1998). For reliable control decision-making in autumn and early spring, our results - like those of Boeve & Weiss (1997) and Jarosík et al. (2003) - clearly demonstrate that larger sample sizes are necessary, as shown in Tab. 4. Furthermore, after comparing typical mean numbers of aphids at the flowering stage of winter wheat, when there are one to six aphids per tiller, the aforementioned authors determined that the minimum sample size was 132 tillers (for 25% precision).

Conclusions

Accurate techniques for estimation of cereal aphid densities are essential for calculation and application of threshold levels in autumn and early spring. The choice of sampling techniques is a delicate matter in early growth stages (GS 11-29), since there is always a trade-off between precision and applicability of the method in terms of required cost and workload, in particular. None of the available techniques is highly accurate and practical over the entire range of aphid densities over time, and at certain points of the sampling scheme or at certain aphid population densities, every technique shows some weaknesses. According to our results, plant sampling resulted in the most accurate cereal aphid classification and enabled further aphid analyses in laboratory. Visual counts were the most effective way to produce a quick rough estimate of the overall population density for management strategies, etc. D-VAC proved to be the least effective technique. Since D-VAC was found to be inappropriate for the collection of cereal aphids in autumnal crops, its use is not advisable. The sampling techniques investigated here are intended to be used by researchers, growers, and field advisers. Additionally, we stress the importance of proper sample size estimates depending on the level of uncertainty (i.e. precision) the users require and the time and effort they are willing to take.

Acknowledgements

The authors are especially grateful to U. Heimbach for providing suction trap and yellow water trap samples from the Braunschweig site (1998), to S. Wandrey for proofreading the manuscript, and to T. Michel for practical assistance. This project was financially supported by the Bundesministerium für Verbraucherschutz, Ernährung und Landwirtschaft, Germany (Federal Ministry of Food, Agriculture, and Consumer Protection; project code: 01HS083).

Global Discussion

The global discussion provides an overall bird's eye view of the cereal aphid immigration and early population development studies described in more detail in the independent chapters and also expatiates detailed points that were not included in the chapter discussions.

Model comparisons

The serious risk of high yield losses caused by cereal aphids is related, in most seasons, to the population density reached relatively late in winter wheat during the phase in which assimilates are produced and transported to the grains and during ripening of the grains. However, the basis for damaging densities to be reached is founded much earlier, during the phase of first establishment of "founder colonies" in the crop stands. It is therefore important to understand immigration and early population development (Carter & Rabbinge, 1980; Loxdale et al., 1993; Vialatte et al., 2007). The population dynamics of cereal aphids have often attracted the attention of modellers (Zhou & Carter, 1989; Rossing, 1991; Hansen, 1999). Population models describing the development and seasonal progression of pest abundances are, in general, important tools for integrated pest management (IPM) strategies. The primary basis for aphid population models is exact knowledge about typical population growth parameters, such as development time, mortality of life stages, reproduction rates and longevity as well as about external influences (e.g. temperature and humidity) on these parameters. Growth rates, which are defined here as the increase in biomass over time, can be important, since damage is not only related to the numbers of aphids, but also to their growth (biomass) level (Leather & Dixon, 1984; Acreman & Dixon, 1989; Awmack & Leather, 2007). Especially in the case of cereal aphids, population growth rates (e.g. mean relative growth rates, MRGR) and development rates (e.g. reproductive maturity, period from birth to adult) have been intensively examined. They are frequently combined as intrinsic rates of natural increase (r_m) to yield estimates of future population growth rates based on the performance of individual aphids (Wyatt & White, 1977; Dixon, 1990). This broad knowledge about cereal aphid growth and development rates explains why detailed population models such as GETLAUS01 faired well in the field situation à posteriori ("retral-calculation"; chapter 1). In à posteriori analyses, the main driving factors can be easily re-calculated (e.g. from climate protocols). Such models are valuable for sensitivity analysis, but they usually failed to accurately describe future (e.g. more than three weeks ahead) aphid developments and future population densities (e.g. model LAUS; chapter 1). Recapitulating, field studies have shown that accurate and species-specific modelling of aphid population developments during the early growth stage (before flowering of winter wheat) is not possible using the available datasets (chapter 1; Gosselke et al., 2001). Even very detailed models like GETLAUS01 failed, when the simulation started as early as four weeks (e.g. on May 17th) before the recommended model start (chapter 1). The major problem seems to be the extremely low density and the aggregated distribution of aphids early in the season. According to Gosselke et al. (2001), the most significant problems in modelling aphid as well as antagonist population dynamics arise from the course of immigration and from the estimation of early-season mortality rates (i.e. survival). The latter are influenced by both abiotic and biotic factors (e.g. morph structure, species composition, antagonists, etc.), which are frequently unknown because of inadequacies of the sampling technique or sample size (chapter 6). We have developed models to simulate the course of immigration in spring (chapter 3), but these models estimate only the migration potential of a given day without quantifying in great detail the numbers of migrating aphids (chapter 3). Therefore, it is still a challenge to forecast in detail the immigration events and early population developments in spring. Moreover, the population models need further revisions to make them applicable to such a difficult period as early spring (e.g. before GS 69; chapter 1). However, reliable predictions of gradations of cereal aphid would be very helpful for economic management of cereal aphids. Due to the extreme data variability and workload associated with forecasting aphid population densities in early spring (before end of May), a drastic simplification of the data structure was required. This was achieved through simple classification of treated case studies those with or without gradation (chapter 2). As a result, lots of information (i.e. on species, morphs, and age-structure) was lost, but this was the only way to make the model applicable and reliable for the aspired decision support system for early insecticide applications in winter wheat, i.e. before flowering (GS 61).

Cereal aphid gradation

Interestingly, the data of predator units evaluated in our case studies did not show substantial impact on the gradations (i.e. during the course of gradation) of cereal aphids, which does not mean that cereal aphid populations are not affected at all by their antagonists. But here, it indicates that gradation models could solely be based on meteorological or suction trap data (chapter 2). Possibly, different resource exploitation strategies among the predators and parasitoids integrated into guilds of predator units might be a reason for that (Freier et al., 1998). For example, when considering only Syrphids (i.e. larvae) as specific predators, one may expect high numbers of eggs (and therefore more developing larvae) with high numbers of cereal aphids. This is based on numerical and functional response found in Syrphids (Freier & Triltsch, 1996; Hemptinne & Dixon, 1997; Freier et al., 2001). Therefore, the summation of cereal aphid antagonists into predator units may be disreputable (Freier et al., 1998). Extensions of predator units, which consider the different patterns of functional and numerical reactions, may be very helpful for definition of predictor variables subsequently influencing cereal aphid gradations. A critical bottleneck between aphids and their antagonists may be related also the questions, when (synchronisation in time) and in which relations (synchronisation in densities) they meet. For example, a certain (high) number of predator units in later growth stages of winter wheat may indicate that large numbers of cereal aphids were present (numerical response of predators like Syrphids or Coccinellids). However, a similar amount of predator units at an early growth stage of winter wheat may not be related to numerical response, but may influence the aphids in different ways. Possibly, the predator units need other weighting in accordance to their composition in respect to decimations of cereal aphid populations.

The gradation models available thus far are based on a simple, fixed control threshold level (Basedow et al., 1994). Here, the control threshold gives evidence that the underlying economic damage threshold level will be achieved or exceeded soon after (Basedow et al., 1994). Threshold levels were considerably investigated elsewhere (Anderson, 1985; Lindqvist, 1985; Barbagallo & Suss, 1986; Bromand, 1990; Rappaport & Freier, 2001), and our study was neither intended to verify nor to update that concept. However, model uncertainty (i.e. failure in correctly forecasting cereal aphid gradations) is not only based on validation results in chapter 2, but additionally with respective to the control threshold level (Basedow et al., 1994). Incorrect decisions derived from the control threshold level may continue in gradation models. Basedow et al. (1994) reported a few cases, when the application of threshold levels failed. Several factors may cause uncertainty in correct forecasting aphid populations (Rappaport & Freier, 2001). This may be especially the case, because we made a “detour” and forecasted if the aphid population exceeded the control threshold, but not of the economic threshold level. Incorrect forecasts were detected in validation studies of independent submodels (chapter 2). The time from the end of ear emergence to the end of flowering was shown to be of great importance for the development of cereal aphids (Leather & Dixon, 1981; Zhou & Carter, 1992). For *S. avenae*, optimal weather conditions during the flowering of winter wheat promoted ear infestation (Watt, 1979), which in turn led to high population levels two to three weeks later and therefore increased yield losses (Freier et al., 2001). Strong rainfalls, moderately low temperatures, and high abundances of cereal aphid antagonists may have negative effects on population development (Rappaport & Freier, 2001). However, the dilemma to forecast future weather parameters (i.e. at the end of flowering GS 69) as early as the time of ear emergence (GS 51) cannot be solved (H. Friesland, pers. comm.). Hence, low hit rates of the gradation model or high discrepancies from real development of infestations in the one or other case have been reported (chapter 2; Basedow et al., 1994; Freier et al., 2001).

Another question is whether a simple, inflexible control threshold level can also incorporate the flexibility of the future economic damage threshold (Rappaport & Freier, 2001). Changes in yield expectations, in climatic conditions (e.g. longer dry summers), in newly developed cultivars, and in further aspects of crop cultivation within a certain region (e.g. increased production of maize to produce energy) will possibly influence the level of aphid density, and expenses for control will be in balance with circumvented yield losses. Therefore, a conscientious revision of the proposed models is a fundamental prerequisite to establish their relevance in practise.

For many researchers and modellers, the afore-mentioned “detour” and the rough classification method may sound too simple (or even inaccurate), because it does not consider many factors that were previously incorporated in detailed population models, and which are known to affect the population development of cereal aphids (Freier & Wetzel, 1980; Pierre & Dedryver, 1985; Papura et al., 2003; Llewellyn et al., 2004). According to our models, those factors are not necessary for the binary classification concerning the use or non-use of insecticides (i.e. case studies with and without gradation). There is no doubt that detailed cereal aphid population models including large numbers of factors are still important for basic scientific research, especially for sensitivity analyses. However, the drawback of detailed models for prediction of aphid population dynamics (in terms of decision support in IPM) is the high sensitivity of output variables (aphid densities) to a multiple set of intrinsic (e.g. size, fecundity, mortality, migration rate) and extrinsic factors (e.g. meteorological parameter). Moreover, detailed population models tend to be very complex, because modellers believe that higher complexity leads to higher accuracy. However, it is often overlooked that such multiple input models are also very sensitive to measurement errors rising with each parameter, hence resulting in highly variable predictions (Stewart & Dixon, 1988). The presented models to forecast gradation (chapter 2) are the best alternatives so far for users (field advisers, farmers) and their working routine. At an early growth stage of winter wheat (GS 51 to 59), they make it possible to reconsider the application of insecticides on farms where economical constraints demand that the final (regular) fungicide treatment and the (irregular) insecticide application must be combined and, thus, must take place clearly before the end of flowering.

Overwintering seems to be a key event in the population dynamics of cereal aphids, which were affected directly (as reported in chapter 4) and indirectly (as reported in chapters 1, 2, and 3). The simulation model SIMLAUS correctly classified the possibility of hibernation type, independent of the population level in the previous autumn (chapter 1). Moreover, gradation models were dependent on predictor variables associated with winter strength (e.g. temperature sums > 0 from November 15th to May 1st; chapter 2). Accordingly, cereal aphid gradation can be forecasted based on winter temperatures, without labour-intensive field counts. Forecasting models based on suction trap data are currently available in representative suction trap catchment areas (i.e. 80 to 160 km radius; Taylor, 1986; Cocu et al., 2005a). Although the models are constrained to rather continental regions of Germany, they cover a large area most important for winter wheat production. Especially in the eastern parts of Germany, large-scale land management prevails (mean field size > 80 ha; European agricultural statistics, 2008). The workload for farmers is high and the decision whether or not to apply insecticides is often focused on a very short time window. The consequences, however, affect very large areas. Therefore, the decision support system can contribute to extending IPM to those regions. Nevertheless, approximations for a wider area (e.g. total Germany) are desirable and only future pilot runs will determine the wider applicability and usefulness of such an early decision support system.

Implications for practice and economic framework

The economic threshold level of Basedow et al. (1989), with one aphid per ear and flag leaf, was originally based on a wheat prices of approx. € 20 per tenth of a ton; this was later adjusted to ≥ 3 aphids per ear and flag leaf when wheat gave only a return of approx. € 12 per tenth of a ton (Basedow et al., 1994). Currently, winter wheat brings higher returns due to increasing demand on the world market than some years ago (European agricultural statistics, 2008). Ideally, a flexible decision support system should be perpetually adapted to the reality of economic parameters (wheat price, costs for vehicle crossing, prime costs, etc.).

Decision systems should weigh the risks (and experience) of wrong decisions against the benefits. The decision system of Basedow et al. (1994), which uses a threshold of ≥ 3 aphids per ear and flag leaf, detected one redundant (superfluous) insecticide treatment in 44 cases, whereas two dignified treatments were not recognised. Using a similar control threshold level, Holz et al. (1994) observed redundant insecticide treatment in 1 out of 10 cases. As shown for the independent submodels of the developed decision support system (gradation models), more false positive than false negative decisions were obtained (chapter 2). Unnecessary treatments are both economically and ecologically undesirable. However, failure to predict necessary treatments is much more destructive for acceptance and establishment of a decision support system. Because farmers are risk aware (Rossberg et al., 2002), they will use a decision support system on a long term basis only if they are convinced of its merits (benefits) from the very beginning. They are particularly disappointed by false negative predictions (Basedow et al., 1994; Rossberg et al., 2002). Like threshold level concepts, the gradation models (i.e. the decision support system) must prevent economic losses in order to convince farmers of their usefulness. Moreover, decision systems should be simple and easy to use. The control threshold level (Basedow et al., 1994) and hence, the gradation models (chapter 2) were designed with such compromises from the user side in mind. Decision support based on the control threshold may occasionally lead to wrong decisions but, overall, it is beneficial to farmers, both economically and ecologically (Basedow et al., 1994; Dixon, 1998). An incorrect forecast apparently leading to yield losses may lose creditability with a novice in IPM. However, our studies have shown that the decision support system actually minimises wrong decisions (chapter 2). Subsequently costs for vehicle crossing and prime costs will be economised, but most importantly, temporal and financial efforts to compare the actual population level on several fields of a given farmer with the control threshold level can be strongly reduced.

The gradation models may also help to optimise the working routine of farmer advisory services. Field advisers can also use the models for negative prognoses, to predict situations in which further action (e.g. visually estimating cereal aphid population levels in the fields) is required only if the gradation model predicts a cereal aphid outbreak.

Besides their practical use, models can generally be used as scientific tools to improve our knowledge of, demonstrate and/or explain population dynamics (depending on driving forces) and trophic interactions. GETLAUS01, a very detailed model, is a prime example (Gosselke et al., 2001). Gradation models (chapter 2) may also show learning effects in a similar way. Farmers may not believe that cereal aphid populations are not worth fighting every year, and that insecticide treatments may be an unnecessary expense. It is most important for farmers unfamiliar with IPM and threshold concepts to learn to trust that small aphid infestation levels can be tolerated.

In general, cereal aphid management strategies in winter wheat before the flowering are not as fine-tuned in time scale as those for other agricultural pests (e.g. *Contarinia tritici* Kirby, *Haplodiplosis equestris* Wagn.) and diseases (e.g. *Puccinia striiformis* Westend., *P. recondite* Rob. ex Desm.). For example, the germination of rust spores must be prevented from the very beginning, i.e., before the germ tube enters the winter wheat leaf. Once rust mycelium infection has occurred within leaves, it is much more difficult to control (eradicate) the pathogen and to avoid yield losses. Models must take such special features into consideration (Kleinhenz, 2007). As sucking pests, aphids in winter wheat can be handled differently, and developing populations can be treated at various times within in a given period (between beginning and end of June). This fact may have contributed to the increased tendency to apply insecticides for cereal aphid control. Moreover, it may have reduced the willingness of farmers to wait until the population densities exceed the critical threshold.

Migration models

The study of migration by weekly sampling of alatae cereal aphids in winter wheat and winter barley fields (the original plan) turned out to be an inconvenient approach (chapter 3). During early population development (the most important phase in our study), no defined periods of immigration or age- or morph - specific population structures indicating immigration processes were detected. In spite of increased sampling frequencies (every four to five days in the Hannover region) and much larger sample sizes (in 2005 and 2006), the “snapshot views” of the situation in the fields were insufficient for elucidation of migration (i.e. immigration) events. Suction trap catches (and partly yellow water trap catches), on the other hand, were better able to provide information about migration events (chapter 6). They are the most important tools used to determine the population of cereal aphids in aerial plankton (Malloch et al., 2006). This was shown using predictor variables in gradation (chapter 2) or migration model calculations (chapter 3). Weekly suction trap catches reliably provided the smallest coefficient of variation among sampling methods (chapter 6).

In spite of detailed daily suction trap catches from many case studies, and in spite of focusing on light hours of a given day, the correlations and regressions between meteorological factors and migration events were rather weak ($R^2 < 0.22$; chapter 3). We can only speculate the reasons. However, vagaries of weather may be partly responsible. In both maritime and continental climate zones, there are days of extreme weather fluctuations. An aphid may not be motivated to take-off on a rainy morning with strong gusts of wind and moderately low temperatures (Mann et al., 1995). However, if the weather conditions improve and the temperatures increase during the afternoon, higher numbers of aphids may take-off and land in suction traps (Friesland, 1994). Adverse weather conditions for the flight of cereal aphids were also shown to delay but not to prevent take-off readiness (Walters & Dixon, 1984). For more exact determination of migration, it might be better to check suction traps several times a day, especially on days when changing weather conditions prevail. Moreover, meteorological parameters may remain near optimum for several consecutive days without any winged cereal aphids landing in suction traps (as discussed in chapter 3).

Comparison of locations

Due to the limited number of case studies, we could not compare suction trap data from different locations in order to assess individual model results among the locations (suction trap sites). It is possible that the developed migration models may primarily be valid in the continental regions (as gradation models in chapter 2), because only a few datasets used for model construction and validation were available from non-continental locations (i.e. Hohenheim and Rostock; chapter 3). Moreover, sites with predominantly (or exclusively) holocyclic aphid development displayed more stable patterns than sites with a balanced proportion of holocyclic or anholocyclic strategies, or with exclusively anholocycle strategies (chapters 1 and 2; Pierre & Dedryver, 1985; Hansen, 1999). However, more case studies are needed to compare the performance of the different models and to detect flight patterns in different locations according to Hullé et al. (1994).

Improvement of migration models

Early research focussed on the effects of temperature thresholds on flight activity of cereal aphids in spring (Wiktelius, 1981; Walter & Dixon, 1984). Predictive models have been developed based on correlations between temperature and specific flight activities, such as the date of the onset of spring migration (Harrington at al., 1990) or weeks with 0, 25, 50, or 75% of seasonal catches (e.g. in spring; Clark et al., 1992). According to Veenker (2000), temperature sum standards (starting from January 1st with a basic temperature of 4°C) are appropriate to indicate the start of flight activity after holocyclic hibernation. Concerning autumnal flight activity, further studies are necessary to clarify the key factors for immigration and early population development. The area of maize (as possible secondary host plant in late summer), the growth (in time and space) of volunteers on harvested areas, and the weather situations (e.g. dry and hot or humid and temperate) may be important qualitative variables for further statistical analyses to improve autumnal migration models.

The waves of migration during a year are commonly divided into three periods: spring, summer, and autumn migration; each period may vary between locations (MaCaulay et al., 1988; Hullé et al., 1994). However, the limits between these migration periods change and have to be adjusted in each year. Using multivariate descriptive analyses (e.g. cluster and discriminant analyses), Hullé et al. (1994) studied global patterns of flight phenology (phenomenological models) for different locations in France. The authors compared the flight phenologies of *R. padi* using data from suction traps set-up throughout France between 1978 and 1988 (91 case studies). They found certain patterns at different locations. In our case studies, no such flight phenology patterns were observed (data not shown). This was mainly a result of variation of the catch periods and a considerable low number of case studies with "complete" datasets (with spring, summer, and autumn migration data). Some trapping sites stopped checking the traps by the end of June, and others collected trap data for only a short period in autumn (e.g. end of September to mid-October). In contrast to Clark et al. (1992), we could not identify certain days on which 10%, 20% or 50% of all spring migrating cereal aphids were caught in suction traps (data not shown). In addition to the above-mentioned problems, certain species (e.g. *M. dirhodum*) or morphs (e.g. males) were not recorded at all in some cases.

The detection of typical, phenomenological flight patterns in certain locations should also make it possible to improve forecasting cereal aphid flight activity (Hullé et al., 1994). Coupling such phenomenological models with the migration models (i.e. the potential migratory events of a given day, chapter 3) may help to predict the range of flight activities in a given season and, finally, to assess the infestation potential with cereal aphids and, furthermore, the infection potential of vectored virus such as BYDV (chapter 3). These results will ultimately lead to efficient monitoring (in time and space) and may help to improve decision support systems to control cereal aphids. However, this requires more datasets with synchronised catch-periods among all suction trap locations throughout the year.

The flight phenology of aphids results from a number of abiotic and biotic factors (chapter 3). Purely descriptive models of flight activity based solely on meteorological parameters are therefore incomplete, as discussed in chapter 3. Although the analysis was time-restricted and based on a simplified data structure, only one significant relation between the numbers of cereal aphids in different seasons was directly detected (i.e. for *R. padi*; chapter 3). As rare as every sixth year, significantly higher aerial populations of *R. padi* in spring have been reported, when a large number of *R. padi* were caught in the suction trap in previous autumn. No such correlation was detected for other cereal aphid species and for field catches. Several factors influencing the spread of cereal aphids, including natural enemies, are known. When estimating the effects of aphid antagonists, both their potential to reduce aphid numbers by predation and their stimulation on aphid dispersal should be considered. Annan et al. (1999) found a positive correlation between the spread of *A. craccivora* and the incidence of antagonists in cowpea fields; however, other factors (e.g. wind speed) also influenced aphid dispersal (chapter 3). Nothing is known about the *relative importance* of antagonists as compared with other factors (such as temperature, wind speed, precipitation, host plant quality or aphid population growth), and the individual contributions of different factors to the total effect of migration events remain unclear (Irwin et al., 2007). Our migration models refer to meteorological influences on take-off activity (i.e. ascent), which is of major importance for dispersal (chapter 3). However, horizontal translocation and stimulation of landing (plant selection) are important activities that also determine the level of potential cereal infestation. Meteorological conditions favouring long-distance transport within the planetary boundary layer are seasonal in occurrence. They might determine migratory events (*sensu stricto*) during specific periods of the year (frequently in late spring, summer, and autumn) in association with meteorological events (Scott & Achtemeier, 1987; Isard & Gage, 2001). However, the relevance of these weather events is not defined and is beyond the scope of this study. Moreover, at some point during its dispersal flight (movement), the aphid's behaviour switches from the migratory mode to the landing mode (plant selection). The mechanisms behind this behavioural change are still largely unknown (Taylor, 1986; Isard et al., 1990), but meteorological conditions, the physiological state of the aphid, and the distance already travelled (duration of flight activity) may play a major role (Isard et al., 1990; Gage et al., 1999; Isard & Gage, 2001). However, the lack of detailed migration data may have contributed to the partial weakness of modelling results, e.g. for the "*S. avenae* and *M. dirhodum* fly" model (chapter 3).

Based on the results of chapters 2 and 3 (i.e. forecast models for gradation and migration), it seems to be possible to improve the spring migration models for *S. avenae* and *M. dirhodum* (model "*S. avenae* and *M. dirhodum* fly"; chapter 3). Case studies with gradation exhibited higher numbers of those aphids, which in turn led to a greater basic population (*n*), as determined based on the daily suction trap catches (chapter 2). It might be of advantage to exclude non-gradation case studies in order to exclude the many days without cereal aphid catches from the analyses. The remaining days might then show more distinct effects of meteorological parameters on migration activities (i.e. higher bias due to reduced overall aphid population).

Validation methods for the developed models

The validation of the gradation (chapter 2) and migration (chapter 3) models were performed with different methods (empirical-, cross classification-, independent data-method, and ROC analyses). Whereas the first methods are frequently used for validation (Afifi & Clark, 1999; Madry, 1997; Ellner & Rees, 2006), the ROC analyses are rare and frequently unknown, and therefore, they will be presented here more in detail (Pepe, 2000; Holmes et al., 2007; Manzato, 2007). Comparing the different ROC curves, excellent predictions were found for gradation models (i.e. submodels “winter conditions” and “real migration”; chapter 2). Here, the reader may refer on the value of ROC analyses, which is specified in detail for the gradation model (i.e. submodel “winter conditions”, Fig. 4 in chapter 2) and for the autumnal migration model “≥ 10 aphids fly”. Even for small values of the fraction of case studies without gradation incorrectly classified as gradation, it is possible to get a large fraction of case studies with gradation correctly classified as gradation. Conversely in the autumnal migration model, it is obvious that a high fraction (e.g. 0.80) of days with migration classified as migration day results in a fraction of about 0.60 of non-migration days classified as days with migration, indeed an unacceptable level. The bisection line in the ROC curves represents the chance-alone assignment (i.e. flipping a coin; Afifi & Clark, 1999). Even when the final model is significant, the ROC curves can estimate the model performance: the closer the ROC curve is to the bisection line, the higher the probability that *other* (but not necessarily *more*) predictor variables are needed in order to ameliorate the logistic regression or discriminative model.

If it is assumed that the prevalence (or frequency) of case studies with gradation in a given region is rather low, then a cut-point (i.e. a cereal aphid threshold level) on the lower part of the ROC curve is chosen (e.g. ≥ 5 cereal aphids per ear and flag leaf; Fig. 4 in chapter 2), since most of the case studies are without cereal aphid gradation (which is congruent to observations; chapter 2; Freier et al., 2001); and (too) many non-gradation case studies should not be classified as gradation case studies (Fig. 4, chapter 2). A case study would be assigned with cereal aphid gradation only if we were quite sure that the actual location-year had extraordinary high cereal aphid populations (i.e. so-called “strict threshold”; Afifi & Clark, 1999). The major drawback of this approach is that many case studies with gradation would be missed; doubtless dramatically and not acceptable for model introduction in practical management systems (Basedow et al., 1994; Pepe, 2000). However, if case studies are assumed from regions with frequently high rates of gradations, then a cut-point higher up the curve should be chosen (Afifi & Clark, 1999). Then, a case study would be referred to as gradation if there is any (small) indication that the location-year might fall in that group. Very few case studies with gradation would be missed, but non-gradation case studies would be grouped as case study with gradation (what is called “lax threshold”; Afifi & Clark, 1999).

In general, the ROC curves are most frequently used in deciding, which of several models (and their accordingly predictor variables) to use (Afifi & Clark, 1999; Pepe, 2000; Holmes et al., 2007). All else being equal, the one with greater area (preferably close to one) should be chosen (Swets, 1973; Metz, 1978). However, it is also possible to choose the model with greatest height to the ROC curve at a desired cut-point (Metz, 1978; Afifi & Clark, 1999; Manzato, 2007).

Dispersal and migration in the context of population genetics

In chapter 4, the relative importance of proximity between winter and summer hosts on the immigration and early population development of host-alternating aphid species in cereal fields was assessed. Significant trends were observed with higher numbers of winter hosts in landscapes associated with higher counts of *R. padi* and *M. dirhodum* in the fields. In the first of three subplots with different distances to the hedge (D_1: 0-8 m, D_2: 8-24 m, D_3: 24-60 m) significantly higher counts of *R. padi* were found in the cereal fields according to weekly evaluation from May to end of July each year. However, tracking the movements of *R. padi* populations from winter to summer hosts did not showed any detailed genetic structuring, and adjacent winter hosts (*Prunus padus*) were found to be a low source of *R. padi* colonizers of cereal fields across the whole colonization period. This was globally true, whatever the distance between the *P. padus* trees and the subplots were. Concerning the migration events, we therefore found indications that migration events in cereal aphids takes place on small-scale (in fields) as well as on large-scale (in landscapes) levels. Subsequently, the pro and cons of large-scale and small-scale migratory movements of cereal aphids, which were not yet discussed in chapter 4, will be disputed in more detail here, including the techniques used for tracking cereal aphid movement.

Holocyclic vs. anholoyclic life strategies

The ratio between asexual and (facultative) sexual lineages is expected to differ among locations, where continental areas (such as eastern Germany) characterized by harsh winters should favour the sexual strategy (Papura et al., 2003; Halkett et al., 2004). Hiddestorf is located in central Germany, where more continental climate is prevailing. The winter 2005/2006 was harsh (e.g. > 105 frost days between November 15th and May 1st), and no anholocyclic hibernation was observed in the study locations. Though, the most asexual lineages in the whole region may have been erased. Moreover, our detailed sampling protocol may have led to the low numbers of clones (as discussed in chapter 4). Contrary, mild winters have been reported from western France and the U.K., where anholocyclic species were frequently observed (Dedryver, 1981; Walters & Dewar, 1986; Helden & Dixon, 2002). Interestingly, it seems that Germany is just situated between the more or less distinct zones of different lifecycle strategies of cereal aphids. That situation may favour the asexual lineages on the costal sides (e.g. at location Carolinensiel) or in the West (at location Wörth), whereas sexual lineages seems to be more prevalent in the middle (at location Hiddestorf) and eastern zones (at location Magdeburg) of Germany.

Several studies (Loxdale et al., 1985; Simon et al., 1999b; Vorburger, 2004) have shown that different life cycle types are geographically distributed. The life cycle types of *S. avenae*, for example, were distributed in the UK. Based on the latitude, the frequency of anholocycly or holocycly decreased or increased, respectively, towards the north (Walters & Dewar, 1986; Helden & Dixon, 2002). Simon et al. (1999b) found that a relation between colour and lifecycle was connected to climatic and photoperiodic conditions based on the latitude. The widespread occurrence of some genotypes was taken as evidence of long-distance migration of *S. avenae* (Simon et al., 1999b). Our results likewise showed that a large number of genotypes were present at the study locations, emphasizing the aspect of long-distance migration and the predominance of holocyclic clones. However, no comparable datasets are available for German *R. padi* populations, and more research is needed to clarify this aspect (chapter 4).

Dispersal behaviour

Migration (*sensu stricto*) might be the driving force behind the dilution effects and responsible for the large exchange in density dependences (chapter 4). Cereal aphids (e.g. *S. avenae*) take-off at higher wind speeds than other aphids (Walters & Dixon 1984) and therefore might passively disperse over large areas. In addition *S. avenae* showed a high disposition to migrate (including walking) within cereal fields (Dean 1974, DeBarro et al. 1995a, b). The high mobility of cereal aphids is supported by studies using molecular markers that revealed a rather homogenous population structure all over Great Britain (Llewellyn et al., 2003). The major benefit from highly mobile aphids might be that possible resources can be captured at optimal leading to higher ecological dimension (including colonisation, reproduction, and survival; Dixon, 1998; VanEmden & Harrington, 2007). However, it can also be argued that migration over great distances would be contra-productive in several ways. Migrating cereal aphids take longer to develop, suffer delayed reproductive development, smaller gonads, and reduced fecundity as costs of flight (Dixon & Wratten, 1971; Dixon & Kindlmann, 1999; Müller et al., 2001). Moreover, they have a low probability of survival, because only few aphids will find and colonize new hosts (Dixon, 1998; Ward et al., 1998). Therefore, the strategy in migration seems to be based on the idea that enough aphids will encounter more favourable environments to colonise, reproduce, and survive. However, this is a critical bottleneck, and further investigations about the sense of migration are needed. Moreover, it is not clear, why increased counts of *R. padi* were found with lower temperatures in May in several locations in 2004 (as discussed in chapter 4). As the angle of ascent in spring is smaller than in autumn, and alatae took-off under predominately stable atmospheric conditions, they were more likely transported short distances. This is mainly because aphids will not escape the surface boundary layer and thus are unaided by positive atmospheric forces and cannot move long distances (Isard & Gage, 2001; Irwin et al., 2007). Increased knowledge about the density dependences may therefore help to better estimate from where and to what extend cereal aphid clones could immigrate and colonise field crops.

Population genetics - subpopulations

Most comparable studies using molecular marker techniques to track movements of flying insects are indirect analyses, because changes in genotype frequencies were evaluated and the subsequent migration events inferred (Loxdale & Lushai, 1998). More direct deduction of movement is achieved when a particular genotype occurs at high frequencies in two comparable populations, and was absent in one of the populations before. Our comparisons of subpopulations of the first evaluation days (June 20th and 27th, chapter 4) were therefore more direct, because *R. padi* populations were absent in the adjacent winter cereal fields (due to missing anholozyclic individuals) before they arrived later (e.g. from their winter hosts).

Interestingly, the first colonisers were replaced, as discussed in chapter 4. Since only a few studies provided long-term seasonal evaluations (several evaluation days within a given season), we cannot determine whether the replacement (or displacement) of certain genotypes is a frequently occurring effect (Reimer, 2004). However, the identified clones of several subpopulations (e.g. tree no. 6 and 9) did not contribute to a shared genotype. This was possibly because the genotype had arrived later or was not detected in sampling due to the predominance of other clones. At this, the sampling effect may have biased the results, as discussed in chapter 4.

Migration models

The migration models describing days with and without flight activity of cereal aphids are rather weak (chapter 3) compared to gradation models (compare validation results in chapters 2 and 3). Full exclusion of certain days (i.e. negative prognosis) without the arrival of cereal aphids in crops (or without landing in suction traps) was not even possible. Firstly, the migration models classify the migration potential of a day (day with or without migration) with moderately low accuracy in autumn and spring (chapter 3), and therefore the reliability of a negative prognosis is also weak. Problems in identifying meteorological parameters that describe optimal conditions for migrating cereal aphids have been reported in field studies (Wiktelius, 1981; Clark et al., 1992). Unfavourable weather conditions were found to retard but not prevent the take-off readiness (Walters & Dixon, 1984), which was corroborated by our datasets (chapter 3). Secondly, we cannot exclude (i.e. in terms of a negative prognosis) the settling (colonisation) of aphids on the different cereal crops or cultivars (as reported in chapter 5). Interestingly, the area with summer hosts (i.e. either winter barley or winter wheat) did not influence the intensity of immigration and early population development, neither for *R. padi* nor for *M. dirhodum*, since the corresponding qualitative variable in ANCOVA was not significant (chapter 4). This is different to immigration and early population development in autumn, because winter barley frequently supports higher levels of cereal aphids than winter wheat (Geissler et al., 1989; Huth, 1990). However, the higher autumnal population levels found in winter barley were often related to earlier sowing than was the case in winter wheat (Aßmann & Hamann, 1991; Kleinhenz, 1994). Concerning the negative prognosis attempt, it should be considered that cultivars can influence the settlement behaviour of cereal aphids (as shown in chapter 5). Moreover, we have not detected a clear influence of a given landscape structure on the settlement behaviour and early population build-up (chapter 4): Comparing early population development between locations, earliest migration and greatest numbers of cereal aphids were found at Wörth, a site situated in a small-scale structured landscape. However, the contrary was found at Wahlbach, which is situated in a similarly structured landscape type only approx. 120 km north of Wörth. At Wahlbach, aphids arrived very late after winter and in numbers lower than those in Wörth. General conclusions should be drawn with care, because data from only a few case studies from such diverse landscapes were available in our study. However, it seems that the effect of landscape structure is lower than that of temperature (e.g. during wintertime): the mean temperature in February in Wörth, the warmest location, was 3.6 ±0.4°C compared to only 1.7 ±0.4°C in Wahlbach, the coldest location. Interestingly, cereal aphids arrived at the low-structure locations Bernburg and Magdeburg (mean temperature in February: 2.2 ±0.4°C) later than at other locations where winter temperatures were not as low as at Wahlbach. Aphid antagonists also arrived late in those locations. However, the scope of our investigation was too small to provide more detailed conclusions on the effects of landscape. Further research activities, including more detailed descriptions of landscape structures (e.g. using GIS-based programs like ARCVIEW), evaluation of cereal aphid antagonists, and genotypic differences in cereal aphids in different locations (Reimer, 2004) and host plants (Vorburger et al., 2003a) are therefore essential.

Host plant interactions

Interactions between host plants (e.g. cultivars) and winged colonizers can be important for immigration and early population development, as different plant growth stages are known to affect aphid growth and development (chapter 5; Leather & Dixon, 1981). Therefore, we also compared cultivars of winter wheat in terms of their attractiveness and suitability as hosts for cereal aphids by performing visual counts and cage experiments, etc. (chapter 5). Since no superiority of a given cultivar was observed, it seems that the attractiveness of wheat cultivars for winged aphids during spring immigration and following antibiosis reactions are of minor importance as input variables for migration and population modelling. Although cereal aphids are considerably poor flyers, visual and olfactory responses were found to influence the settlement behaviour among different plant species (Hardie, 1989; Nottingham et al., 1991a, b; Petterson et al., 1994; Park et al., 2000). After landing, aphid behaviour is affected by plant morphology and chemistry, which is tested in sequence by the aphid's probing behaviour. However, the differences among cultivars in the field have been shown to be more or less marginal (Havlickova, 1997, 2001; Bundessortenamt, 2006), and the cultivars showed a similar nutritional status or plant growth stages (chapter 5). Host plant resistance may have a far greater potential for reducing cereal aphid populations than previously assumed. The prime example for highly effective and dramatic host plant resistance is the 'Avoncrisp' lettuce to *Pemphigus bursarius* L. Although the cultivars covered a broad range of genotypes and qualities, we assume that the genetic range of the prevailing material of current winter wheat cultivars is rather narrow. Concerning the overall population level in a given season, other factors like plant nutrition or weather conditions that determine the growth pattern of the host plants (e.g. the duration of sensitive growth phases) are of major importance for aphid population dynamics and subsequent yield reactions (as discussed in chapter 5).

Mean relative growth rate (MRGR)

More detailed criticisms may focus on the techniques used to compare the performances of aphids (i.e. antibiosis) on different cultivars. Growth rates (i.e. increase in aphid size) and developmental rates (i.e. increase in fecundity or longevity) of individual aphids can be reliable indicators of future population growth rates (Leather & Dixon, 1984; Leszczynski et al., 1989). Growth rates are a function of aphid birth weight. Since large aphids grow faster than small ones, growth rate analyses must be corrected for differences in initial weight. Radford (1967) therefore proposed use of the mean relative growth rate (MRGR, in µg / µg / day), which is based on the logarithmic weight gain of an aphid. The MRGR has been used in many studies requiring quick estimates of aphid performance under different treatment conditions outside the field (VanEmden, 1969; Leszczynski et al., 1989; Telang et al., 1999). However, we used clip cages (antibiosis experiments) and have therefore focussed more on potential fecundity (the reproductive potential of an individual aphid), as was frequently reported in similar studies (Berg, 1984; Carroll & Hoyt, 1986; Lamb et al., 1987; Lamb, 1992). When studying aphid development under different treatment conditions (i.e. different cultivars), clip cages have the advantage that aphids can develop inside the cages without frequent disturbances (Dixon, 1998; Telang et al., 1999). When MRGR analyses are performed, a very accurate micro balance and skilled manual handling of aphids are required, because aphids can weigh as little as 30 µg (Dixon, 1998). The slightest inaccuracy in initial weight measurement can have a tremendous effect on the final MRGR value, which is based on the logarithmic nature of insect growth. In order to obtain precise weighing results, one must therefore perform a large number of replications, which results in frequent disturbances of development rates of aphids in cages, for example (Dixon, 1998; Awmack & Leather, 2007).

Genotypic heterogeneity

A further important aspect and possible point of criticism is that we used only one aphid genotype to assess the attractiveness and host suitability of winter wheat cultivars (e.g. in settlement experiments). Earlier studies using molecular marker techniques demonstrated adaptation (and resistance) to host plants and the prevalence of certain genotypes with host preference (DeBarro et al., 1995a,b; Lushai et al., 2002). The authors found that populations of *S. avenae* were recognized by their performance on different hosts. Moreover, different life cycle characteristics (anholocycly, holocycly) and body colours indicated that aphids collected from barley, oats or wheat can differ considerably (DeBarro et al., 1995a, b). Similar host-clone relations have been shown in many other studies in aphids in general (Weber 1985b; Sunnucks et al., 1997a; Haack et al., 2000; Figueroa et al., 2005). However, the scope of our investigations were not detailed enough to relate similar selection strategies in the wheat-aphid complex, as immigrating aphids were counted on tillers (settlement behaviour experiments; chapter 5).

Concerning the antibiosis experiments, it can be argued that we did not test enough clones of cereal aphids to draw conclusions, since not all clones adapted to winter wheat will necessarily show the same cultivar-specific reactions. Increasing the number of clones multiplies the work tremendously while hardly increasing the probability of detecting an extremely rare, virulent genotype (Figueroa et al., 2004). Therefore, it is appropriate to use a single clone when characterising and searching for resistance to an aphid pest, as long as that clone is known to be adapted and virulent to the target crop in the study area. The aim of our cultivar experiments was neither to show the factors involved in the resistance of winter wheat cultivars towards cereal aphids nor to detect every single resistance effect in every cultivar. We assessed the attractiveness and host suitability of eight current productive winter wheat cultivars. None of the cultivars (covering a broad range of different genotypes and qualities) showed a superior impact of resistance. This may not exclude the possibility that other cultivars or aphid genotypes will react differently but, according to the current knowledge of current winter wheat cultivars, it seems to be quite implausible (Rossberg et al., 2005; D. Rentel, pers. comm.). Moreover, literature reviews came to similar conclusions (Riedell et al., 1999; Havlickova et al., 2000; Schotzko & Bosque-Perez, 2000).

Evaluation techniques for insect populations

Cereal aphid population dynamics

The appropriate sample technique and sample size are possibly the most crucial factors, to assess either cereal aphids, or their antagonists in fields (as pointed out above). Jarosík et al. (2003) could not demonstrate population growth of cereal aphids at very low densities (in early spring), when they assessed 300 tillers in individual field plots. However, after pooling all field plots, sample sizes ranged from 2,400 to 30,600 (with mean numbers of 12,900 tillers per field plot) and exponential growth became obvious, even at low cereal aphid densities early in the years. Ward et al. (1985b) pointed out that estimations of sample size are frequently unreliable at very low aphid densities and that the required sample size increases rapidly to “infinity”, if the densities are less than e.g. one aphid per tiller (chapter 6). Such densities are typical for the start of the population growth (e.g. after immigration) as shown in our study and Kindlmann et al. (2007) added that the same problem applies to suction trap catches.

Sample size is critical, and it is always a battled compromise between efforts in terms of technique equipment, time, labour, and the desired sensitivity. Getting no significance in differences between subplots when using a sample size of 300 tillers for the assessment of settlement behaviour in different wheat cultivars (chapter 5), or in plots adjacent to winter hosts (chapter 4), thus does not necessary mean that there is no influence. However, the probability for false results is small. Subsequently, the scattered appearance of cereal aphids (i.e. evaluation days with and without insects) during weekly field evaluations in early spring (i.e. until mid or end of May) does not mean that these populations were present/absent or not growing at all (Jarosík et al., 2003). Therefore, either the sample size must be very high (as pointed out in chapter 6), or the results from studies with small sample sizes (i.e. at an early population development before May) must be regarded with caution (i.e. predator units in small scale experiments in chapter 4).

Comparing the different sampling techniques for cereal aphids in autumn and spring (chapter 6), we have used sets per sampling point (i.e. sampling units) comprising 50 to 60 plants or 10 tillers. Elliott et al. (1990) stated that sampling sets of several plants or tillers is advantageous over sampling individual plants or tillers (especially on large-scale fields in eastern Germany; Freier et al., 2001). These sets should be systematically spaced within the field depending on size of the sample area to ensure the coverage of the majority of the sample area. This resulted in a relatively high number of sampling points, where counts are made on absolute numbers of plants or of tillers. These high numbers of sampling points are necessary to reflect the aggregated distribution of cereal aphids (as discussed above; chapter 6).

Sampling populations of small arthropods such as aphids in winter cereals is indeed laborious; and the numbers of high sample sizes needed for a certain level of precision are found of discouraging at first sight, but they will pay-off by detailed specifications on the population developments. In our study, estimates were based on numerical, visual counts. Binomial sampling is based on parameters, which describe a relationship between mean density and the proportion of sample units with no more than a certain number of aphids (so-called tally thresholds "T", which represent thresholds of individual pests). While being easier and less costly, binomial sampling usually requires more samples than complete (or detailed) counts, because from each sample unit only the presence or absence of the pest could be extracted. This trade-off may discourage the use of binomial sampling plans in population monitoring. However, if a given pest species follows the Negative Binomial distribution, there exists an optimal value of "T" for which the binomial sampling is most robust (Binns & Bostanian, 1990). These "T" values would be best considered when aphid populations are sampled at a density of one or more aphids per tiller using binomial counts. In late spring and summer, populations of more than three aphids per tiller are frequently found. At low densities, i.e. less than one aphid per tiller, binomial sampling is practically feasible only if based on empty tillers rather than any other tally thresholds (Feng et al., 1993). However, when no tillers are available (i.e. GS 11-29), it remains questionable if the sampling burden of a low aphid population density may be further reduced by sampling methods such as the binominal sampling. Conversely to spring and summer, colonies of five to eight cereal aphids per sampling point (i.e. per 50 or 60 plants, or per 0.25 m²) were rarely found in autumn. Moreover, plants are very small in autumn and have to be inspected rigorously, regardless of whether binomial or numerical counts are performed. We can neither provide sufficient data on binomial counts using the visual sampling technique, nor about the feasibility (during autumn and early spring), which therefore remains speculative. But, it intuitively seemed that there were no huge differences between the two modes of counts and the subsequent reductions in sampling time, searching aphids visually on small plants. Probably, there may be a greater advantage using binomial counts with the evaluation technique of plant samplings. However, the use of presence / absence data, is not always a solution as discussed by Ward et al. (1985a, b). The saving in time is associated with a decrease in accuracy, or an increase in the sample size is required to obtain the same data quality (Elliott et al., 1990). Further investigations are a must, which than allow to shed light on the appropriateness of binomial sampling plans for aphids in autumnal cereals.

Effects of natural enemies

In recent years, an impressive body of knowledge on the biology and ecology of cereal aphid antagonists has been accumulated (Dedryver, 1981; Storck-Weyhermüller, 1988; Hoeller, 1990; Volkmar et al., 1994; Bothe & Heimbach, 1995; Freier & Triltsch, 1996). For example, aphid specific predators (Coccinellids, Syrphids) showed high voracity and a good synchronisation in time and space with cereal aphids in winter wheat (Freier & Triltsch, 1996; Tenhumberg, 1997). This can greatly reduce the rate of population increase as supposed by Poehling (1988) and Elliott et al. (1997). In practice, however, the careful choice and application of pesticides as well as habitat modifications are so far the only resulting IPM activities related to enhanced biological control (Poehling et al., 2007). Moreover, some researchers questioned that aphid metapopulation dynamics (i.e. before cereal aphid population crash in mid or end of July) are driven by predators or that predators are responding to aphid abundance (Kindlmann & Dixon, 1996, 1999). Similarly, we could not detect influences of predators when using the approach of predator units to summarize the possible effects of antagonists on aphid gradation (chapter 2). However, confusion about effects of antagonists may be most frequently related to survey techniques, especially when time periods early in the season with low aphid and antagonist densities are considered. Rappaport (1998) ascertained that the evaluation method of predators in the form of visual counts (during GS 69 to 85) may cause underestimations of the whole antagonist potential. Even sample sizes of e.g. 800 tillers may not be sufficient for reliable estimations of density (e.g. relative abundance) and subsequent classification will lead to rough statements of high or low predator units per area (chapter 6). The same was observed in our studies, when individual antagonists of aphids were compared among evaluation times. Even the summarisation into predator units showed scattering mean values with high standard deviations, which were clearly based on sample size and sampling techniques. Moreover, apart from sample size, the sampling technique itself may be inconvenient to get a clear picture about the abundance of different predators. The evaluation of ear and flag leaves for example underestimates mainly the larval stages of aphid specific predators such as Coccinellids or Syrphids (data not shown). Kuo-Sell und Hasken (1989) tracked well the population dynamics of adult specific predators (i.e. red shining ladybeetles) using 50 whole tillers at milky stage (GS 77). Doubling the sample sizes, they were also able to register larval stages of hoverflies (i.e. Syrphids), but not those of ladybirds or of common green lacewing. Therefore, visual counting of tillers seems to give only an approximate estimation of stenophagous predator larvae. Most antagonists of cereal aphids are highly mobile, not very abundant insects, and their survey - a compromise between reliability and work load - is extraordinary difficult as discussed in chapter 6 (Freier et al., 1998).

Most scientific methods, e.g. repeated measurement (e.g. counting) or the use of mobile suction samplers, are very labour- and time-intensive and therefore not appropriate for practical survey by farmers (Iperti et al., 1988, Elliott et al., 1991). Moreover, several methods are strongly dependent on the weather conditions or on the daily rhythmic of scanned species (and their preys) (Frazer, 1973; Neuenschwander, 1984; Schotzko & O'Keefee, 1989). In consideration of these factors, however, Elliott et al. (1991) und Rappaport (1998) showed that e.g. the densities of Coccinellids were well estimated using sweep net catches and transects counting (at later growth stages). This was also approved with own datasets in 2005, when higher numbers were observed. Problematically in terms of visual counts (GS 71 to 85) is that adults of *Propylea quatuordecimpunctata* L. were more likely overlooked compared to red-shining *Coccinella septempunctata* L. Moreover, field advisers are sometimes more willing to count just those tillers, where they have perceived the red-shining from far. Using small sample sizes, the precision fell considerably (chapter 6) and especially non-experienced field advisers evaluated error-prone. Subsequently, techniques for early evaluations of cereal aphids using high sample sizes appeared to be not convenient to include counts of antagonists. However, visual counting is labour- and time-saving compared to other trapping techniques (as shown for cereal aphids in chapter 6). Concerning trapping only sweep net catches permitted a rough estimation of predator densities in the fields with relatively low labour input, when using a minimal number of 4×50 hits (sweeps), but considerably variability was observed among and between fields (chapter 6).

Future prospects

Problems encountered during predator analyses may have contributed to the fact that there was no predator-related predictor variable significantly associated with the formation of gradation (as discussed above). In future, precision farming (Werner, 2008) will be extended and in addition to GIS-based small-scale field datasets, information systems for crop density (e.g. crop meter; Quinckhardt, 2008) and optical surveys (Rath, 2008) might also be used. GIS-based datasets provide information about field altitude profiles (Brunsch, 2008) and, at the same time, site-specific data concerning the expected yield (based on yield calculations from previous years) are immediately calculated. Fertilisation will be adapted accordingly (exactly per square meter). Such systems are currently being tested in large-scale trials for practical application in Magdeburg (Brunsch, 2008). Concerning plant protection, it is advantageous to use GIS-controlled single nozzles, which prevent repeated treatments, for example, in sloping field areas. This technique permits a more uniform application of pesticides.

Furthermore, optical systems for weeds were recently developed (Rath, 2008). Whether these optical systems (i.e. image detection systems) can be extended to cereal aphids or all their antagonists during early maintenance activities (e.g. the first herbicide or fungicide application after winter) remains speculative. However, these systems may well detect the first occurrence of red-shiny old lady bugs (e.g. *C. septempunctata*, *Harmonia axyridis* Pallas, *Rodolia cardinalis* Mulsant, *Epilachna argus* Geoffroy) because they stand out from the green background. They may also provide very detailed information concerning the overall abundance of red lady bugs in a given location and year, which might be useful in modelling and decision support systems.

Closing statements

Cereal aphids are sedentary for most of their lives. However, their ability to *move* is so pivotal that several authors have elevated them to the status of super pests (Loxdahle et al., 1993; Irwin et al., 2007; H.D. Loxdahle, pers. comm.). Even though only a few aphid species are pests in cereal crops, they are able to move across large spatial scales, even transcending continents. Because of their high reproduction rate and vectoring capacity, cereal aphids can devastate crops within a very short time span (e.g. within the four weeks between flowering and the milky stage of winter wheat). If aphid movements were limited to very small spatial scales, even those species that are excellent vectors would play a much smaller role in spreading plant diseases such as BYDV. Research conducted during the past decades has provided a good theoretical understanding of aphid population dynamics. However, implementation of this knowledge into management decision-making practice continues to be rather disappointing. Therefore, aphids are both fascinating and frustrating (Dixon, 1998). As described in this work, forecasting the immigration and early population developments of aphids in agricultural systems is still challenging (e.g. modelling early population dynamics, chapter 1 and 2; forecasting models for immigration into cereal crops in autumn and spring, chapter 3). It is still difficult to determine, where the cereal aphids came from before arriving in a given field (chapter 4; Vialatte et al., 2007). However, this information would enhance the ability to forecast qualitative and quantitative aspects of aphid immigration into cereal crops. Thus, more research activities (long-term field studies) are needed to obtain a detailed understanding of how aphid immigration movement and early population development takes place. The subsequent understanding of how to modify it will then be the key to designing useful aphid control strategies in accordance with IPM concepts.

References

A'Brook J. 1968: The effect of plant spacing on the numbers of aphids trapped over the groundnut crop. *Annals of Applied Biology* **61**: 289-294.

Acreman S.J. & Dixon A.F.G. 1989: The effects of temperature and host quality on the rate of increase of the grain aphid (*Sitobion avenae*) on wheat. *Annals of Applied Biology* **115**: 3-9.

Afifi A.A. & Azen S.P. 1979: *Statistical Analysis: A Computer-oriented Approach*. Academic Press, New York, U.S.A., 442 pp.

Afifi A.A. & Clark V. 1999: *Computer-aided Multivariate Analysis*. Chapman and Hall, Boca Raton, U.S.A., 455 pp.

Agrawal A.A., Underwood N. & Stinchcombe J.R. 2004: Intraspecific variation in the strength of density dependence in aphid populations. *Ecological Entomology* **29**: 521-526.

Ahlers D. & Hindorf H. 1987: Epidemiologische Untersuchungen über den Schaderreger *Sclerotinia sclerotiorum* an Winterraps im Hinblick auf eine Prognose. *Nachrichtenblatt Deutscher Pflanzenschutzdienst* **39**: 113-119.

Anderson K. 1985: Situation of the integrated control of cereal aphids in Sweden. *SROP Bulletin* **8**: 54-55.

Annan I.B., Schaefers G.A. & Syxena K.N. 1999: Pattern and rate of within-field dispersal and bionomics of the cowpea aphid, *Aphis craccivora* (Aphididae), on selected cowpea cultivars. *Insect Science and its Application* **19**: 1-16.

Antignus Y., Lapidot M., Hadar D., Messika Y. & Cohen S. 1998: Ultraviolet - absorbing screens serve as optical barriers to protect crops from virus and insect pests. *Journal of Economic Entomology* **91**: 1401-1405.

Archetti M. & Leather S.R. 2005: A test of the co-evolution theory of autumn colors: color preference of *Rhopalosiphum padi* L. on *Prunus padus* L. *Oikos* **110**: 339-343.

Armitage P. 1955: Test for linear trend in proportions and frequencies. *Biometrics* **11**: 375-386.

Armitage P., Berry G. & Matthews J.N.S. 2002: *Statistical Methods in Medical Research*. Blackwell, Oxford, U.K., 277 pp.

Arzani A., Peng J.H. & Lapitan N.L.V. 2004: DNA and morphological markers for a Russian wheat aphid resistance gene. *Euphytica* **139**: 167-172.

Aßmann G. & Hamann M. 1991: Virusvektorenbekämpfung im Winterweizen - Ab wann ist eine Behandlung sinnvoll? *Gesunde Pflanzen* **43**: 149-151.

Awmack C.S. & Leather S.R. 2007: Growth and Development. In: VanEmden H.F. & Harrington R. (eds.): *Aphids as Crop Pests*. CAB International, Wallingford, U.K., 135 - 151 pp.

Backhaus G.F. 2008: *Kleinstrukturen in Agrarlandschaften*. Biologische Bundesanstalt für Land- und Forstwirtschaft. http://www.bba.bund.de/cln_044/nn_813794/DE/Home/pflanzen__schuetzen/integriert/kleinstruktur/kleinstruktur__node.html__nnn=true. Status: January, 2008.

Bailey S.M., Irwin M.E., Kampmeier G.E., Eastman C.E. & Hewings, A.D. 1995: Physical and biological perturbations: Their effect on movement of apterous *Rhopalosiphum padi* (Homoptera: Aphididae) and localized spread of barley yellow dwarf virus. *Environmental Entomology* **24**: 24-33.

Barbagallo S. & Suss L. 1986: Towards the integrated pest control in cereals in Italy. In: Cavalloro R. & Sunderland K.D. (eds.): *Integrated Crop Protection in Cereals.* Vol. 33. Balkema, Rotterdam, Netherlands, 25-31 pp.

Basedow T. 1980: Studies on the ecology and control of the cereal aphid (Homoptera: Aphididae) in northern Germany. *IOBC Bulletin* **3**: 67-84.

Basedow T., Bauers C. & Lauenstein G. 1989: Ergebnisse vierjähriger Untersuchungen zur gezielten Bekämpfung der Getreideblattläuse (Homoptera: Aphididae) im intensiven Winterweizenanbau: optimaler Termin und Bekämpfungsschwellen. *Mitteilungen der Biologischen Bundesanstalt* **254**: 1-63.

Basedow T., Poehling H.-M. & Lauenstein G. 1994: Untersuchungen zur Anpassung der Bekämpfungsschwelle der Getreideblattläuse (Homoptera: Aphididae) (Saugschäden an Weizen im Sommer) an die veränderten ökonomischen Rahmenbedingungen im Ackerbau. *Journal of Plant Diseases and Protection* **101**: 337-349.

Berg G.N. 1984: The effect of temperature and host species on the population-growth potential of the cowpea aphid, *Aphis craccivora* Koch (Homoptera, Aphididae). *Australian Journal of Zoology* **32**: 345-352.

Berry R.E. 1969: Effects of temperature and light on take-off of *Rhopalosiphum maidis* and *Schizaphis graminum* in field (Homoptera: Aphididae). *Annals of the Entomological Society of America* **62**: 1176-1184.

Berzonsky W.A., Ding H., Haley S.D., Harris M.O., Lamb R.J., McKenzie R.I.H., Ohm H.W., Patterson F.L., Pearis F.B., Porter D.R., Ratcliffe R.H. & Shanower T.G. 2003: Breeding wheat for resistance to insects. *Plant Breeding Reviews* **22**: 221-296.

Bianchi F.J.J.A. & VanDerWerf W. 2003: The effect of the area and configuration of hibernation sites on the control of aphids by *Coccinella septempunctata* (Coleoptera: Coccinellidae) in agricultural landscapes: a simulation study. *Environmental Entomology* **32**: 1290-1304

Bianchi F.J.J.A. & VanDerWerf W. 2004: Model evaluation of the function of prey in non-crop habitats for biological control by ladybeetles in agricultural landscapes. *Ecological Modelling* **171**: 177-193.

Binns M.R. & Bostanian N.J. 1990: Robust binomial decision rules for integrated pest management based on the Negative Binomial distribution. *Bulletin of the Entomological Society of America* **36**: 50-54.

Binns M.R., Nyrop J.P. & VanDerWerf W. 2000: *Sampling and Monitoring in Crop Protection: The theoretical basis for developing practical decision guides*. CAB International, Wallingford, U.K., 284 pp.

Blackman R.L. 1990: Specifity in aphid/plant genetic interactions, with particular attention to the role of the alatae coloniser. In: Campbell F.K. & Eikenbary R.D. (eds.): *Aphid - Plant Genotype Interactions*. Elsevier, Amsterdam, Netherlands, pp. 251-274.

Boeve P.J. & Weiss M.J. 1997: Binomial sequential sampling plans for cereal aphids (Homoptera: Aphididae) in spring wheat. *Journal of Economic Entomology* **90**: 967-975.

Boller E.F., Häni F. & Poehling H.-M. 2004: *Ecological Infrastructures: Ideabook on Functional Biodiversity at the Farm Level. IOBC/WPRS Commission on Integrated Production Guidelines and Endorsement.* Swiss Centre for Agricultural Extension and Rural Development (LBL), Eschikon, Switzerland, 83pp.

Bommarco R., Wetterlind S. & Sigvald R. 2007: Cereal aphid populations in non-crop habitats show strong density dependence. *Journal of Applied Ecology* **44**: 1013-1022.

Borgemeister C. 1992: Primär- und Hyperparasitoide von Getreideblattläusen: Interaktionen und Beeinflussung durch Insektizide. In: Nentwig W. & Poehling H.M. (eds.): *Agrarökologie*. Vol. 3. Haupt, Bern, Switzerland, 1-191 pp.

Bosque-Perez N.A., Johnson J.B., Schotzko D.J. & Unger L. 2002: Species diversity, abundance, and phenology of aphid natural enemies on spring wheat resistant and susceptible to Russian wheat aphid. *Biocontrol* **47**: 667-684.

Bothe S. & Heimbach U. 1995: Untersuchungen zur Erfassung und Bedeutung von Kurzflügelkäfern (Coleoptera: Staphylinidae) unter Berücksichtigung der Blattlauspopulation in Winterweizen. *Archives of Phytopathology and Plant Protection* **29**: 429-436.

Bottenberg H. & Irwin M.E. 1991: Influence of wind speed on residence time of *Uroleucon ambrosiae* alatae (Homoptera: Aphididae) on bean plants in bean monocultures and bean-maize mixtures. *Environmental Entomology* **20**: 1375-1380.

Bottenberg H. & Irwin M.E. 1992a: Flight and landing activity of *Rhopalosiphum maidis* (Homoptera: Aphididae) in bean monocultures and bean-corn mixtures. *Journal of Entomological Science* **27**: 143-153.

Bottenberg H. & Irwin M.E. 1992b: Canopy structure in soybean monocultures and soybean-sorghum mixtures: Impact on aphid (Homoptera: Aphididae) landing rates. *Environmental Entomology* **21**: 542-548.

Bromand B. 1990: Reduced dosages by chemical control of aphids in cereals. Danish plant protection conference. *Pest and Disease* **7**: 231-247.

Brunsch R. 2008: *Nachhaltige Ressourcenbewirtschaftung*. Leibniz-Institut für Agrartechnik Potsdam-Bornim e.V. http://www.atb-potsdam.de. Status: January, 2008.

Bundessortenamt (Federal Institute for protection and national listing of new plant varieties in Hannover) 2006: *Beschreibende Sortenliste 2006. Getreide, Mais, Ölfrüchte Leguminosen (großkörnig) und Hackfrüchte (außer Kartoffeln).* Deutscher Landwirtschaftsverlag, Hannover, Germany, 271 pp.

Caillaud C.M., Dedryver C.A., DiPietro J.P., Simon J.C., Fima F. & Chaubet B. 1995: Clonal variability in the response of *Sitobion avenae* (Homoptera: Aphididae) to resistant and susceptible wheat. *Bulletin of Entomological Research* **85**: 189-195.

Carroll D. & Hoyt S. 1986: Some effects of parental rearing conditions and age on progeny birth weight, growth, development, and reproduction in the apple aphid, *Aphis pomi* (Homoptera: Aphididae). *Environmental Entomology* **15**: 614-619.

Carter N. 1985: Simulation modelling of the population-dynamics of cereal aphids. *Biosystems* **18**: 111-119.

Carter N. & Rabbinge R. 1980: Simulation models of the population development of *Sitobion avenae*. *Bulletin SROP* **3**: 93-98.

Carter N., Dixon A.F.G. & Rabbinge R. 1982: *Cereal Aphid Populations: Biology, Simulation and Prediction*. Simulation Monograph. Pudoc, Wageningen, Netherlands, 91 pp.

Carter N., Entwistle J.C., Dixon A.F.G. & Payne, J.M. 1989: Validation of models that predict the peak density of grain aphid *Sitobion avenae* and yield loss in winter wheat. *Annals of Applied Biology* **115**: 31-37.

Castro V., Isard S.A., Gamez R., Fletcher J. & Irwin M.E. 1991: The microclimate of maize and bean crops in tropical America: A comparison between monocultures and polycultures planted at high and low density. *Agricultural and Forest Meteorology* **57**: 49-67.

Clark S.J., Tatchell G.M., Perry J.N. & Woiwod I.P. 1992: Comparative phenologies of two migrant cereal aphid species. *Journal of Applied Ecology* **29**: 571-580.

Cochran W.G. 1954: Some methods for strengthening the common χ^2 tests. *Biometrics* **10**: 417-454.

Cocu N., Harrington R., Hullé M. & Rounsevell M.D.A. 2005: Spatial autocorrelation as a tool for identifying the geographical patterns of aphid annual abundance. *Agricultural and Forest Entomology* **7**: 31-43.

Cooley W.W. & Lohnes P.R. 1971: *Multivariate Data Analysis.* Wiley & Sons, New York, U.S.A., 176 pp.

Constanza M.C. & Afifi A.A. 1979: Comparison of stopping rules for forward stepwise discriminant analysis. *Journal of the American Statistical Association* **74**: 777-785.

Corander J., Waldmann P. & Sillanpa M.J. 2003: Bayesian analysis of genetic differentiation between populations. *Genetics* **163**: 367-374.

Corkum L.D., Ciborowski J.J.H. & Dolan D.M. 2006. Timing of Hexagenia (Ephemeridae: Ephemeroptera) mayfly swarms. *Canadian Journal of Zoology - Revue canadienne de Zoologie* **84**: 1616-1622.

Cytel Cooperation 2008: The StatXact User Manual. http://www.cytel.com/home/default.asp. Status: January, 2008.

Dean G.J. 1974: Overwintering and abundance of cereal aphids. *Annals of Applied Biology* **76**: 1-7.

DeBarro P.J. 1991: Attractiveness of 4 colours of traps to cereal aphids (Homoptera: Aphididae) in South-Australia. *Journal of the Australian Entomological Society* **30**: 263-264.

DeBarro P.J., Sherratt T.N., Brookes C.P., David O. & Maclean N. 1995a: Spatial and temporal genetic variation in the population structure of the grain aphid, *Sitobion avenae* F. (Hemiptera: Aphididae). *Proceedings of the Royal Society of London* **262**: 321-327.

DeBarro P.J., Sherratt T.N., Carvalho G.R., Nicol D., Iyengar A. & Maclean N. 1995b: Geographic and micro-geographic genetic differentiation in two aphid species over southern England using the multilocus $(GATA)_4$ probe. *Molecular Ecology* **4**: 375-382.

Dedryver C.A. 1981: Biology of the cereal aphids in the West of France. 2. Spatial and temporal distribution and field pathogenicity of 3 species of entomophthoraceae. *Entomophaga* **26**: 381-393.

Dedryver C.A. & Gelle A. 1982: Biology of the cereal aphids in the west of France. 4. Overwintering of anholocyclic populations of *Rhopalosiphum padi* L., *Metopolophium dirhodum* Wlk., and *Sitobion avenae* F. on cereal volunteers in 3 places in Brittany and in the Basin of Paris. *Acta Oecologica - Oecologia Applicata* **3**: 321-342.

Dedryver C.A. & DiPietro J.P. 1986: Biologie des pucerons des céréales dans l'ouest de la France: VI-Étude comparative des fluctuations au champ de *Sitobion avenae* F., *Metopolophium dirhodum* Wlk. et *Rhopalosiphum padi* L. sur différents cultivars de blé d'hiver. *Agronomie* **6**: 75-84.

Dedryver C.A., Riault G., Tanguy S., LeGallic J.F., Trottet M. & Jacquot E. 2005: Intra-specific variation and inheritance of BYDV-PAV transmission in the aphid *Sitobion avenae*. *European Journal of Plant Pathology* **111**: 341-354.

Delmotte F., Leterme N., Gauthier J.P., Rispe C. & Simon J.C. 2002: Genetic architecture of sexual and asexual populations of the aphid *Rhopalosiphum padi* based on allozyme and microsatellite markers. *Molecular Ecology* **11**: 711-723.

Dennis P., Thomas M.B. & Sotherton N.W. 1994: Structural features of field boundaries which influence the overwintering densities of beneficial arthropod predators. *Journal of Applied Ecology* **31**: 361-370.

DeRoos A.M., Diekmann O. & Metz J.A.J. 1990: Studying the dynamics of structured populations. A versatile technique and its application to Daphnia. *American Naturalist* **139**: 123-147.

Dewar A.M., Dean G.F. & Cannon R. 1982: Assessment of methods for estimating the numbers of aphids (Hemiptera: Aphididae) in cereals. *Bulletin of Entomological Research* **72**: 675-685.

Dewdney M.M., Biggs A.R. & Turechek W.W. 2007: A statistical comparison of the blossom blight forecasts of *Maryblyt* and *Cougarblight* with receiver operating characteristic curve analysis. *Phytopathology* **97**: 1164-1176.

Dinter A. 1995: *Untersuchungen zur Populationsdynamik von Spinnen (Arachnida: Araneae) in Winterweizen und deren Beeinflussung durch insektizide Wirkstoffe.* Ph.D. thesis, University of Göttingen, Göttingen, Germany, 383 pp.

Dixon A.F.G. 1971: Life-cycle and host preferences of bird cherry-oat aphid, *Rhopalosiphum padi* L., and their bearing on theories of host-alternation in aphids. *Annals of Applied Biology* **68**: 135-139.

Dixon A.F.G. 1990: Ecological interactions of aphids and their host plants. In: Campbell R.K. & Eikenbary R.D. (eds.): *Aphid-Plant Genotype Interaction*. Elsevier, Amsterdam, Netherlands, 7-19 pp.

Dixon A.F.G. 1992: Constraints on the rate of parthenogenetic reproduction and pest status of aphids. *Invertebrate Reproduction and Development* **22**: 159-163.

Dixon A.F.G. 1998: *Aphid Ecology: An Optimisation Approach*. Chapman & Hall, London, U.K., 300 pp.

Dixon A.F.G & Wratten S.D. 1971: Laboratory studies on aggregation, size, and fecundity in the black bean aphid, *Aphis fabae* Scop. *Bulletin of Entomological Research* **61**: 97-111.

Dixon A.F.G. & Kindlmann P. 1999: Cost of flight apparatus and optimum body size of aphid migrants. *Ecology* **80**: 1678-1690.

Dong Q.Z., Wei K., Meng Q.X., Wu F.Z., Zhang G.X., Zhong T.S. & Liu D.H. 1987: Investigation on long-distance migration of grain aphid *Macrosiphum avenae* Fabr. in Ningxia. *Acta Entomologica Sinica* **30**: 277-284.

Doodson J.K. & Saunders P.J.W. 1970: Some effects of barley yellow dwarf virus on spring and winter cereals in field trials. *Annals of Applied Biology* **66**: 361-374.

Duffey E. 1980: The efficiency of the Dietrick vacuum sampler (D-VAC) for invertebrate population studies in different types of grassland. *Bulletin d´Ecologie* **11**: 421-431.

Dusi A.N., Peters D. & VanDerWerf W. 2000: Measuring and modelling the effects of inoculation date and aphid flights on the secondary spread of Beet mosaic virus in sugar beet. *Annals of Applied Biology* **136**: 131-146.

Efron B. 1975: The efficiency of logistic regression compared to normal discriminant-analysis. *Journal of the American Statistical Association* **70**: 892-898.

Ekbom B.S. 1985: Spatial-distribution of *Rhopalosiphum padi* L. (Homoptera: Aphididae) in spring cereals in Sweden and its importance for sampling. *Environmental Entomology* **14**: 312-316.

Ekbom B.S. 1987: Incidence counts for estimating densities of *Rhopalosiphum padi* (Homoptera: Aphididae). *Journal of Economic Entomology* **80**: 933-935.

Ekbom B.S., Wiktelius S. & Chiverton P.A. 1992: Can polyphagous predators control the bird cherry-oat aphid (*Rhopalosiphum padi*) in spring cereals? A simulation study. *Entomologia Experimentalis et Applicata* **65**: 215-223.

Elliott N.C. & Kieckhefer R.W. 1986: Cereal aphid populations in winter wheat - spatial distributions and sampling with fixed levels of precision. *Environmental Entomology* **15**: 954-958.

Elliott N.C, Kieckhefer R.W. & Walgenbach D.D. 1990: Binomial sequential sampling methods for cereal aphids in small grains. *Journal of Economic Entomology* **83**: 1381-1387.

Elliott N.C, Kieckhefer R.W. & Kauffman W.C. 1991: Estimating adult coccinellid populations in wheat fields by removal, sweepnet, and visual count sampling. *Canadian Entomologist* **123**: 13-22.

Elliott N.C., Michels G.J., Kieckhefer R.W. & French B.W. 1997: Sequential sampling for adult Coccinellids in wheat. *Entomologia Experimentalis et Applicata* **84**: 267-273.

Elliott N.C., Giles K.L., Royer T.A., Kindler S.D., Tao F.L., Jones D.B. & Cuperus G.W. 2003: Fixed precision sequential sampling plans for the greenbug and bird cherry-oat aphid (Homoptera: Aphididae) in winter wheat. *Journal of Economic Entomology* **96**: 1585-1593.

Ellner S.P. & Rees M. 2006: Integral projection models for species with complex demography. *American Naturalist* **167**: 410-428.

Entwistle J.C. & Dixon A.F.G. 1986: Short-term forecasting of peak population-density of the grain aphid (*Sitobion avenae*) on wheat. *Annals of Applied Biology* **109**: 215-222.

Entwistle J.C. & Dixon A.F.G. 1987: Short-term forecasting of wheat yield loss caused by the grain aphid (*Sitobion avenae*) in summer. *Annals of Applied Biology* **111**: 489-508.

Escobar C.A., Sicker D. & Niemeyer H.M. 1999: Evaluation of DIMBOA analogs as antifeedants and antibiotics towards the aphid *Sitobion avenae* in artificial diets. *Journal of Chemical Ecology* **25**: 1543-1554.

European agricultural statistics 2008: *The use of pesticides in Europe*. http://ec.europa.eu/agriculture/agrista/2004/tabl_en/index.htm. Status: January, 2008.

Examine 2008: *Exploitation of aphid monitoring systems in Europe. Examine project.* http://examine.rothamsted.bbsrc.ac.uk/examine/. Status: January, 2008.

Fabre F., Dedryver C.A., Leterrier J.L. & Plantegenest M. 2003: Aphid abundance on cereals in autumn predicts yield losses caused by barley yellow dwarf virus. *Phytopathology* **93**: 1217-1222.

Fabre F., Pierre J.S., Dedryver C.A. & Plantegenest M. 2006: Barley yellow dwarf disease risk assessment based on Bayesian modelling of aphid population dynamics. *Ecological Modelling* **193**: 457-466.

FAO (Food and Agriculture Organization) 2008: *Provisional 2004 Production Data. Agricultural production, crops primary*. http://apps.fao.org/faostat. Status: January, 2008.

Feng M.G. & Nowierski R.M. 1992: Spatial-distribution and sampling plans for 4 species of cereal aphids (Homoptera: Aphididae) infesting spring wheat in south-western Idaho. *Journal of Economic Entomology* **85**: 830-837.

Feng M.G., Nowierski R.M. & Zeng Z. 1993a: Populations of *Sitobion avenae* and *Aphidius ervi* on spring wheat in the northwestern United States: Spatial distribution and sequential sampling plans based on numerical and binomial counts. *Entomologia Experimentalis et Applicata* **67**: 109-117.

Feng M.G., Nowierski R.M. & Zeng Z. 1993b: Binomial sampling plans for the English grain aphid, *Sitobion avenae* (Homoptera, Aphididae) based on an empirical relationship between mean density and proportion of tillers with different tally thresholds of aphids. *Bulletin of Entomological Research* **83**: 187-196.

Fereres A., Kampmeier G.E. & Irwin M.E. 1999: Aphid attraction and preference for soybean and pepper plants infected with Potyviridae. *Annals of the Entomological Society of America* **92**: 542-548.

Fievet V., Dedryver C.A., Plantegenest M., Simon J.C. & Outreman Y. 2007: Aphid colony turn-over influences the spatial distribution of the grain aphid *Sitobion avenae* over the wheat growing season. *Agricultural and Forest Entomology* **9**: 125-134.

Figueroa C.C., Simon J.C., LeGallic J.F., Prunier-Leterme N., Briones L.M., Dedryver C.A. & Niemeyer H.M. 2004: Effect of host defence chemicals on clonal distribution and performance of different Genotypes of the cereal aphid *Sitobion avenae. Journal of Chemical Ecology* **30**: 2515-2525.

Figueroa C.C., Simon J.C., LeGallic J.F., Prunier-Leterme N., Briones L.M., Dedryver C.A. & Niemeyer H.M. 2005: Genetic structure and clonal diversity of an introduced pest in Chile, the cereal aphid *Sitobion avenae*. *Heredity* **95**: 24-33.

Fischer R.A. 1936: The use of multiple measurements in taxonomic problems. *Annals of Eugenics* **7**: 179-188.

Foster G., Blake S., Tones S., Barker I., Harrington R., Taylor M., Walters K., Northing P. & Morgan D. 2004: Decision support for BYDV control in the United Kingdom: Can a regional forecast be made field specific? In: Simon J.-C., Dedryver C.A., Rispe C. & Hullé M. (eds.): *Aphids in a New Millennium. Proceedings of the VIth International Symposium on Aphids*. INRA Rennes, Versailles, France: pp. 287-291.

Fraser L.H. & Grime J.P. 1999: Aphid fitness on 13 grass species: A test of plant defence theory. *Canadian Journal of Botany - Revue Canadienne de Botanique* **77**: 1783-1789.

Frazer J.F.D. 1973: Estimating butterfly numbers. *Biological Conservation* **5-6**: 271-276.

Freier B. & Wetzel T. 1980: Der Verlauf der Progradation der Getreidelaus *Macrosiphum avenae* im Winterweizen und die Möglichkeit der kurzfristigen Befallsvorhersage. *Beiträge zur Entomologie* **30**: 137-143.

Freier B. & Triltsch H. 1996: Climate chamber experiments and computer simulations on the influence of increasing temperature on wheat - aphid - predator interactions. *Aspects of*

Applied Biology **45**: 293-298.

Freier B., Triltsch H. & Rossberg D. 1996: GTLAUS: A model of wheat - cereal aphid - predator interaction and its use in complex agro-ecological studies. *Journal of Plant Diseases and Protection* **103**: 543-554.

Freier B., Triltsch H., Möwes M. & Rappaport V. 1997a: Der relative Wert von Prädatoren bei der natürlichen Kontrolle von Getreideblattläusen und die Verwendung von Prädatoreinheiten. *Nachrichtenblatt Deutscher Pflanzenschutzdienst* **49**: 215-222.

Freier B., Triltsch H., Pluschkell U., Jahn M., Pallut B., Lindner K. & Burth U. 1997b: *Integrierter Pflanzenschutz im Ackerbau: Ein Leitfaden für Landwirte*. Biologische Bundesanstalt für Land- und Forstwirtschaft, Berlin, 56 pp.

Freier B., Möwes M., Triltsch H. & Rappaport V. 1998: Predator units - an approach to evaluate coccinellids within the aphid predator community in winter wheat. *IOBC Bulletin* **21**: 103-111.

Freier B., Triltsch H. & Gosselke U. 1999: Die Dimension der natürlichen Kontrolle von Getreideblattläusen durch Prädatoren. *Gesunde Pflanzen* **51**: 65-71.

Freier B., Triltsch H. & Gosselke U. 2001: Potential and limitations of long term field data to identify numerical and functional responses of predators to aphid density in wheat. *IOBC Bulletin* **24**: 65-71.

Freier B., Rossberg D., Gosselke U. & Triltsch H. 2002: Bewertung von Nützlingsleistungen in Weizenfeldern mit Hilfe von Computersimulationen. *Gesunde Pflanzen* **54**: 188-193.

Freier B., Triltsch H., Möwes M. & Moll E. 2007: The potential of predators in natural control of aphids in wheat: Results of a ten-year field study in two German landscapes. *Biocontrol* **52**: 775-788.

Frere I., Fabry J. & Hance T. 2007: Apparent competition or apparent mutualism? An analysis of the influence of rose bush strip management on aphid population in wheat field. *Journal of Applied Entomology* **131**: 275-283

Friedt W., Scheurer K.S., Huth W., Habekuss A. & Ordon F. 2003: Genetic analyses of BYDV-tolerance in barley (*Hordeum vulgare* L.). *Journal of Plant Diseases and Protection* **110**: 278-286.

Friesland H. 1986: Entwicklung eines Prognosemodells für die Populationsdichte der Großen Getreideblattlaus in Winterweizen auf meteorologischer Grundlage. *Beiträge zur Agrarmeteorologie Nr. 9, Deutscher Wetterdienst, Zentrale Agrarmeteorologische Forschungsberichte, Braunschweig*, 92 pp.

Friesland H. 1994: "LAUS", ein Prognosemodell für den Getreideblattlausbefall als Beispiel aus dem agrarmeteorologischen Softwarepaket "AMBER". *Nachrichtenblatt Deutscher Pflanzenschutzdienst* **46**: 287-291.

Gage S.H., Isard S.A. & Colunga M. 1999: Ecological scaling of aerobiological dispersal processes. *Agricultural and Forest Meteorology* **97**: 249-261.

Garve E. 1994: *Atlas der gefährdeten Farn- und Blütenpflanzen in Niedersachsen und Bremen. Kartierung 1982-1992. Naturschutz und Landschaftspflege in Niedersachsen, 30/2.* Niedersächsisches Landesamt für Ökologie, Hannover, Germany, 722 pp.

Geissler K., Proeseler G. & Lehmann C.O. 1989: Resistenzeigenschaften im Gersten- und Winterweizensortiment Gatersleben. 28. Prüfung von Gersten auf ihr Verhalten gegenüber den Blattlausarten *Rhopalosiphum padi* (L.) und *Macrosiphum (Sitobion) avenae* (F.). *Kulturpflanze* **37**: 155-161.

Geissler K., Schliephake E. & Karl E. 1995: Zum Massenwechsel von Getreideaphiden und zu ihrer Bedeutung als Vektoren des Gerstengelbverzwergungsvirus (barley yellow dwarf virus) in Mitteldeutschland. Eine Übersicht. *Archives of Phytopathology and Plant Protection* **30**: 99-107.

Gianoli E. & Niemeyer H.M. 1998: DIBOA in wild Poaceae: Sources of resistance to the Russian wheat aphid (*Diuraphis noxia*) and the Greenburg (*Schizaphis graminum*). *Euphytica* **102**: 317-321.

Giesecke J. 1983: Gebietsniederschlag. *Wasserwirtschaft* **73**: 1-7.

Giles K.L., Jones D.B., Royer T.A., Norman C., Elliott N.C. & Kindler S.D. 2003: Development of a sampling plan in winter wheat that estimates cereal aphid parasitism levels and predicts population suppression. *Journal of Economic Entomology* **96**: 975-982.

Gosselke U., Triltsch H., Rossberg D. & Freier B. 2001: GETLAUS01 - the latest version of a model for simulating aphid population dynamics in dependence on antagonists in wheat. *Ecological Modelling* **145**: 143-157.

Goudet J. 2008: *FSTAT, a program to estimate and test gene diversities and fixation indices (version 2.9.3)*. http://www.unil.ch/izea/softwares/fstat.html. Status: January, 2008.

Graf R.F., Bollmann K., Bugmann H. & Suter W. 2007: Forest and landscape structure as predictors of capercaillie occurrence. *Journal of Wildlife Management* **71**: 356-365.

Greenwood J.J.D. & Robinson R.A. 2006: Principles of sampling. In: Sutherland W.J. (ed.): *Ecological census technique: a handbook*. Cambridge University Press, Cambridge, U.K., 11-86 pp.

Gurr G.M., Wratten S.D. & Altieri M.A. 2004: *Ecological Engineering for Pest Management*. CABI, Wallingford, U.K., 232 pp.

Gutsche V. & Enzian S. 2002: Quantifizierung der Ausstattung einer Landschaft mit naturbetonten terrestrischen Biotopen auf der Basis digitaler topographischer Daten. *Nachrichtenblatt Deutscher Pflanzenschutzdienst* **54**: 92-101.

Haack L., Simon J.C., Gauthier J.P., Plantegenest M. & Dedryver C.A. 2000: Evidence for predominant clones in a cyclically parthenogenetic organism provided by combined demographic and genetic analyses. *Molecular Ecology* **9**: 2055-2066.

Häckel H. 2005: *Meteorologie*. Ulmer-Verlag, Stuttgart, Germany, 447 pp.

Hahlen J. 2004: Pressemitteilung vom 21. Januar 2004 des Statistischen Bundesamtes auf der "Internationalen Grünen Woche" in Berlin. *Aktuelle Ergebnisse der Agrarstrukturerhebung 2003*. http://www.destatis.de/presse/deutsch/pm2004/p0340141.htm. Status: January, 2008.

Haine E. 1955: Aphid take-off in controlled wind speeds. *Nature* **175**: 474-475.

Halkett F., Harrington R., Hullé M., Kindlmann P., Menu F., Rispe C. & Plantegenest M. 2004: Dynamics of production of sexual forms in aphids: Theoretical and experimental evidence for adaptive "coin-flipping" plasticity. *American Naturalist* **163**: E112-E125.

Halkett F., Plantegenest M., Prunier-Leterme N., Mieuzet L., Delmotte F. & Simon, J.C. 2005: Admixed sexual and facultatively asexual aphid lineages at mating sites. *Molecular Ecology* **14**: 325-336.

Hand S.C. 1980: Overwintering of cereal aphids. *IOBC Bulletin* **3**: 59-61.

Hand S.C. 1986: The capture efficiency of Dietrick vacuum insect net for aphids on grasses and cereals. *Annals of Applied Biology* **108**: 233-241.

Hansen L.M. 1999: Effect of weather during spring on the time of arrival of bird cherry-oat aphid (*Rhopalosiphum padi* L.) in spring barley (*Hordeum vulgare* L.) fields. *Acta Agriculturae Scandinavica Section B - Soil and Plant Science* **49**: 117-121.

Hardie J. 1993: Flight behavior in migration insects. *Journal of Agricultural Entomology* **10**: 239-245.

Hardie J. & Campbell C.A.M. 1998: The flight behaviour of spring and autumn forms of the Samson-hop aphid, *Phorodon humuli*, in the laboratory. In: NietoNafria J.M. & Dixon A.F.G. (eds.): *Aphids in Natural and Managed Ecosystems*. Universidad de León, León, Spain, 205-212 pp.

Harrington R., Tatchell G.M. & Bale J.S. 1990: Weather, life cycle strategy, and spring populations of aphids. *Acta Phytopathologica Academiae Scientiarum Hungaricae* **25**: 423-432.

Harrington R., Verrier P., Denholm C., Hullé M., Maurice D., Bell N., Knight J., Rounsevell M., Cocu N., Barbagallo S., Basky Z., Coceano P.G., Derron J., Katis N., Lukášová H., Marrkula I., Mohar J., Pickup J., Rolot J.L., Ruszkowska M., Schliephake E., Seco-Fernandez M.V., Sigvald R., Tsitsipis J. & Ulber B. 2004: Examine (EXploitation of Aphid Monitoring IN Europe): An European thematic network for the study of global change impacts on aphids. In: Simon J.C., Dedryver C.A., Rispe C. & Hullé M. (eds.): *Aphids in a New Millennium. Proceedings of the VIth International Symposium on Aphids*. INRA Editions, France, 45-49 pp.

Harrington R., Hullé M. & Plantegenest M. 2007: Monitoring and forecasting. In: VanEmden H.F. & Harrington R. (eds.): *Aphids as Crop Pests*. CAB International, Wallingford, U.K., 515-536 pp.

Hasken K.H. & Poehling H.-M. 1995: Effects of different intensities of fertilisers and pesticides on aphids and aphid predators in winter wheat. *Agriculture, Ecosystems and Environment* **52**: 45-50.

Havlickova H. 1993: Level and nature of the resistance to the cereal aphid, *Sitobion avenae* (F.), in thirteen winter wheat cultivars. *Journal of Agronomy and Crop Science* **171**: 133-137.

Havlickova H. 1997: Differences in level of tolerance to cereal aphids in five winter wheat cultivars. *Rostlinna Vyroba* **43**: 593-596.

Havlickova H. 2001: Screening of productive Czech winter wheat cultivars on resistance to aphids. *Rostlinna Vyroba* **47**: 326-329.

Havlickova H., Cvikrova M. & Eder J. 2000: Polyamine accumulation in ears of winter wheat cultivars infested by *Sitobion avenae* (F.). *Journal of Plant Diseases and Protection* **107**: 505-513.

Helden A.J. & Dixon A.F.G. 2002: Life-cycle variation in the aphid *Sitobion avenae*: Costs and benefits of male production. *Ecological Entomology* **27**: 692-701.

Hemptinne J.L. & Dixon A.F.G. 1997: Biological control of aphids: The effectiveness of ladybird beetles is limited by their foraging behavior. In: Powell W. (ed.): *Arthropod Natural Enemies in Arable Land, 3: The individual, the Population and the Community*. Acta Jutlandica Vol. 72, Aarhus University, Aarhus, Denmark, 11-19 pp.

Henderson I.F. & Whitaker T.M. 1977: The efficiency of an insect suction sampler in grassland. *Ecological Entomology* **2**: 57-60.

Hesler L.S. & Tharp C.I. 2005: Antibiosis and antixenosis to *Rhopalosiphum padi* among triticale accessions. *Euphytica* **143**: 153-160.

Hodgson C. 1991: Dispersal of apterous aphids (Homoptera: Aphididae) from their host plant and its significance. *Bulletin of Entomological Research* **81**: 417-427.

Hoeller C. 1990: Overwintering and hymenopterous parasitism in autumn of the cereal aphid *Sitobion avenae* (F.) in northern FR Germany. *Journal of Applied Entomology* **109**: 21-28.

Holland J.M. 1998: The effectiveness of exclusion barriers for polyphagous predatory arthropods in wheat. *Bulletin of Entomological Research* **88**: 305-310.

Holland J.M., Brikett T., Begbie M., Southway S. & Thomas C.F.G. 2003: The spatial dynamics of predatory arthropods and the importance of crop and adjacent margin habitats. *Landscape Management for Functional Biodiversity, IOBC Bulletin* **26**: 65-70.

Holmes S.B., Venier L.A., Naylor B.J. & Zirnmerling J.R. 2007: A test of Ontario's Habitat Suitability Matrix as a forest management planning tool for forest birds. *Forestry Chronicle* **83**: 570-579.

Holz F. 1991: A model-based catalogue of case studies as a tool for decision making in the control of the cereal aphid *Macrosiphum* (*Sitobion*) *avenae* in winter wheat. *IOBC Bulletin* **14**: 35-41.

Holz F. & Wetzel T. 1989: Ein Fallstudienkatalog als schlagbezogene Entscheidungshilfe für die gezielte Bekämpfung der Getreideblattlaus (*Macrosiphum avenae*). *Nachrichtenblätter des Pflanzenschutzdienstes der DDR* **42**: 58-60.

Holz F., Wetzel, T. & Freier B. 1994: 3 bis 5 Blattläuse pro Ähre im Winterweizen - eine neue

Bekämpfungsschwelle? *Gesunde Pflanzen* **46**: 8-12.

Hosmer D. & Lemeshow S. 2000: *Applied Logistic Regression*. Wiley & Sons, New York, U.S.A., 373 pp.

Hullé M., Coquio S. & Laperche V. 1994: Patterns in flight phenology of a migrant cereal aphid species. *Journal of Applied Ecology* **31**: 49-58.

Hullé M., Rispe C., Gauthier J.P. & Harrington R. 1996: Analysis of the flight activity of *Rhopalosiphum padi* males in relation with a population biology model. *IOBC Bulletin* **19**: 79-89.

Huth W. 1990: Barley Yellow Dwarf - ein permanentes Problem für den Getreidebau in der Bundesrepublik Deutschland? *Nachrichtenblatt Deutscher Pflanzenschutzdienst* **42**: 33-39.

Huth W. & Lauenstein G. 1991: Zum Problem der Gelbverzwergung in Getreidebeständen. *Gesunde Pflanzen* **43**: 139-148.

Huth W. & Züchner S. 1996: Untersuchungen zur Anfälligkeit von Weidelgras (*Lolium perenne*) gegenüber dem Gelbverzwergungsvirus der Gerste (Barley yellow dwarf virus). *Journal of Plant Disease and Protection* **103**: 125-133.

ICC (International Association for Cereal Science and Technology) 2008: *Bestimmung des Rohproteins in Getreide und Getreideprodukten für Nahrungs- und Futtermittel: Kjeldahl-Methode 105/2.* Standardmethoden der Internationalen Gesellschaft für Getreidewissenschaft und -technologie, Wien.
http://www.icc.or.at/index.php. Status: January, 2008.

Iperti G., Lapchin L., Ferran A., Rabasse J.M. & Lyon J.P. 1988: Sequential sampling of adult *Coccinella septempunctata* L. in wheat fields. *Canadian Entomologist* **120**: 773-778.

Isard S.A. & Irwin M.E. 1996: Formulating and evaluating hypotheses on the ascent phase of aphid movement and dispersal. In: Jerome D. & Heilman W.E. (eds.): *Proceedings of the XIIth Conference on Biometeorology and Aerobiology*. American Meteorological Society, Boston, U.S.A.: pp 430-433.

Isard S.A. & Gage S.H. 2001: *Flow of Life in the Atmosphere: An Air-scape Approach to Understanding Invasive Organisms*. Michigan State University Press, East Lansing, Michigan, U.S.A., 240 pp.

Isard S.A., Irwin M.E. & Hollinger S.E. 1990: Vertical-distribution of aphids (Homoptera: Aphididae) in the planetary boundary-layer. *Environmental Entomology* **19**: 1473-1484.

Irwin M.E., Kampmeier G.E. & Weisser W.W. 2007: Aphid movement: Process and consequences. In: VanEmden H.F. & Harrington R. (eds.): *Aphids as Crop Pests*. CAB International, Wallingford, U.K., 311-329 pp.

Jarosík V. & Dixon A.F.G. 1999: Population dynamics of a tree-dwelling aphid: Regulation and density independent processes. *Journal of Animal Ecology* **68**: 726-732.

Jarosík V., Honek A. & Dixon A.F.G. 2003: Natural enemy ravine revisited: The importance of sample size for determining population growth. *Ecological Entomology* **28**: 85-91.

Jensen R.E. & Wallin J.R. 1965: *Weather and Aphids: A Review*. United States Department of Commerce Technology. Note, 5-AGMET-1, 19 pp.

Jimenez-Martinez E.S., Bosque-Perez N.A., Berger P.H. & Zemetra R.S. 2004: Life history of the bird cherry-oat aphid, *Rhopalosiphum padi* (Homoptera: Aphididae), on transgenic and untransformed wheat challenged with Barley yellow dwarf virus. *Journal of Economic Entomology* **97**: 203-212.

Johnson C.G. & Taylor L.R. 1957: Periodism and energy summation with special reference to flight rhythms in aphids. *Journal of Experimental Biology* **34**: 209-221.

Karandinos M.G. 1976: Optimum sample size and comments on some published formulae. *Bulletin of the Entomological Society of America* **22**: 417-421.

Kavallieratos G., Tomanovic Z., Stary P., Athanassiou C.G., Sarlis G.P., Petrovic O., Niketic M. & Veroniki M.A. 2004: A survey of aphid parasitoids (Hymenoptera: Braconidae: Aphidiinae) of south-eastern Europe and their aphid-plant associations. *Applied*

Entomology and Zoology **39**: 527-563.

Kazemi M.H. & VanEmden H.E. 1992: Partial antibiosis to *Rhopalosiphum padi* in wheat and some phytochemical correlations. *Annals of Applied Biology* **121**: 1-9.

Kendall D.A. & Chinn N.E. 1990: A comparison of vector population indices for forecasting barley yellow dwarf virus in autumn sown cereal crops. *Annals of Applied Biology* **116**: 87-102.

Kennedy J.S. 1990: Behavioural post-inhibitory rebound in aphids taking flight after exposure to wind. *Animal Behaviour* **39**: 1078-1088.

Kenny G.J. & Chapman R.B. 1988: Effects of an intercrop on the insect pests, yield, and quality of cabbage. *New Zealand Journal of Experimental Agriculture* **16**: 67-72.

Kindlmann P. & Dixon A.F.G. 1989: Developmental constraints in the evolution of reproductive strategies: Telescoping of generations in parthenogenetic aphids. *Functional Ecology* **3**: 531-537.

Kindlmann P. & Dixon A.F.G. 1996: Population dynamics of tree-dwelling aphid: Individuals to populations. *Ecological Modelling* **89**: 23-30.

Kindlmann P. & Dixon A.F.G. 1998: Patterns in the population dynamics of the Turkey-oak aphid. In: NietoNafria J.M. & Dixon A.F.G. (eds.): *Aphids in Natural and Managed Ecosystems*. Universidad de León, León, Spain, 219-225 pp.

Kindlmann P. & Dixon A.F.G. 1999: Strategies of aphidophagous predators: Lessons for modelling insect predator-prey dynamics. *Journal of Applied Entomology* **123**: 397-399.

Kindlmann P., Jarosík V. & Dixon A.F.G. 2007: Population dynamics. In: VanEmden H.F. & Harrington R. (eds.): *Aphids as Crop Pests*. CAB International, Wallingford, U.K. 311-329 pp.

Kleinhenz B. 1994: *Entwicklung von Simulationsmodellen zur Beschreibung der Populationsdynamik von Virusübertragenden Getreideblattläusen in der Herbst- und Winterperiode auf der Basis von im Freiland und Labor ermittelten Daten*. Ph.D. thesis, University of Bonn, Bonn, Germany, 98 pp.

Kleinhenz B. & Sengonca C. 1993: Das unterschiedliche Auftreten und die Vermehrung der Getreideblattläuse auf Wintergerste und Winterweizen zweier aufeinander folgender Herbst- und Winterperioden. *Mitteilungen Deutsche Gesellschaft Angewandte Entomologie* **8**: 609-613.

Kleinhenz B. & Jörg E. 1998: Integrierter Pflanzenschutz - Rechnergestützte Entscheidungshilfen. *Angewandte Wissenschaft* **473**: 168 pp.

Knudsen G.R. & Schotzko D.J. 1999: Spatial simulation of epizootics caused by *Beauveria bassiana* in Russian wheat aphid populations. *Biological Control* **16**: 318-326.

Köhler W., Schachtel G. & Voleske P. 1984. *Biometrie - Einführung in die Statistik für Biologen und Agrar-Wissenschafter*. Springer, Berlin, Germany, 255 pp.

Krebs C.J. 1989: *Ecological Methodology*. Harper and Row, New York, U.S.A., 654 pp.

Kuo-Sell H.-L. & Hasken K.-H. 1989: Eignung verschiedener Methoden zur Erfassung der Populationsentwicklung stenophager Prädatoren und deren Wirkung auf Getreideblattläuse (Homoptera: Aphididae) im Winterweizen. *Mitteilungen Deutsche Gesellschaft für Angewandte Entomologie* **7**: 180-189.

Kuo-Sell H.-L. 1993: *Resistenz von Getreide gegen Blattläuse und ihre Kompatibilität mit Blattlausfeinden*. Ph.D. thesis, University of Göttingen, Göttingen, Germany, 139 pp.

Kuroli G. & Lantos Z. 2006: Long-term study of flight activity and abundance of wheat colonizing aphid species. *Cereal Research Communications* **34**: 1093-1099.

Lachenbruch P.A. & Kupper L.L. 1973: Discriminant analysis when one population is a mixture of normals. *Biometrics* **15**: 191-197.

Ländis D., Wratten S.D. & Gurr G.M. 2000: Habitat management for natural enemies. *Annual Review of Entomology* **45**: 175-201.

Lamb R.J. 1992: Developmental rate of *Acyrthosiphon pisum* (Homoptera: Aphididae) at low-temperatures - implications for estimating rate parameters for insects. *Environmental*

Entomology **21**: 10-19.

Lamb R.J., Mackay P.A. & Gerber G.H. 1987: Are development and growth of pea aphids, *Acyrthosiphon pisum*, in North-America adapted to local temperatures? *Oecologia* **72**: 170-177.

Latteur G. & Nicolas J. 1987: Piège à succion et prognose aphidienne en cereales. In: Cavalloro R. (ed.): *Aphid migration and forecasting 'Euraphid' systems in European community countries*. Commission of the European Communities, Luxembourg, Luxembourg, 75-86 pp.

Lawrence R. & Labus M. 2003: Early detection of Douglas-Fir beetle infestation with sub-canopy resolution hyper-spectral imagery. *Western Journal of Applied Forestry* **18**: 202-206.

Leather S.R. 1980: Egg survival in the bird cherry-oat aphids, *Rhopalosiphum padi* (L.). *Entomologia Experimentalis et Applicata* **27**: 96-97.

Leather S.R. 1983: Forecasting aphid outbreaks using winter egg counts: An assessment of its feasibility and an example of its application in Finland. *Journal of Applied Entomology* **100**: 510-513.

Leather S.R. 1985: Atmospheric humidity and aphid reproduction. *Journal of Applied Entomology* **100**: 510-513.

Leather S.R. 1996: *Prunus padus* L. *Journal of Ecology* **84**: 125-132.

Leather S.R. & Dixon A.F.G. 1981: The effects of cereal growth stage and feeding site on the reproduction activity of the bird cherry-oat aphid, *Rhopalosiphum padi* L. *Annals of Applied Biology* **97**: 135-142.

Leather S.R. & Lethi J.P. 1981: Abundance and survival of eggs of the bird cherry-oat aphid, *Rhopalosiphum padi* L. in southern Finland. *Annales Entomologici Fennici* **47**: 125-130.

Leather S.R. & Dixon A.F.G. 1984: Aphid growth and reproductive rates. *Entomologia Experimentalis et Applicata* **35**: 137-140.

Leather S.R., Walters K.F.A. & Dixon A.F.G. 1989: Factors determining the pest status of the bird cherry oat aphid, *Rhopalosiphum padi* L. (Hemiptera: Aphididae), in Europe: a study and review. *Bulletin of Entomological Research* **79**: 345-360.

Leclercq-LeQuillec F., Plantegenest M., Riault G. & Dedryver C.A. 2000: Analyzing and modelling temporal disease progress of Barley Yellow Dwarf Virus serotypes in barley fields. *Phytopathology* **90**: 860-866.

Leszcynski B., Wright L.C. & Bakowski T. 1989: Effect of secondary plant-substances on winter-wheat resistance to grain aphid. *Entomologia Experimentalis et Applicata* **52**: 135-139.

Liebig W. 2001: *Desktop - GIS mit - ArcView GIS. Leitfaden für Anwender*. Wichmann, Heidelberg, Germany, 86 pp.

Lindqvist B. 1985: Some information about cereal aphids in Finland. *SROP Bulletin* **8**: 49-51.

Llewellyn K.S., Loxdale H.D., Harrington R., Brookes C.P., Clark S.J. & Sunnucks P. 2003: Migration and genetic structure of the grain aphid (*Sitobion avenae*) in Britain related to climate and clonal fluctuation as revealed using microsatellites. *Molecular Ecology* **12**: 21-34

Llewellyn K.S., Loxdale H.D., Harrington R., Clark S.J. & Sunnucks P. 2004: Evidence for gene flow and local clonal selection in field populations of the grain aphid (*Sitobion avenae*) in Britain revealed using microsatellites. *Heredity* **93**: 143-153.

Loxdale H.D. 2001: Tracking flying insects using molecular markers. *Bulletin of the Royal Entomological Society (Antenna)* **25**: 242-250.

Loxdale H.D. & Lushai G. 2001: Use of genetic diversity in movement studies of flying insects. In: Woiwod I.P., Reynolds D.R. & Thomas C.D. (eds.): *Insect Movement: Mechanisms and Consequences*. CAB International, Wallingford, U.K., 361-386 pp.

Loxdale H.D., Tarr I.J., Weber C.P., Brookes C.P. & Digby P.G.N. 1985: Electrophoretic study of enzymes from cereal aphid populations. 3. Spatial and temporal genetic-variation of populations of *Sitobion avenae* F. (Hemiptera: Aphididae). *Bulletin of Entomological Research* **75**: 121-141.

Loxdale H.D., Hardie J., Halbert S., Foottit R., Kidd N.A.C. & Carter C.I. 1993: The relative importance of short- and long-range movement of flying aphids. *Biological Review* **68**: 291-311.

Lushai G. & Loxdale H.D. 2004: Tracking movement in small insect pests, with special reference to aphid populations. *International Journal of Pest Management* **50**: 307-315.

Lushai G., Markovitch O. & Loxdale H.D. 2002: Host-based genotype variation in insects revisited. *Bulletin of Entomological Research* **92**: 159-164.

Lushai G., Foottit R., Maw E. & Barette R. 2004: Genetic variation in the green apple aphid, *Aphis pomi* DeGeer (Homoptera: Aphididae) detected using microsatellite DNA flanking sequences. In: Simon J.-C., Dedryver C.A., Rispe C. & Hullé M. (eds.): *Aphids in a New Millennium. Proceedings of the VIth International Symposium on Aphids*. INRA Rennes, Versailles, France: 245-251 pp.

Ma C. 2000: *Modelling and simulation of the population dynamics of the cereal aphid Metopolophium dirhodum in northern Germany*. Ph.D. thesis, University of Hannover, Hannover, Germany, 67 pp.

MaCaulay E.D.M., Tatchell G.M. & Taylor L.R. 1988: The Rothamsted Insect Survey ’12-metre’ suction trap. *Bulletin of Entomological Research* **78**: 121-129.

Mackauer M. & Way M.J. 1976: *Myzus persicae* Sulz., an aphid of world importance. In: Delucchi V.L. (ed.): *Studies in Biological Control*. Cambridge University Press, Cambridge, U.K., 51-119 pp.

Mackenzie A. & Dixon A.F.G. 1991: An ecological perspective of host-alternation in aphids (Homoptera: Aphididae). *Entomologia Generalis* **16**: 265-284.

Madry W. 1997: A statistical approach to multivariate evaluation of diversity with respect to quantitative characteristics in cereal germplasm collections. *Journal of Applied Statistics* **24**: 573-588

MAFF - Ministry of agriculture, fisheries, and food, 1988. Cereal pest control. *ADAS Pest Management* **858**: 2-6.

Malloch G., Highet F., Kasprowicz L., Pickup J., Neilson R. & Fenton B. 2006: Microsatellite marker analysis of peach-potato aphids (*Myzus persicae*, Homoptera: Aphididae) from Scottish suction traps. *Bulletin of Entomological Research* **96**: 573-582.

Mann B.P. & Wratten S.D. 1991: A computer-based advisory system for cereal aphids - field-testing the model. *Annals of Applied Biology* **118**: 503-512.

Mann J.A., Tatchell G.M., Dupuch M.J., Harrington R., Clark S.J. & McCartner H.A. 1995: Movement of apaterous *Sitobion avenae* (Homoptera: Aphididae) in response to leaf disturbances caused by wind and rain. *Annals of Applied Biology* **126**: 417-427.

Manzato A. 2007: A note on the maximum Peirce Skill Score**.** *Weather and Forecasting* **22**: 1148-1154.

McCullagh P. & Nelder J.A. 1989: *Generalized Linear Models*. Chapman and Hall, London, U.K., 511 pp.

Mehta C.R., Patel N.R. & Senchaudhuri P. 1998: Exact power and sample-size computations for the Cochran-Armitage trend test. *Biometrics* **54**: 1615-1621.

Metz C.E. 1978: Basic principles of ROC analysis. *Seminars in Nuclear Medicine* **8**: 283-298.

Meyer U. 2008: *Entwicklungsstadien mono- und dikotyler Pflanzen. BBCH Monographie.* http://www.bba.de/veroeff/bbch/bbchdeu.pdf. Status: January, 2008.

MeyerZuBrickwedde W. & Poehling H.-M. 1996: Überwachung der ersten Flugaktivitäten von *Rhopalosiphum padi* (L.)., *Sitobion avenae* (F.) und *Metopolophium dirhodum* (W.) mit Hilfe stationärer Saugfallen und Farbschalen. *Mitteilungen Biologische Bundesanstalt für Land- und Forstwirtschaft, Berlin-Dahlem* **321**: 349 pp.

Meynen E., Schmithüsen J., Gilbert J., Nelf E., Müller-Ming H. & Schultze J.H. 1962: *Handbuch der naturräumlichen Gliederung Deutschlands*. Bundesanstalt für Landeskunde und Raumforschung, Bad Godesberg, Germany, 139 pp.

Migui S.M. & Lamb R.J. 2003: Patterns of resistance to three cereal aphids among wheats in the genus *Triticum* (Poaceae). *Bulletin of Entomological Research* **93**: 323-333.

Migui S.M. & Lamb R.J. 2004: Seedling and adult plant resistance to *Sitobion avenae* (Homoptera: Aphididae) in *Triticum monococcum* (Poaceae), an ancestor of wheat. *Bulletin of Entomological Research* **94**: 35-46.

Mila A.L., Carriquiry A.L. & Yang X.B. 2004: Logistic regression modelling of prevalence of soybean *Sclerotinia* stem rot in the north-central region of the United States. *Phytopathology* **94**: 102-110.

Moericke H. 1951: Eine Farbschale zur Kontrolle des Fluges von Blattläusen, insbesondere der Pfirsichblattlaus, *Myzodes persicae* (Sulz.). *Nachrichtenblatt Deutscher Pflanzenschutzdienst* **3**: 23-24.

Möwes M., Freier B. & Heimann J. 1997: Variation in yield loss per aphid-day due to *Sitobion avenae* - infestation in high yielding winter wheat. *Journal of Plant Diseases and Protection* **104**: 569-575.

Moharramipour S., Tsumuki H., Sato K., Murata S. & Kanehisa K. 1997: Effects of leaf colour, epicuticular wax amount, and gramine content in barley hybrids on cereal aphid populations. *Applied Entomology and Zoology* **32**: 1-8.

Morgan D. 1996: Temperature changes and insect pests: a simulation study. *Aspects of Applied Biology* **45**: 277-283.

Mühlenberg M. 1993: *Freilandökologie*. Quelle & Meyer, Heidelberg, Germany, 512 pp.

Müller C.B., Williams I.S. & Hardie J. 2001: The role of nutrition, crowding and interspecific interactions in the development of winged aphids. *Ecological Entomology* **26**: 330-340.

Neuenschwander P. 1984: Sampling procedures for chrysopid populations. In: Canard M., Séméria Y. & New T.R. (eds.): *Biology of Chrysopidae*. Dr. W. Junk Publisher, The Hague, Netherlands: 205-211 pp.

Newman J.A. 2004: Climate change and cereal aphids: The relative effects of increasing CO_2 and temperature on aphid population dynamics. *Global Change Biology* **10**: 5-15.

Newman J.A., Gibson D.J., Parsons A.J. & Thornley J.H.M. 2003: How predictable are aphid population responses to elevated CO_2? *Journal of Animal Ecology* **72**: 556-566.

Nicolino M., Bost M., David M. & Chaussain J.L. 1995: Familial Blepharophimosis - An uncommon marker of ovarian digenesis. *Journal of Pediatric Endocrinology & Metabolism* **8**: 127-133.

Niehoff B. & Stäblein J. 1998: Vergleichende Untersuchungen zum Schadpotential der Getreideblattlausarten *Metopolophium dirhodum* (Wlk.) und *Sitobion avenae* (F.) in Winterweizen. *Journal of Applied Entomology* **122**: 223-229.

Nottingham S.F., Hardie J. & Tatchell G.M. 1991: Flight behaviour of the bird cherry aphid, *Rhopalosiphum padi* L. *Physiological Entomology* **16**: 223-229.

O'Gorman T.W. & Woolson R.F. 1991: Variable selection to discriminate between 2 groups - stepwise logistic-regression or stepwise discriminant-analysis. *American Statistician* **45**: 187-193.

Ohnesorge B. 1991: *Tiere als Pflanzenschädlinge*. Thieme, Stuttgart, Germany, 336 pp.

Papura D., Simon J.C., Halkett F., Delmotte F., LeGallic J.F. & Dedryver C.A. 2003: Predominance of sexual reproduction in Romanian populations of the aphid *Sitobion avenae* inferred from phenotypic and genetic structure. *Heredity* **90**: 397-404.

Parker W.E., Howard J.J., Foster S.P. & Denholm I. 2006: The effect of insecticide application sequences on the control and insecticide resistance status of the peach-potato aphid, *Myzus persicae* (Hemiptera: Aphididae), on field crops of potato. *Pest Management Science* **62**: 307-315.

Parsons S. & Jones G. 2000: Acoustic identification of twelve species of echo-locating bat by discriminant function analysis and artificial neural networks. *Journal of Experimental Biology* **203**: 2641-2656.

Parry H.R., Evans A.J. & Morgan D. 2006: Aphid population response to agricultural landscape change: A spatially explicit, individual-based model. *Ecological Modelling* **199**: 451-463.

Passioura J.B. 1973: Sense and nonsense in crop simulation. *Journal of the Australian Institute of Agricultural Science* **39**: 181-183.

Pepe M.S. 2000: An interpretation for the ROC curve and inference using GLM procedures. *Biometrics* **56**: 352-359.

Pickett S.T.A. & Cadenasso M.L. 1995: Landscape ecology: Spatial heterogeneity in ecological systems. *Science* **269**: 331-334.

Pierre J.S. & Dedryver C.A. 1985: Un modèle de prevision des pullulations du puceron *Sitobion avenae* sur blé d'hiver. *Phytoma* **369**: 13-17.

Pluschkell U. 1997: Zum Zeitbedarf für das Monitoring im integrierten Pflanzenschutz. *Nachrichtenblatt Deutscher Pflanzenschutzdienst* **49**: 146-149.

Poehling H.-M. 1988: Zum Auftreten von Syrphiden- und Coccinellidenlarven in Winterweizen von 1984-1987 in Relation zur Abundanz von Getreideblattläusen. *Mitteilungen der Deutschen Gesellschaft für Allgemeine und Angewandte Entomologie* **6**: 248-254.

Poehling H.-M., Freier B. & Klüken A.M. 2007: IPM case study: Grain. In: VanEmden H.F. & Harrington R. (eds.): *Aphids as Crop Pests*. CAB International, Wallingford, U.K., 597-611 pp.

Polis G.A., Anderson W.B. & Holt R.A. 1997: Toward an integration of landscape and food web ecology: The dynamics of spatially subsidized food webs. *Annual Review Ecological Systems* **28**: 289-316.

Porter J.R., Jamieson P.D. & Wilson D.R. 1992: Comparison of the wheat simulation models AFRCWHEAT2, CERES-Wheat, and SWHEAT for non-limiting conditions of crop growth. *Field Crops Research* **33**: 131-157.

Press S.J. & Wilson S. 1978: Choosing between logistic regression and discriminant-analysis. *Journal of the American Statistical Association* **73**: 699-705.

Quinckhardt M. 2008: *The crop meter*. Plant Production by Agrocom. http://www.agrocom.com/index.php. Status: January, 2008.

Rabbinge R. & Vereijken P.H. 1979: Effects of aphids and honeydew on the yield of winter wheat. *Acta Botanica Nederlandica* **28**: 240-240.

Radford P.J. 1967: Growth analysis formulae - Their use and abuse. *Crop Science* **7**: 171-175.

Rappaport V. 1998: Ein situationsbezogenes Schwellenwertkonzept für Getreideblattläuse am Winterweizen unter Berücksichtigung der natürlichen Gegenspieler. In: Nentwig W. & Poehling H.-M. (eds.): *Agrarökologie*. Vol. 33. Haupt, Bern, Switzerland, 1-137 pp.

Rappaport V. & Freier B. 2001: Erprobung eines flexiblen Schwellenswertkonzepts für Getreideblattläuse an Winterweizen unter Berücksichtigung der natürlichen Gegenspieler. *Nachrichtenblatt Deutscher Pflanzenschutzdienst* **53**: 113-119.

Rath T. 2008: *Bio-Robotics and Automation Techniques in Plant Cultivation*. Biosystems and Horticultural Engineering Section, Institute of Biological Production Systems. http://www.bgt.uni-hannover.de/index.php. Status: January, 2008.

Rautapäa J. 1976: Population dynamics of cereal aphids and method of prediction population trends. *Annales Agricultura Fennici* **15**: 272-293.

Rautapäa J. 1979: Humidity reaction of cereal aphids (Homoptera, Aphididae). *Annales Entomologici Fennici* **45**: 33-41.

Reimer L. 2004: *Clonal diversity and population genetic structure of the grain aphid Sitobion avenae F. in central Europe*. Ph.D. thesis, University of Göttingen, Göttingen, Germany, 102 pp.

Richter L. 2000: Langfristige Populationsentwicklung der Großen Getreideblattlaus (*Sitobion* *avenae* (Fabr.)) im Winterweizen. *Mitteilungen Biologische Bundesanstalt für Land- und Forstwirtschaft, Berlin-Dahlem* **376**, 289 pp.

Riedell W.E., Kieckhefer R.W., Haley S.D., Langham M.A.C. & Evenson P.D. 1999: Winter wheat responses to bird cherry-oat aphids and barley yellow dwarf virus infection. *Crop Science* **39**: 158-163.

Roa C.R. 1973: *Linear Inference and its Application*. Wiley, New York, U.S.A., 103 pp.

Robert Y. 1987: Dispersion and migration. In: Minks A.K. & Harrwijn E. (eds.): *Aphids, their Biology, Natural Enemies and Control.* Vol. A. Elsevier, Amsterdam, Netherlands, 299-313 pp.

Robert Y., Dedryver C.A. & Pierre J.S. 1988: Sampling techniques. In: Minks A.K. & Harrewijn P. (eds.): *Aphids, their Biology, Natural Enemies and Control*. Vol. B. Elsevier, Amsterdam, Netherlands, 1-364 pp.

Rogerson J.P. 1947: The oat bird-cherry aphid, *Rhopalosiphum padi* L. and comparison with *R. crataegellum* Theo (Hemiptera, Aphididae). *Bulletin of Entomological Research* **38**: 157-176.

Roschewitz I., Hucker M., Tscharntke T. & Thies C. 2005: The influence of landscape context and farming practices on parasitism of cereal aphids. *Agriculture, Ecosystems and Environment* **108**: 218-227.

Rossberg D., Holz F., Freier B. & Wenzel V. 1986: PESTSIM-MAC, a model for simulation of *Macrosiphum avenae* Fabr. populations. *Tagungsberichte der Akademie der Landwirtschaftswissenschaften der DDR, Berlin,* **242**: 87-100.

Rossberg D., Gutsche V., Enzian S. & Wick M. 2002: NEPTUN2000 - Erhebung von Daten zum tatsächlichen Einsatz von chemischen Pflanzenschutzmitteln im Ackerbau Deutschlands. *Berichte aus der biologischen Bundesanstalt für Land- und Forstwirtschaft* **98**: 1-78.

Rossberg D., Jörg E. & Falke K. 2005: SIMONTO - ein neues Ontogenesemodell für Wintergetreide und Winterraps. *Nachrichtenblatt Deutscher Pflanzenschutzdienst* **57**: 74-80.

Rossing W.A.H. 1991: Simulation of damage in winter wheat caused by the grain aphid *Sitobion avenae*. 3. Calculation of damage at various attainable yield levels. *Netherlands Journal of Plant Pathology* **97**: 87-103.

Rossing W.A.H., Eggenschwiler L. & Poehling H.-M. 2006: Landscape management for functional biodiversity. *IOBC Bulletin* **29**: 165-168.

Sachs L. 1999: *Angewandte Statistik.* Springer, Berlin, Germany, 884 pp.

Sandström J. 2000: Nutritional quality of phloem sap in relation to host plant-alternation in bird cherry-oat aphid. *Chemoecology* **10**: 17-24.

SAS 2008: *The statistical analyses systems for windows V8*. SAS program 8.2. http://www.sas.com/index.html. Status: January, 2008.

Schmidtmann E.T. 2006: Testing the relationship between dissolved salts in aquatic habitats and immature populations of the *Culicoides variipennis* complex (Diptera: Ceratopogonidae). *Environmental Entomology* **35**: 1154-1160.

Scholz S. 1994: *Untersuchungen zur Abundanz, Mobilität und Überwinterung von Getreideblattläusen in Wintergerste (Herbst/Frühjahr, 1992/1993) und Laboruntersuchungen zum Einfluss von Insektiziden (Imidacloprid, Lambda-Cyhalothrin) auf Verhaltensparameter von Sitobion avenae*. Ph.D. thesis, University of Göttingen, Göttingen, Germany, 193 pp.

Schotzko D.J. & O'Keeffee L.E. 1989: Comparison of sweep net, D-VAC, and absolute sampling, and variation of sweep net sampling estimates in lentils for pea aphid (Homoptera, Aphididae), nabids (Hemiptera, Nabidae), lady beetles (Coleoptera, Coccinellidae), and lacewings (Neuroptera, Chrysopidae). *Journal of Economic Entomology* **82**: 491-506.

Schotzko D.J. & Bosque-Perez N.A. 2000: Seasonal dynamics of cereal aphids on Russian wheat aphid (Homoptera: Aphididae) susceptible and resistant wheat. *Journal of Economic Entomology* **93**: 975-981.

Schultz G.A., Irwin M.E. & Goodman R.M. 1985: Relationship of aphid (Homoptera: Aphididae) landing rates to the field spread of soybean mosaic virus. *Journal of Economic Entomology* **78**: 143-147.

Scott R.W. & Achtelmeier G.L. 1987: Estimating pathways of migrating insects carried in atmospheric winds. *Environmental Entomology* **16**: 1244-1254.

Selhorst T. 2000: *Modellierung, Simulation und optimale Steuerung von Insektenpopulationen in Agrar-Ökosystemen*. Dr. Hänsel-Hohenhausen AG, Frankfurt A.M., Germany, 172 pp.

Sengonca C., Hoffmann A. & Kleinhenz B. 1992: Laboruntersuchungen zur Entwicklung, Lebensdauer und Fruchtbarkeit der Getreideblattlausarten *Sitobion avenae* (F.) und *Rhopalosiphum padi* (L.) (Homoptera, Aphididae) bei verschiedenen tieferen Temperaturen. *Journal of Applied Entomology* **117**: 224-233.

Sequeira R. & Dixon A.F.G. 1997: Population dynamics of tree-dwelling aphids: The importance of seasonality and time scale. *Ecology* **78**: 2603-2610.

Sherlock P.L., Bowden J. & Digby P.G.N. 1986: Studies of elemental composition as a biological marker in insects. 5. The elemental composition of *Rhopalosiphum padi* L. (Hemiptera, Aphididae) from *Prunus padus* L. at different localities. *Bulletin of Entomological Research* **76**: 621-632.

Simon J.C. & Hebert P.D.N. 1995: Patterns of genetic variation among Canadian populations of the bird cherry-oat aphid, *Rhopalosiphum padi* L. (Homoptera: Aphididae). *Heredity* **74**: 346-353.

Simon J.C., Blackman R.L. & LeGallic J.F. 1991: Local variability in the lifecycle of the bird cherry-oat aphid *Rhopalosiphum padi* L. in western France. *Bulletin of Entomological Research* **81**: 315-322.

Simon J.C., Martinez-Torres D., Latorre A., Moya A. & Hebert P.D.N. 1996a: Molecular characterization of cyclic and obligate parthenogens in the aphid *Rhopalosiphum padi* L. *Proceedings of the Royal Society of London series B - Biological Science* **263**: 481-486.

Simon J.C., Carrel E., Herbert P.D.N., Dedryver C.A., Bonhomme J. & LeGallic J.F. 1996b: Genetic diversity and mode of reproduction in French populations of the aphid *Rhopalosiphum padi*. *Heredity* **76**: 305-313.

Simon J.C., Baumann S., Sunnucks P., Herbert P.D.N., Pierre J.S., LeGallic J.F. & Dedryver C.A. 1999: Reproductive mode and population genetic structure of the cereal aphid *Sitobion avenae*, studied using phenotypic and microsatellite markers. *Molecular Ecology* **8**: 531-545.

Simon J.C., Leterme N., Delmotte F., Martin O. & Estoup A. 2001: Isolation and characterization of microsatellite loci in the aphid species *Rhopalosiphum padi*. *Molecular Ecology Notes* **1**: 4-5.

Simon J.C., Delmotte F., Rispe C. & Crease T. 2003: Phylogenetic relationships between parthenogens and their sexual relatives: the possible routes to parthenogenesis in animals. *Biological Journal of the Linnean Society* **79**: 151-163.

Skirvin DJ., Perry J.N. & Harrington R. 1997: A model describing the population dynamics of *Sitobion avenae* and *Coccinella septempunctata*. *Ecological Modelling* **96**: 29-40.

Smith C.M., Havlickova H., Starkey S., Gill B.S. & Holubec V. 2004: Identification of Aegilops germplasm with multiple aphid resistance. *Euphytica* **135**: 265-273.

Southwood T.R.E. & Henderson P.A. 2000: *Ecological Methods*. Blackwell Science, Oxford, U.K., 575 pp.

Spiller N.J. & Llewellyn M. 1987: Honeydew production and sap ingestion by the cereal aphids *Rhopalosiphum padi* and *Metopolophium dirhodum* on seedling of resistant and susceptible wheat species. *Annals of Applied Biology* **110**: 585-590.

Stewart L. & Dixon A.F.G. 1988: Quantification of the effect of natural enemies on the abundance of aphids: Precision and statistics. In: Niemcyzyk E. & Dixon A.F.G. (eds.): *Ecology and Effectiveness of Aphidophaga*. Academic Publishing, The Hague, Netherland: 187-197 pp.

Storck-Weyhermüller S. 1988: Einfluss natürlicher Feinde auf die Populationsdynamik der Getreideblattläuse im Winterweizen Mittelhessens (Homoptera: Aphididae). *Entomologia Generalis* **13**: 189-206.

Sunnucks P. & Hales D.F. 1996: Numerous transposed sequences of mitochondrial cytochrome oxidase I-II in aphids of the genus *Sitobion* (Hemiptera: Aphididae). *Molecular Biology and Evolution* **13**: 515-524.

Sunnucks P., England P.R., Taylor A.C. & Hales D.F. 1996: Microsatellite and chromosome evolution of parthenogenetic *Sitobion* aphids in Australia. *Genetics* **144**: 747-756.

Sunnucks P., DeBarro P.J., Lushai G., McLean N. & Hales D.F. 1997: Genetic structure of an aphid using microsatellites: Cyclic parthenogenesis, differential lineages, and host specialization. *Molecular Ecology* **6**: 1059-1073.

Sutherland J.W. 2006: *Ecological Census Techniques: A Handbook*. Cambridge University Press, Cambridge, U.K., 352 pp.

Swets J.A. 1973: Relative operating characteristic in psychology. *Science* **182**: 990-1000.

Tatchell G.M. 2007: IPM case study: Leafy salad crops. In: VanEmden H.F. & Harrington R. (eds.): *Aphids as Crop Pests*. CAB International, Wallingford, U.K., 587-596 pp.

Tatsuoka M.M. 1971: Statistical theories of mental test scores. *Journal of the American Statistical Association* **66**: 651-652.

Tayler L.R. 1955: The standardization of air-flow in insect suction traps. *Annals of Applied Biology* **43**: 390-408.

Taylor L.R. 1961: Aggregation, variance and the mean. *Nature* **189**: 732-735.

Taylor L.R. 1986: Synoptic dynamics, migration, and the Rothamsted insect survey. *Journal of Animal Ecology* **55**: 1-38.

Telang A., Sandstrom J., Dyreson E. & Moran N.A. 1999: Feeding damage by *Diuraphis noxia* results in a nutritionally enhanced phloem diet. *Entomologia Experimentalis et Applicata* **91**: 403-412.

Teng P.S. 1981: Validation of computer models of plant disease epidemics: A review of philosophy and methodology. *Journal of Plant Diseases and Protection* **88**: 49-63.

Tenhumberg B. 1997: Estimating predatory efficiency of *Episyrphus balteatus* (Diptera: Syrphidae) in cereal fields. *Environmental Entomology* **24**: 687-691.

Thies C. & Tscharntke T. 1999: Landscape structure and biological control in agro-ecosystems. *Science* **285**: 893-895.

Thies C., Steffan-Dewenter I. & Tscharntke T. 2003: Effects of landscape context on herbivory and parasitism at different spatial scales. *Oikos* **101**: 18-25.

Thies C., Roschewitz I. & Tscharntke T. 2005: The landscape context of cereal aphid-parasitoid interactions. *Proceedings of the Royal Society of London B* **272**: 203-210.

Thieme T. & Heimbach U. 1996: Development and reproductive potential of cereal aphids (Homoptera: Aphididae) on winter wheat cultivars. *IOBC Bulletin* **19**: 1-8.

Thomas C.F.G. & Marshall E.J.P. 1999: Arthropod abundance and diversity in differently vegetated margins of arable fields. *Agriculture, Ecosystems and Environment* **72**: 131-144.

Thompson J.N. 1988: Coevolution and alternative hypotheses on insect/plant interactions. *Ecology* **69**: 893-895.

Topping C.J. & Sunderland K.D. 1994: A spatial population-dynamics model for *Lepthyphantes tenuis* (Araneae: Linyphiidae) with some simulations of the spatial and temporal effects of farming operations and land-use. *Agriculture, Ecosystems and Environment* **48**: 203-217.

Tottman D.R. & Broad H. 1987: The decimal code for the growth stages of cereals with illustrations. *Annals of Applied Biology* **110**: 441-454.

Tsai J.H. & Wang J.J. 2001: Effects of host plants on biology and life table parameters of *Aphis spiraecola* (Homoptera: Aphididae). *Environmental Entomology* **30**: 44-50.

Tscharntke T., Rand T.A. & Bianchi F.J.J.A. 2005: The landscape context of tritrophic interactions: Insect spill-over across the crop - non-crop interface**.** *Annals Zoologici Fennici* **42**: 421-432.

Tsumuki H., Kanehisa K. & Kawada K. 1989: Leaf surface wax as a possible resistance factor of barley to cereal aphids. *Applied Entomology and Zoology* **24**: 295-301.

Twengström E., Sigvald R., Svensson C. & Yuen J. 1998: Forecasting *Sclerotinia* stem rot in spring sown oilseed rape. *Crop Protection* **17**: 405-411.

VanEmden H.F. 1969: Plant resistance to *Mycus persicae* induced by a plant regulator and measured by aphid relative growth rate. *Entomologia Experimentalis et Applicata* **12**: 125-131.

VanEmden H.F. & Harrington R. 2007: *Aphids as Crop Pests*. CAB International, Wallingford, U.K., 717 pp.

Veenker H. 2000: *Untersuchungen zur Überwachung der Initialbesiedlung und Abundanzdynamik der Getreideblattläuse mit Hilfe von Saugfallenfängen.* Ph.D. thesis, University of Göttingen, Göttingen, Germany, 115 pp.

Veenker H. & Ulber B. 2004: Phenology and population structure in the autumn flight of *Rhopalosiphum padi* in northern Germany. In: Simon J.-C., Dedryver C.A., Rispe C. & Hullé M. (eds.): *Aphids in a New Millennium. Proceedings of the VI*th *International Symposium on Aphids*. INRA Rennes, Versailles, France: 375-381 pp.

Veenker H., MeyerZuBrickwedde W., Ulber B. & Poehling H.-M. 1998: First flight activities and immigration of cereal aphids in spring 1994-1996 at Göttingen (northern Germany). *IOBC Bulletin* **21**: 39-49.

Vialatte A., Simon J.C., Dedryver C.A., Fabre F. & Plantegenest M. 2005: Tracing individual movements of aphids reveals preferential routs of population transfers in agro-ecosystems. *Ecological Applications* **16**: 839-844.

Vialatte A., Plantegenest M., Simon J.C. & Dedryver C.A. 2007: Farm-scale assessment of movement patterns and colonization dynamics of the grain aphid in arable crops and hedgerows. *Agricultural and Forest Entomology* **9**: 337-346.

Volkmar C., Bothe S., Kreuter T., Lübke-Al Hussein M., Richter L., Heimbach U. & Wetzel T. 1994: Epigäische Raubarthropoden in Winterweizenbeständen Mitteldeutschlands und ihre Beziehung zu Blattläusen. *Mitteilungen Biologische Bundesanstalt für Land- und Forstwirtschaft, Berlin-Dahlem* **299**: 1-134.

Vorburger C. 2004**:** Cold tolerance in obligate and cyclical partheogens of the peach-potato aphid, *Mycus persicae*. *Ecological Entomology* **29**: 498-505.

Vorburger C., Lancaster M. & Sunnucks P. 2003**:** Environmentally related patterns of reproductive modes in the aphid *Myzus persicae* and the predominance of two 'superclones' in Victoria, Australia. *Molecular Ecology* **12**: 3493-3504.

Walters K.F.A. & Dixon A.F.G. 1984: The effects of temperature and wind on the flight activity of cereal aphids. *Annals of Applied Biology* **104**: 17-26.

Walters K.F.A. & Dewar A.M. 1986: Overwintering strategy and the timing of the spring migration of the cereal aphids *Sitobion avenae* and *Sitobion fragariae*. *Journal of Applied Ecology* **23**: 905-915.

Ward S.A., Rabbinge R. & Mantel W.P. 1985a: The use of incidence counts for estimation of aphid populations. 1. Minimum sample size for required accuracy. *Netherlands Journal of Plant Pathology* **91**: 93-99.

Ward S.A., Rabbinge R. & Mantel W.P. 1985b: The use of incidence counts for estimation of aphid populations. 2. Confidence intervals from fixed sample sizes. *Netherlands Journal of Plant Pathology* **91**: 100-104.

Ward S.A., Leather S.R., Pickup J. & Harrington R. 1998: Mortality during dispersal and the cost of host-specificity in parasites: how many aphids find hosts? *Journal of Animal*

Ecology **67**: 763-773.

Wardiatno Y. & Tamaki A. 2001: Bivariate discriminant analysis for the identification of *Nihonotrypaea japonica* and *N. harmandi* (Decapoda: Thalassinidea / Callianassidae). *Journal of Crustacean Biology* **21**: 1042-1048.

Watt A.D. 1979: The effect of cereal growth stages on the reproductive activity of *Sitobion avenae* and *Metopolophium dirhodum*. *Annals of Applied Biology* **91**: 147-157.

Weber G. 1985: Genetic variability in host plant adaptation of the green peach aphid, *Myzus persicae*. *Entomologia Experimentalis et Applicata* **38**: 49-56.

Weir B.S. & Cockerham C.C. 1984: Estimating F-Statistics for the analysis of population-structure. *Evolution* **38**: 1358-1370.

Weng Y., Michels G.J., Lazar M.D. & Rudd J.C. 2005: Spatial and temporal distribution of induced resistance to greenbug (Homoptera: Aphididae) herbivory in preconditioned resistant and susceptible near isogenic plants of wheat. *Journal of Economic Entomology* **98**: 1024-1031.

Wenks P. 1981: Bionomicas of adult blackflies. In: Laird M. (ed.): *Blackflies: The Future for Biological Methods in Integrated Control*. Academic Press, New York, U.S.A., 259-276 pp.

Werner A. 2008: *Precision farming*. Collaborative Research Project: pre agro. http://www.preagro.de/index.php. Status: January, 2008.

Wetzel T. 2004: *Integrierter Pflanzenschutz und Agroökosysteme*. Pause, Halle/Saale, Germany, 288 pp.

Wetzel T., Freier B. & Heyer W. 1980: Zur Modellierung von Befall-Schadens-Relationen wichtiger Schadinsekten des Winterweizens. *Journal of Applied Entomology* **89**: 330-344.

Wiktelius S. 1981: The diurnal flight periodicities and temperature thresholds for flight for different migrants forms of *Rhopalosiphum padi* L. (Homoperta: Aphididae). *Journal of Applied Entomology* **93**: 449-457.

Wiktelius S. 1984: Long-range migration of aphids into Sweden. *International Journal of Biometeorology* **28**: 185-200.

Wiktelius S. 1992: The induction of alatea in *Rhopalosiphum padi* L. (Homoptera: Aphididae) in relation to crowding and plant growth stage in spring sown barley. *Journal of Applied Entomology* **114**: 491-496.

Williams I.S. & Dixon A.F.G. 2007: Life cycles and polymorphism. In: VanEmden H.F. & Harrington R. (eds.): *Aphids as Crop Pests*. CAB International, Wallingford, U.K., 69-85 pp.

Wilson A.C.C., Sunnucks P. & Hales D.F. 1999: Microevolution, low clonal diversity and genetic affinities of parthenogenetic *Sitobion* aphids in New Zealand. *Molecular Ecology* **8**: 1655-1666.

Wilson A.C.C., Massonnet B., Simon J.-C., Prunier-Leterme N., Dolatti L., Llewellyn K.S., Figueroa C.C., Ramirez C.C., Blackman R.L., Estoup A. & Sunnucks P. 2004: Cross-species amplification of microsatellite loci in aphids: assessment and application. *Molecular Ecology Notes* **4**: 104-109.

Winder L., Alexander C.J., Holland J.M., Symondson W.O.C., Perry J.N. & Woolley C. 2005: Predatory activity and spatial pattern: the response of generalist carabids to their aphid prey. *Journal of Animal Ecology* **74**: 443-454.

Wolf J., Evans L.G., Semenov M.A., Eckersten H. & Iglesias A. 1996: Comparison of wheat simulation models under climate change. I. Model calibration and sensitivity analyses. *Climate Research* **7**: 253-270.

Wratten S.O. & George K.S. 1985: Effects of cereal aphids on yield and quality of wheat and barley. *IOBC Bulletin* **8**: 10-26.

Wyatt I.J. & White P.F. 1977: Simple estimation of intrinsic increase rates for aphids and tetranychid mites. *Journal of Applied Ecology* **14**: 757-766.

Yuen J., Twengström E. & Sigvald R. 1996: Calibration and verification of risk algorithms using logistic regression. *European Journal of Plant Pathology* **102**: 847-854.

Zhou X. & Carter N. 1989: A simulation model describing the population dynamics and damage potential of the rose grain aphid, *Metopolophium dirhodum* (Walker) (Hemiptera: Aphididae), in the U.K. *Bulletin Entomological Research* **79**: 373-380.

Zhou X. & Carter N. 1992: Effects of temperature, feeding position and crop growth stage on the population-dynamics of the rose grain aphid, *Metopolophium dirhodum* (Hemiptera: Aphididae). *Annals of Applied Biology* **121**: 27-37.

Zhou X., Harrington R., Woiwod I.P., Perry J.N. & Clark S.J. 1996: Impact of climate change on aphid flight phenology. *Aspects of Applied Biology* **45**: 299-305.

Zuniga E. 1985: Efecto de la Iluvia en la abundancia de afidos y afidos momificados en trigo (Homoptera: Aphididae). *Revista Chilena de Entomologia* **12**: 205-208.

Acknowledgements

I am especially grateful to both my supervisors Prof. Dr. Bernhard HAU and Prof. Dr. Hans-Michael POEHLING for the challenging topic of my dissertation. I also thank Prof. Dr. Bernd FREIER for taking over the second survey report.

You always supported my work in many ways: to construct the models, to use the different statistical methods (including ROC-analyses), to discuss statistical analyses, to catch the aphids, to discuss the ecology of aphids and their natural enemies, and to present the results on international conferences. Excellent advice, detailed discussions, and a critical reading of the manuscripts rounded off the supervision.

This project was made possible by a lot of helping hands and brains:

Firstly, I thank all the staff of ISIP (Informationssystem Integrierter Pflanzenschutz), ZEPP (Zentralstelle der Länder für EDV-gestützte Entscheidungshilfen und Programme im Pflanzenschutz), and the plant protection service in Rhineland Palatinate, but mainly Benno Kleinhenz, Erich Jörg, and Frank Burghause. You are a funny bunch over there in Bad Kreuznach. Thanks for your kind support.

Secondly, I thank those of the plant protection services, who provided technical support and collected aphid data, mainly: Mechthild Hübner, Adelheid Gneist, Stefan Krüssel, Gerd Lauenstein, Peter Matthes, Walter Rickmann, Christian Wolff, and Vera Wüstefeld.

I thank Hans Friesland and his collegues from the German weather service (Deutscher Wetterdienst, DWD) in Braunschweig and Offenbach for providing millions of numbers determining the weather.

Special thanks goes to Bernd Ulber and his colleagues from the Institute of Plant Pathology and Plant Protection, University of Göttingen, for suction trap construction and for the data on aphids.

Manuscripts were greatly improved by proofreading of Florence B. Boshold and Suzyon Wandrey, and by discussions with Charles-Antoine Dedryver, Bernd Freier, Hans Friesland, Christian C. Figueroa, Hugh D. Loxdale, Benno Kleinhenz, and especially Jean-Christophe Simon.

I thank the colleagues at the Institute of Plant Disease and Plant Protection, including the entomology working-group; with special thanks to Peter Hondelmann, Inga Koepke, Christine Warmke, and Timo Michel. Counting aphids was not always fun, but eating Wal-markt Döner and listening to E-books prepared the ground for opulence of aphids.

I thank the Institute for Biostatistics, mainly Ludwig A. Hothorn and Frank Schaarschmidt, for stimulating discussions about statistical tests and techniques.

I thank Udo Heimbach, Maurice Hullé, and Thomas Thieme for help with the identification of aphids.

I thank Simone Seling, Federal Research Institution for Alimentation and Food (Bundesforschungsanstalt für Ernährung und Lebensmittel, in Detmold), for the accurate determination of crude protein contents.

I thank all of the farmers, who let us work in their fields, giving us space and time, doing without insecticide applications, and thereby providing a lot of aphids.

Finally, I am infinitely grateful to my lovely wife Meike, my family, and all friends (including “Halb-Eins-Mensa”); you were really great to give everlasting courage and helped to keep-up with the funny sides of life!

Last but not least I thank all the **aphids** that were migrating and developing in variable numbers though all years, thereby providing insights in their complex life cycles, showing various migration behaviours, developing in cages as well as in fields, being open to count, attracting their natural enemies, and providing “broad-minded” their DNA. They really demonstrated to be more than ugly cereal pests but incredible complex organisms.

This work was financially supported by the Bundesministerium für Verbraucherschutz, Ernährung und Landwirtschaft, Germany (Federal Ministry of Food, Agriculture, and Consumer Protection; project code: 01HS083).

Curriculum Vitae (English)

Personal data

Name:	A. Michael KLÜKEN
Address:	Wilhelm-Bluhm-Str. 51, 30451 Hannover, www.klueken.de
Born:	15.09.1973 in Krefeld
Marital status:	married, no children
Nationality:	German

School education

1980-1993	Bischöfliche Maria-Montessori Schule, Krefeld
1993	Final school exam grade “B“

Social service

1994-1995	Social service in the Körperbehinderten-Schule, Krefeld-Traar

Professional training

09/1995-09/1998	Train as gardener (garden- and landscaping) in the company LHG-Gartengestaltung, Krefeld
06/1998	Final vocational exam grade “A“

Universitary training

10/1998-10/2003	Study of Horticultural Science at the Leibniz Universität Hannover, Final University exam grade “A“
10/2003	Diploma thesis in the issue of "Population structure and within-field variability of *Aspergillus flavus* field populations of a single small-scale field in West African maize production systems" (Department of Phytomedicine, exam grade “A“)
11/2003-12/2007	Project-bound assistantship at the Institute for Plant Diseases and Protection, Leibniz Universität Hannover: Doctoral thesis project: "Migration and early population development of cereal aphids in winter cereals" (Funding: BLE)
02/2008	Final doctoral exam grade

Publications

- Klüken A.M., Borgemeister C. & Hau B. 2008: Field releases of an atoxigenic *Aspergillus flavus* L-strain in central Benin. *Journal of Plant Diseases and Protection* (submitted).
- Klüken A.M., Poehling H.-M. & Hau B. 2007: Analyses of factors influencing the population dynamics of cereal aphids and their relevance to model extensions. *Mitteilungen der Deutschen Gesellschaft für allgemeine und angewandte Entomologie* **16**.
- Poehling H.-M., Freier B. & Klüken A.M. 2007: IPM case study: Grain. In: VanEmden H.F. & Harrington R. (eds.): *Aphids as crop pests*. CAB International, Wallingford, U.K., pp. 311-329.

Memberships

since 03/2004	Deutsche Phytomedizinische Gesellschaft, DPG (German Phytomedical Society)
since 03/2004	Deutsche Gesellschaft für allgemeine und angewandte Entomologie, DGaaE (German Society for general and applied Entomology)
since 06/2005	Deutsche Landwirtschafts Gesellschaft, DLG (German Agricultural Society)

Voluntary services

09/2005 - 09/2006	Main chairman of the “offspring” in the German Phytomedical Society
09/2004 - 09/2005	Assistance chairman of the “offspring” in the German Phytomedical Society
04/2000 - 03/2002	Chairman of the students in special field of the (ancient) Department of Horticultural Science
10/1998 - 08/2002	Chairman of students unit of the (ancient) Department of Horticultural Science and selected committees

Curriculum Vitae (Deutsch)

Persönliche Daten

Name: A. Michael KLÜKEN
Adresse: Wilhelm-Bluhm-Str. 51, 30451 Hannover,
www.klueken.de
Geboren: 15.09.1973 in Krefeld
Familienstand: verheiratet, ohne Kinder
Staatsangehörigkeit: deutsch

Schullaufbahn

1980-1993	Bischöfliche Maria-Montessori Schule, Krefeld
1993	Allgemeine Hochschulreife, Note „gut“

Zivildienst

1994-1995	Pflegedienst in der Körperbehinderten-Schule, Krefeld-Traar

Berufsausbildung

09/1995-09/1998	Ausbildung zum Gärtner (Garten- und Landschaftsbau) bei der Firma LHG-Gartengestaltung, Krefeld
06/1998	Abschlussprüfung: „sehr gut“

Universitäre Ausbildung

10/1998-10/2003	Studium der Gartenbauwissenschaften an der Leibniz Universität Hannover, Abschlussnote: „sehr gut“
10/2003	Diplomarbeit zum Thema "Population structure and within-field variability of *Aspergillus flavus* field populations of a single small-scale field in West African maize production systems" (Fach: Phytomedizin, Note: „sehr gut“)
11/2003-12/2007	Projektgebundene Assistentenstelle am Institut für Pflanzenkrankheiten und Pflanzenschutz, Leibniz Universität Hannover: Promotionsvorhaben zum Thema "Migration and early population development of cereal aphids in winter cereals" (Finanzierung: BLE)
02/2008	Promotion mit Abschluss

Weitere Publikationen

- Klüken A.M., Borgemeister C. & Hau B. 2008: Field releases of an atoxigenic *Aspergillus flavus* L-strain in central Benin. *Journal of Plant Diseases and Protection* (submitted).
- Klüken A.M., Poehling H.-M. & Hau B. 2008: Analyses of factors influencing the population dynamics of cereal aphids and their relevance to model extensions. *Mitteilungen der Deutschen Gesellschaft für allgemeine und angewandte Entomologie* **16**.
- Poehling H.-M., Freier B. & Klüken A.M. 2007: IPM case study: Grain. In: VanEmden H.F. & Harrington R. (eds.): *Aphids as crop pests*. CAB International, Wallingford, U.K., pp. 311-329.

Mitgliedschaften

seit 03/2004	Deutsche Phytomedizinische Gesellschaft, DPG
seit 03/2004	Deutsche Gesellschaft für allgemeine und angewandte Entomologie, DGaaE
seit 06/2005	Deutsche Landwirtschafts Gesellschaft, DLG

Ehrenamtliche Tätigkeiten

09/2005 - 09/2006	Hauptverantwortlicher Sprecher der Nachwuchswissenschaftler in der Deutschen Phytomedizinischen Gesellschaft
09/2004 - 09/2005	Stellvertretender Sprecher der Nachwuchswissenschaftler in der Deutschen Phytomedizinischen Gesellschaft
04/2000 - 03/2002	Vertreter der Studenten im (ehem.) Fachbereichsrat Gartenbau
10/1998 - 08/2002	Vertreter der Studenten im Fachschaftsrat Gartenbau und in verschiedenen Kommissionen

NOTES: