Agronomic and Physiological Parameters of Genotypic Nitrogen Efficiency in Oilseed Rape (*Brassica napus* L.)

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GENERAL ABSTRACT

In European agriculture winter oilseed rape (*Brassica napus* L.) is characterized by the highest N-balance surpluses as compared to other agricultural crops. This is mainly due to low N-uptake rates during reproductive growth and incomplete N retranslocation from the source organs to the seeds, leaving high soil mineral N contents and high N amounts in crop residues in the field. A main approach to solve the large problem of N balance surpluses of this crop is the breeding and cultivation of cultivars which efficiently use the available nitrogen. However, to facilitate the breeding process of N-efficient cultivars, the identification of secondary plant traits contributing to N efficiency is necessary.

The objectives of the present study were: (1) to determine genotypic differences in N efficiency (seed yield at limiting N supply) and the importance of N uptake and N utilization efficiency (grain yield per unit N taken up) for genetic variation in seed yield under different levels of N supply, (2) to estimate the significance of root growth and morphology for genotypic differences in N efficiency, (3) to identify morphological and physiological leaf traits contributing to genotypic differences in N efficiency and (4) to quantify the relative importance of radiation interception and radiation use efficiency for crop growth rate. Different sets of cultivars and DH lines were evaluated in field experiments conducted in 1999/2000, 2000/2001 and 2001/2002 cropping periods at two experimental sites near Göttingen under three different levels of N supply (N0: soil mineral N, N1: 120 kg N ha^{-1}, N2: 240 kg N ha^{-1}).

In the experiments significant genotypic differences in N efficiency were found. Also the yield response to supplied N, i.e. the interaction between N and genotype, was highly significant. High N efficiency was mainly achieved by those cultivars which maintained high N-uptake activity during the reproductive growth phase. The root investigations showed that the N-efficient cultivar also had a more vigorous root system. Also, this cultivar was able to achieve a higher light interception at limiting N supply. On the other hand, N losses by dropped leaves were found to be generally low and not important for genotypic differences in grain yield.

In conclusion, the results suggest that N uptake and crop growth during the reproductive growth phase are more important for N efficiency than N retranslocation from vegetative plant parts to the seeds.

KURZZUSAMMENFASSUNG

Winterraps (*Brassica napus* L.) ist innerhalb der europäischen Landwirtschaft im Vergleich zu anderen Kulturarten durch die höchsten Stickstoff (N) Bilanzsalden gekennzeichnet. Verantwortlich dafür sind niedrige N-Aufnahmeraten während der reproduktiven Wachstumsphase und eine unvollständige N-Verlagerung in die Samen, so dass hohe mineralische N-Gehalte und hohe N-Mengen in den Ernterückständen auf dem Feld verbleiben. Hauptansatz zur Reduzierung der Bilanzüberschüsse ist die Entwicklung und der Anbau von N-effizienten Sorten, die den verfügbaren Stickstoff effizient nutzen. Um den Züchtungsprozess von N-effizienten Sorten zu vereinfachen, ist jedoch die Identifizierung von sekundären pflanzlichen Eigenschaften mit Einfluss auf die N-Effizienz notwendig.

Die Zielsetzungen der vorliegenden Arbeiten waren: (1) genotypische Unterschiede in der N-Effizienz (Kornertrag bei limitierendem N-Angebot) und die Bedeutung von N-Aufnahme- und Nutzungseffizienz für die genetische Variation im Ertrag bei unterschiedlichen N-Angebotsstufen zu bestimmen, (2) die Bedeutung von Wurzelwachstum und –morphologie für die N-Effizienz zu beurteilen, (3) morphologische and physiologische Blattmerkmale mit Einfluss auf die N-Effizienz zu untersuchen und (4) die relative Bedeutung von Lichtaufnahme und –nutzung für das Wachstum zu quantifizieren. Verschiedene Sorten und DH-Linien wurden in drei Feldversuchen in den Wachstumsperioden 1999/2000, 2000/2001 und 2001/2002 an zwei Standorten in der Nähe von Göttingen und bei drei N-Angebotsstufen (N0: mineraler Boden-N, N1: 120 kg N ha^{-1}, N2: 240 kg N ha^{-1}) untersucht.

In den Versuchen unterschieden sich die Genotypen signifikant in der N-Effizienz. Auch die Ertragssteigerung nach N-Düngung, d.h. die Interaktion zwischen N-Angebot und Genotyp, war hochsignifikant. Eine hohe N-Effizienz wurde v. a. von Sorten mit einer hohen N-Aufnahmekapazität während des reproduktiven Wachstums erreicht. Die Wurzeluntersuchungen zeigten, dass die N-effiziente Sorte auch ein größeres Wurzelsystem besaß. Außerdem wies diese Sorte eine höhere Lichtaufnahme auf. Andererseits waren N-Verluste durch abgefallene Blätter insgesamt gering und nicht entscheidend für Sortenunterschiede im Ertrag.

Abschließend kann aus den Ergebnissen gefolgert werden, dass N-Aufnahme und Wachstum während der reproduktiven Wachstumsphase für die N-Effizienz von größerer Bedeutung sind als die N-Retranslokation aus vegetativen Pflanzenorganen in die Samen.

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ABREVIATIONS

˚C	Degree Celsius
µl	Microliter
µM	Micromolar
ANOVA	Analysis of variance
BF	Beginning of flowering
BS	Beginning of shooting
Chap.	Chapter
cm	Centimetre
CO_2	Carbon dioxide
Cult	Cultivar
DAT	Days after starting the treatment
DH	Double haploid
Drop	Dropping
EF	End of flowering
Fig.	Figure
g	Gram
GSL	Gluconsinolate
ha	Hectare
kg	Kilogram
kJ	Kilo joule
kW	Kilo watt
l	Litre
LAD	Leaf area duration
LAI	Leaf area index
m	Meter
m^2	Meter square
MA	Maturity
mg	Milligram
min	Minute
MJ	Mega Joule
ml	Milliliter
mM	Millimolar
N	Nitrogen
n.s	Statically non significant
NH_4	Ammonium
N_{min}	Mineral N
NO_3	Nitrate
PAR	Photosynthetic active radiation
RL	Root length
RLD	Root length density
RUE	Radiation use efficiency
s	Second
SLN	Specific leaf N
SPAD	Single Photon Avalande Diode
t	Ton
Tab.	Table

GENERAL INTRODUCTION

The world population is increasing at a rate of 80 million per year and expected to be around 8.04 billion for the year 2025 and 9.37 billion for 2050 (FAO, 2009). A rapidly increasing world population demands ever-increasing food production. Therefore, to keep food production at the same level as population growth without using up or devastate the non-renewable resources is not an easy task. Nevertheless, the challenge should be providing food for an increasing population whilst maintaining soil fertility and taking care of the precious natural environment.

In the 1960s, the efforts of agricultural scientists began to be realized in increased crop production in many areas of the world, especially in Asia, which as called "Green Revolution" brought remarkable increases in crop production. World grain output was expanded by a factor of 2.6 from the 1950s to the 1980s (Camemark, 2005). The global increase in grain yield was the result of using high-yielding varieties of cereal crops and application of an energy intensive agriculture. These high yielding varieties performed best under high applications of fertilizer, and also required more expenditure for pesticides, irrigation, and farm machinery (Bumb, 1996).

Today, mineral fertilizers are still an important resource and essential input for crop growth and yield in both high-input and low-input agricultural systems. Particularly, nitrogen (N) is the most common and widely used fertilizer nutrient in crop production. After application of mineral N fertilizer, the immediate positive effect on crop growth makes this fertilizer very popular. To secure yields, growers apply more fertilizer than recommended and so the global use of N fertilizers in the world increased largely during the past 4 decades (Byrnes and Bumb, 1998). On the other hand, the available N is often a more limiting factor influencing plant growth than is any other nutrient in both high-input and low-input agriculture systems (Grindlay, 1997).

Due to the use of low levels of N fertilizers by the small-scale farmers, the soil fertility is declining in low-input agriculture. On the other hand, the concerns are rising on environmental pollution of both air and water due to use of intensive N fertilizers in high-input agriculture (Wiesler, 1998; Brégard et al., 2000). However, the efficiency of N fertilizers is frequently low, since, plants take up often less than 50% of the applied N (Raun and Johnson, 1999), and the proportion of fertilizer N not utilized by the crop is left in the soil

and/or lost from the plant/soil system through volatilisation, leaching and denitrification (Byrnes and Bumb, 1998; Laegreid et al., 1999). Therefore, to improve N efficiency in agriculture, integrated N management strategies that take into consideration improved fertilizers and soil and crop management practices are necessary (Wiesler et al., 2001b). Among these, breeding and cultivation of N-efficient cultivars can play an important role in both low-input and high-input sustainable agricultural production (Horst et al., 2002).

The nutrient efficiency is related to the genetic variation among the crop plants and has been well known for at least 84 years (Hoffer, 1926). Recently, due to ecological, economical and socio-economical grounds, many plant physiologists and plant breeders draw increasing attention to genotypic differences in nutrient efficiency (Wright, 1976; Seifert et al., 2004). However, the discussion on genotypic differences in nutrient efficiency is complicated in the first place by the absence of a generally accepted definition of N efficiency, and the term is used in various ways in the literature. A genotype can be characterized as N-efficient either when realizing a yield above average under conditions of low or suboptimal N supply (Graham, 1984) or when converting N fertilizer efficiently into yield under conditions of high N supply (Sattelmacher et al., 1994).

The N efficiency of crops depends on two primary components: the uptake efficiency and the utilization efficiency (Moll et al., 1982). Moll et al. (1982) expressed uptake efficiency as the efficiency with which the soil N can be taken up by the plant (Nt/Ns), and utilization efficiency as the seed dry weight per unit of absorbed N fertilizer (Gw/Nt); Gw is the seed dry weight, Ns is N supply and Nt is total N in the plant at maturity. However, the definition of Moll et al. (1982) covers the entire range of N fertilizer levels except zero-N application. Therefore, in the present study, the N efficiency was defined according to Graham (1984) as grain yield at low or sub-optimal N supply. Grain yield at high N supply was considered as yield potential or, in relation to N efficiency, the responsiveness to increased N supply. The N uptake efficiency was, accordingly, defined as N uptake at low N supply. The N utilization efficiency was calculated as the ratio between grain yield (kg/ha) and total N (kg/ha) in the aboveground plant at maturity.

Genotypic variation in N efficiency could generally be attributed to high N uptake and/or high N utilisation (Sattelmacher et al., 1994). Several studies demonstrated the genotypic differences in N uptake and N utilisation with many field crops including wheat (Spanakakis,

2000), maize (Moll et al., 1982; Presterl et al., 2000), sorghum (Gardner et al., 1994), barley (Maidl et al., 2000) and winter oilseed rape (Barszczak et al., 1993; Möllers et al., 2000; Wiesler et al., 2001a,b) at different levels of N supply.

The winter oilseed rape (*Brassica napus* L.) is an important agricultural crop cultivated primarily for its oil, which can be used as an edible product or for industrial application (Malagoli et al., 2005). Also, after oil extraction the seed residue has a high protein content which can be used as animal feed supplement (Schjoerring et al. 1995). Around 60% of the world production of oilseed rape are grown in temperate regions (America and Europe), whereas the production in the tropical areas (Africa, Malaysia and Indonesia) is less than 6% (Hatje, 1989). Due to economic grounds and as an important crop to diversify cereal-dominated crop rotations, many EU countries have a great interest in oilseed rape production. Among the EU countries France, Germany and the UK show the largest oilseed rape production (FAO. 2009).

To obtain maximum seed yield, high rates of nitrogen fertilizer are usually applied to oilseed rape crops (Barraclough, 1989; Holmes, 1979; Schjoerring et al., 1995). However, oilseed rape has a relatively poor N efficiency (Aufhammer et al., 1994, Schjoerring et al., 1995). Usually, only about 50% of applied fertilizer N is recovered in the harvested seeds (Augustinussen, 1987). Therefore, in European agriculture, winter oilseed rape crop is characterized by low recoveries of soil and fertilizer N in harvested organs, i.e. largest N-balance surpluses as compared to other agricultural crops (Gäth, 1997). The large N-balance surpluses, which increase the risk of environmental quality by leaching to the ground water (Lickfett, 1993) or trough volatilisation and denitrification to the atmosphere (Byrnes and Bumb, 1998; Laegreid et al., 1999), are the characteristic results of the "traditional oilseed rape cultivars" which always show a high nitrogen (N) uptake until flowering, low N uptake during the reproductive growth phase and incomplete N retranslocation from the source organs to the seeds (Aniol 1993; Lickfett 1993), leaving high soil mineral N contents and high N amounts in crop residues (Aufhammer et al., 1994; Lickfett et al., 2001).

In the past, while little attention was paid on the genotypic differences in N efficiency of winter oilseed rape (Wright, 1976; Baligar and Duncan, 1990; Yau and Thurling, 1987), recently, many studies (Barszczak et al., 1993; Möllers et al., 2000; Wiesler et al., 2001; Horst et al., 2002, Kahm et al., 2005; Schulte auf´m Erley et al., 2007) were carried out on

genotypic differences in N efficiency of oilseed rape cultivars. A main approach to solve the large N balance surpluses problem of this crop was the development and cultivation of cultivars which efficiently use the available nitrogen (N). However, to facilitate the breeding process of N-efficient cultivars, the identification of secondary plant traits contributing to N efficiency is necessary. On the basis of these results, two possible ideotypes of N-efficient rape cultivars have been hypothesized in a previous study by Wiesler et al. (2001a): an "improved traditional ideotype" with vigorous growth and high N uptake until flowering and efficient N retranslocation into the seeds during reproductive growth and an "alternative ideotype" with comparatively slow growth and N-uptake rates until flowering, which, however, continue during reproductive growth. Depending on the ideotype hypothesis of Wiesler et al. (2001a), various long-term field (1996/97, 1997/98, 1998/99) and nutrient solution (1997/98, 1998/99) experiments, were conducted. It has been found that N-efficient rape cultivars can be assigned to the "alternative ideotype" because positive correlations of seed yield with N uptake during reproductive growth under conditions of low N supply have been found, but not with N uptake up to flowering.

To maintain high N uptake activity during the reproductive growth, the "alternative rape ideotype" needs more resourceful and vigorous root growth, since the leaves, stems and pods are depended on an efficient N supply from the soil. On the other hand, for the new root formation and longevity of the roots a continuous assimilate allocation from the leaves to the roots is a prerequisite. This can be supplied by the leaves which are able to delay the leaf senescence process and thus prolong the leaf area duration to intercept more radiation and to maintain photosynthetic activity. On the basis of this "alternative rape ideotype" hypothesis, the objectives of the study were assessed in four areas:

(i) Agronomic parameters of genotypic nitrogen efficiency (Chapter I)
(ii) Significance of root growth and morphology for genotypic differences in nitrogen efficiency (Chapter II)
(iii) Role of leaves for genotypic differences in nitrogen efficiency (Chapter III)
(iv) Genotypic differences in radiation use efficiency (Chapter IV)

Thus, the objectives of the present study were: (1) to determine genotypic differences in N efficiency (seed yield at limiting N supply) and the importance of N uptake and N utilization efficiency (grain yield per unit N taken up) for genetic variation in seed yield under different

levels of N supply, (2) to estimate the significance of root growth and morphology for genotypic differences in N efficiency, (3) to identify morphological and physiological leaf traits contributing to genotypic differences in N efficiency and (4) to quantify the relative importance of radiation interception and radiation use efficiency for crop growth rate.

CHAPTER I

AGRONOMIC PARAMETERS OF GENOTYPIC NITROGEN EFFICIENCY IN OILSEED RAPE (*BRASSICA NAPUS* L.)

1. Abstract

Previous work revealed that genotypic differences in grain yield at limiting N supply (N efficiency) exist among winter oilseed rape (*Brassica napus* L.) cultivars. So far, information on the underlying morphological and physiological mechanisms is scarce. The objectives of this study were i) to assess genotypic differences among pre-selected rapeseed cultivars and new DH lines with respect to their grain yield under low N supply, ii) to evaluate the importance of N uptake and N utilization efficiency, and iii) to identify parameters contributing to N uptake or N utilization. Eight cultivars and four DH lines were evaluated under three N rates (N0: soil mineral N, N1: 120 kg N ha^{-1}, N2: 240 kg N ha^{-1}) in field experiments in 2000, 2001 and 2002 performed at two sites near Göttingen. Increasing N supply significantly increased shoot dry matter, seed yield, seed protein content (%), harvest index (HI), total N uptake and N concentration, whereas it decreased seed oil content (%), N harvest index (NHI), and N-utilization. Averaged over three experimental years and two sites, highly significant genotypic variation in grain yield among twelve genotypes existed. Also the yield response to supplied N, i.e. the interaction between N and genotype, was highly significant. High N efficiency correlated significantly with N-uptake and moderately with N-utilization efficiency in 2000. In the second field trial (2001) high N efficiency was achieved by the cultivars which maintained high N-uptake activity during reproductive growth at N0. Due to the use of DH lines in 2002, N efficiency correlated significantly with high N utilization efficiency at N0. Consequently, both N efficiency components can play an important role in N efficiency. Main strategy to improve N efficiency was a high N uptake during reproductive growth, but single N-efficient cultivars were instead characterized by a high N utilization.

Key words: *Brassica napus* L., genotypic variation, cultivar, DH line, N efficiency, uptake, utilization,

2. Introduction

Nitrogen (N) is the most common and widely used fertilizer nutrient in crop production. Although it forms an important resource and essential input for crop growth and yield, the available N is more often a limiting factor influencing plant growth than any other nutrient in both high-input and low-input agriculture systems (Grindlay, 1997). Often, less than 50% of the fertilizer N is recovered by the crop (Raun and Johnson 1999, Schjoerring et al., 1995). Due to the low levels of N fertilizer used by the small-scale farmers, soil fertility is declining dramatically in low-input agriculture. On the other hand the concerns are rising on environmental pollution of both air and water due to use of intensive N fertilizer in high-input agriculture (Wiesler, 1998; Brégard et al., 2000).

In European agriculture winter oilseed rape (*Brassica napus* L.) is an important crop due to economic reasons and it is largely used to diversify cereal dominated crop rotations. As compared to other annual crops, winter oilseed rape has the longest growing period, about 350 days from sowing to maturity, depending on site (Macdonald et al., 1997), weather (Jackson, 2000), fertilization (Schroeder and Makjowski, 1996), crop density (Leach et al., 1999) and sowing date (Jenkins and Leitch, 1986). To obtain maximum seed yields, high rates of nitrogen fertilizer are usually applied for this crop. It has been shown that depending on soil type and yield the fertilizer requirement of this crops ranges from 200 to 330 kg N/ha (Barraclough, 1989; Aufhammer et al., 1994; Schjoerring et al., 1995; Wiesler et al., 2001a,b).

Due to its high capacity to take up nitrate from the soil, several studies proposed to use winter oilseed rape as a catch crop to reduce N leaching during autumn-winter period (Cramer, 1993; Malagoli et al., 2005). On the other hand, this crop has relatively poor N efficiency (Aufhammer et al., 1994, Schjoerring et al., 1995), since usually only about 50% of applied fertilizer N is recovered in the harvested seeds (Augustinussen, 1987). Therefore, in European agriculture winter oilseed rape crop is characterized by low recoveries of soil and fertilizer N in harvested organs, i.e. largest N-balance surpluses as compared to other agricultural crops (Gäth, 1997).

The large N-balance surpluses are mainly due to the characteristics of the traditional oilseed rape cultivars which always show a high nitrogen uptake until flowering, low N uptake during reproductive growth and incomplete N retranslocation from the source organs to the seeds

(Aniol, 1993; Lickfett, 1993), leaving high soil mineral N contents and high N amounts in crop residues in the field (Aufhammer et al., 1994; Lickfett et al., 2001). An improvement in fertilizer, soil and crop management practices may help to improve the N efficiency of this crop in both low- and high-input agriculture systems (Wiesler et al., 2001b). Among these, breeding and cultivation of N-efficient cultivars could contribute to a reduction of the large N balance surpluses of this crop (Schulte auf´m Erley et al., 2007) and thus optimize yields and minimize the environmental impact in high-input agriculture (Lynch, 1998). However, to facilitate the breeding process of N-efficient cultivars, the identification of secondary plant traits correlating with N efficiency is necessary (Schulte auf´m Erley et al., 2007).

Nutrient efficiency related to genetic variation among crop plants has been well known for at least 84 years (Hoffer, 1926). Previously, genotypic differences in N efficiency have been demonstrated widely with many field crops studied in various field and nutrient solution experiments. Significant differences in grain yield among twelve old and new wheat genotypes under low and high N conditions were reported by Austin et al (1980). A comparison of 25 maize hybrids at low and high N supply indicated significant yield variations among hybrids, and the genotype x N interaction was highly significant for grain yield as well as for N uptake and N-utilization (Presterl et al., 2002). Sinebo et al. (2004) elucidated significant genotypic differences in grain yield and total N uptake of twenty-six Ethiopian barley genotypes under two N rates. The field and nutrient solution studies of Gardner et al. (1994) demonstrated significant genetic diversity among five sorghum cultivars in grain yield that correlated mostly with leaf canopy structure and leaf N concentrations at low N supply. Significant yield variations among 16 rice lines under fertilized and non-fertilized conditions were reported by Inthapanya et al. (2000).

Several authors also reported the existence of genotypic differences in N efficiency of oilseed rape. Yau and Thurling (1987b) demonstrated significant differences in grain yield among 40 diverse spring rape genotypes under limiting N supply and in yield response to higher N application rates. Genotype x N interaction was significant for all characters except harvest index (HI) and growth rate. Long-term and multi-locational field trials were carried out by Möllers et al. (1999) with 18 winter oilseed rape cultivars at three N rates. The authors reported significant genotypic differences in grain, oil and protein yields as well as for total N uptake. They further elucidated highly significant genotype x N fertilizer interactions for grain yield and total N uptake. Another long-term field study was carried out by Kessel and Becker

(1999) with 90 oilseed rape genotypes from five different groups at two N rates clearly demonstrated significant genotypic variation in several characters (seed and straw yields, chlorophyll content, N amounts in seed and straw, oil and glucosinolate content in the seeds) which possibly are related to N efficiency. However, except N content in the biomass no significant interactions between genotype and N occurred.

To solve the high N-balance surplus problem of oilseed rape crop similar long-term field trials were conducted previously by members of our institute (Behrens, 2002; Wiesler 2001a,b). Two possible ideotypes of N-efficient rape cultivars have been hypothesized by Wiesler et al. (2001a): an "improved traditional ideotype" with vigorous growth and high N-uptake until flowering and efficient N retranslocation into the seeds during reproductive growth and an "alternative ideotype" with comparatively slow growth and N-uptake rates until flowering, which, however, continue during reproductive growth. It has been found that N-efficient rape cultivars can most probably be assigned to the "alternative ideotype" because positive correlations of seed yield with N-uptake during reproductive growth under conditions of low N supply have been found, but not with N-uptake up to flowering (Behrens, 2002; Wiesler 2001a).

The high N uptake activity of the "alternative N-efficient ideotype" during reproductive growth might be related to a range of agronomic and physiological parameters that contributed to the higher seed yield under limiting N supply. Biological processes that determine seed yield formation are highly variable and depend on genetic and environmental factors and their mutual interactions (Sidlauskas and Bernotas, 2003). A further characterization of the underlying morphological and physiological mechanisms determining N efficiency in oilseed rape is necessary. Therefore, the objectives of this study were i) to assess genotypic differences among pre-selected cultivars and newly introduced DH lines in grain yield under low N supply, ii) to evaluate the importance of N uptake and N utilization efficiency, and iii) to identify parameters contributing to N uptake or N utilization. These results thus present the basis for the more in-depth root and leaf studies that will be described in the following chapters.

3. Materials and Methods

3.1 Experimental Sites

Three field experiments in the 1999/2000, 2000/2001 and 2001/2002 cropping periods were conducted by the Institute of Plant Nutrition, Leibniz University of Hannover in cooperation with the Institute of Agronomy and Plant Breeding, University of Göttingen. The experiments were carried out at two sites, namely Zuchtgarten and Dragoneranger, which are located near to Göttingen (51.32° northern latitude and 09.56° eastern longitude) in northern Germany. The experimental station Zuchtgarten is located at the southern side of Göttingen whereas other station Dragoneranger is located at the northern side. During three years field experiments the intensive studies and investigations were carried out at Zuchtgarten, whereas only the seed yield was considered at Dragoneranger.

The soils at both experimental sites were classified as silty clayey gleyic Luvisol. Soil particle size distribution and chemical properties at different layers of the soil profile are summarized in Table 1. Both experimental sites contained high silt contents at 0-90 cm soil depth. The A_p-horizon (0-30 cm depth) at Zuchtgarten contained slightly more total N and organic C than Dragoneranger. As compared to Zuchtgarten, the soil pH was higher at 0-90 cm soil depth at Dragoneranger.

Table MM I-1: Soil particle size distribution and chemical properties at different layers of the soil profile in the experimental sites Zuchtgarten and Dragoneranger.

		Particle size distribution					
	Soil depth	Sand	Silt	Clay	pH	N	C
Site	[cm]		[%]			[%]	[%]
Zuchtgarten	0-30	13	70	17	7.00	0.15	1.33
	30-60	8	76	16	7.06	0.11	0.98
	60-90	7	73	21	7.18	0.07	0.71
Dragoneranger	0-30	10	73	17	7.22	0.13	1.26
	30-60	10	72	18	7.32	0.10	1.51
	60-90	5	81	14	7.49	0.07	1.30

The agro-meteorological parameters of both experimental sites were collected from the Meteorological Institute of Göttingen. For the period of the three field experiments, the monthly rainfall, monthly temperature and long-term average of monthly rainfall and monthly temperature measured from 1961 to 1990 are shown for each experimental year in Figure MM I-1.

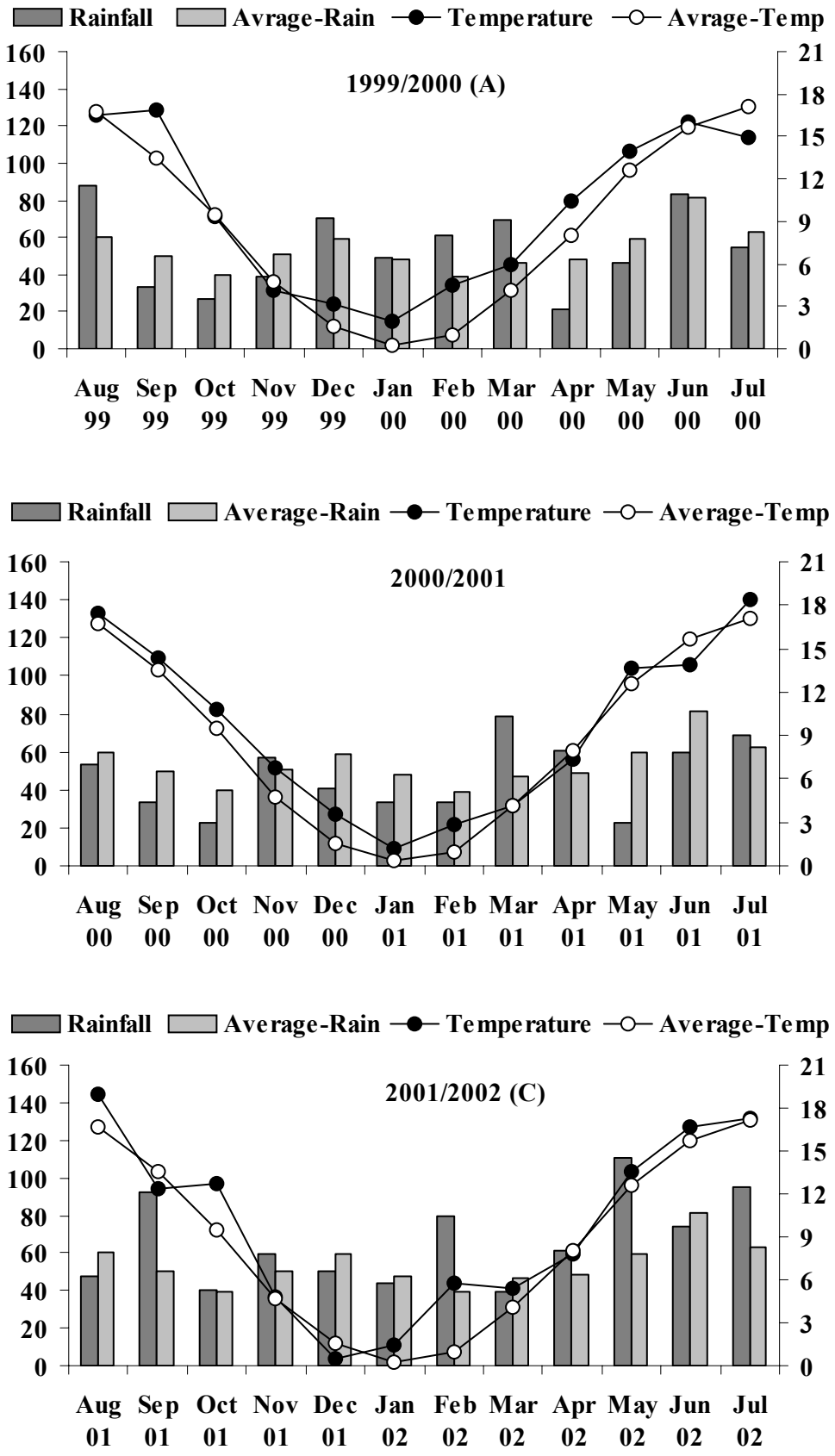


Figure MM I-1: Monthly rainfall and temperature in Göttingen in 2000 (A), 2001(B) and 2002 (C) and as long-term average. Source: Meteorological Institute of Göttingen.

In comparison to the long-term average rainfall and temperature, the growth condition was unfavorable in the first field experiment (1999/2000). A dry season due to lower monthly rainfall particularly between September and November (1999) and between April and May (2000) (annual rainfall 591 mm) and a warm season due to higher monthly temperature from December (1999) up to June (2000) was recorded. In the second field experiment (2000/2001) growth condition was more favorable due to higher monthly temperature during winter period (December- February) and due to sufficient rainfall (annual rainfall 647 mm) particularly in March and April (2001). However, unfavorable growth conditions due to heavy rainfall (annual rainfall 863 mm) were found again in the last field experiment (2001/2002).

3.2 Plant Material and Experimental Design

In total, 12 rapeseed cultivars and the lines were grown in the three field experiments both at Zuchtgarten and Dragoneranger (Tab. MM I-2). Eight commercial winter oilseed rape cultivars were used in the first field experiment (1999/2000). Considering the first year results, the cultivar number was restricted to five commercial rape cultivars in the second year (2001/2002). In the last field experiment (2001/2002), two contrasting rape cultivars (Apex and Capitol) from the previous experiments and four double haploid (DH) lines derived from the crosses between the cultivars ‘Apex’ and ‘Mohican’ were used.

The experiments were layout as split-plot design with three levels of N supply (N0: soil mineral N, N1: 120 kg N ha^{-1}, N2: 240 kg N ha^{-1}) and four replications in a block arrangement. The nitrogen levels were the main plots and the cultivars the subplots. Each research plot consisted of six plant rows with 7.5 m length and 1.5 m width. The distance between two rows was 25 cm. The research plot was accompanied by one adjacent plot of the same treatment in 2000 and by two adjacent plots in 2001 and 2002 field experiments. One plot was kept for the machine harvest at maturity and the other plots were used for the various measurements that were performed before maturity. As N source, calcium ammonium nitrate fertilizer was used. Before application of the N fertilizer, the soil N_{min} content (0-90 cm soil depth) was considered and subtracted from the proposed N rate, 50% of the total amount of N was applied at the start of the vegetation period in March and the remaining 50% was applied at the beginning of shooting.

Table MM I-2: Overview about the field experiments in 2000, 2001 and 2002 in two experimental sites. Intermediate harvests and intensive studies were carried out at Zuchtgarten, whereas only the seed yield was considered at Dragoneranger.

Site/Year	Cultivar/Line	N treatment	N_{min}/ Date
Zuchtgarten 1999/2000	Apex, Bristol, Capitol, Express Lirajet, Mansholt Mohican, Prospa	N0: soil mineral N N1: 120 kg N ha^{-1} N2: 240 kg N ha^{-1}	23 kg N ha^{-1} (13.01.2000)
Dragoneranger 1999/2000	Apex, Bristol, Capitol, Express Lirajet, Mansholt Mohican, Prospa	N0: soil mineral N N1: 120 kg N ha^{-1} N2: 240 kg N ha^{-1}	34 kg N ha^{-1} (13.01.2000)
Zuchtgarten 2000/2001	Apex, Bristol, Capitol, Lirajet Mohican	N0: soil mineral N N1: 120 kg N ha^{-1} N2: 240 kg N ha^{-1}	18 kg N ha^{-1} (14.02.2001)
Dragoneranger 2000/2001	Apex, Bristol, Capitol, Lirajet Mohican	N0: soil mineral N N1: 120 kg N ha^{-1} N2: 240 kg N ha^{-1}	33 kg N ha^{-1} (14.02.2001)
Zuchtgarten 2001/2002	Apex, Capitol DH4, DH15 DH28, DH42	N0: soil mineral N N1: 120 kg N ha^{-1} N2: 240 kg N ha^{-1}	13 kg N ha^{-1} (12.02.2001)
Dragoneranger 2001/2002	Apex, Capitol DH4, DH15 DH28, DH42	N0: soil mineral N N1: 120 kg N ha^{-1} N2: 240 kg N ha^{-1}	28 kg N ha^{-1} (12.02.2001)

3.3 Trial Management

Seeds were sown using a plot drill machine (Öyjord) into 1.5 cm soil depth at a densitiy of 80 seeds per m^2. The seeding was done on 23.08.1999, 22.08.2000 and 23.08.2001 respectively, at Zuchtgarten and 31.08.1999, 28.08.2000 and 29.08.2001 at Dragoneranger. Each year 225 kg ha^{-1} Potassium Magnesia (30% K_2O, 10% MgO, and 17% S), was applied at shooting. 2.0 l ha^{-1} herbicide (Butisan Top) and 2.5 l ha^{-1} fungicide (1.5 l ha^{-1} Folicur + 1.0 l ha^{-1} CCC) were sprayed and 0.15 kg ha^{-1} insecticide (Fastrac SC) was applied in the solid form in almost equal amounts in each year. Herbicide application was done around 15-20 days after seeding and insecticide and fungicide applications were performed around 23-35 days after seeding.

3.4 Measurements and Analysis

3.4.1 Harvest, Dry Weight and Yield Determination

Harvests were performed at the beginning of shooting, beginning of the flowering, end of the flowering and maturity at Zuchtgarten (Tab. MM I-3). For the intermediate harvests, on either 1.0 or 2.0 m^2 plants were cut at the soil surface with the aid of a garden-scissor. Manually harvested plants were collected as a bunch and counted. To determine the total plant fresh weight of the harvested area, the bunch was weighed with the aid of a balance. From this bunch 20 representative plants were selected and weighed again. Afterwards, the representative 20 plants were separated into leaves, stems and pods and the fractions were weighed separately again. The harvested plant samples were transported from Göttingen to Hannover in order to determine the dry weight and for further analysis. All fresh plant fractions were stored separately in paper bags and dried at 65 °C in an oven of the Institute of Plant Nutrition, Leibniz University of Hannover, until a constant dry weight was attained.

Yield determination was carried out by harvesting the untreated research plot with a Hege 160 reaper-thresher (Hege GmbH & Co, Waldenburg) at maturity. From each plot the seeds were collected and transported to the Institute of Agronomy and Plant Breeding Laboratory, University of Göttingen for further analysis. Seed dry matter (t ha^{-1}) was calculated by the moisture content based on the Near Infrared Spectroscopy measurements.

After harvesting each 11.25 m^2 plot, the straw was collected in a canvas attached to the reaper-thresher. To determine the fresh weight of the two straw fractions (stem and pod hulls), the straw was weighed at first and then stems were separated by hand from the mixture and the rest (pod hulls) was weighed again. After registration of each fraction weight, representative sub-samples were taken for dry weight and mineral element determination. The separated stem and pod hulls biomass was stored in paper bags and dried at 65 °C in an oven. Dry weight was determined separately for each plant fraction. For the further analysis in laboratory, each plant fraction was separately pulverized with an automatic mill (Schlagkreuzmühle SK 1 Retsch GmbH, Haan).

Table MM I-3: Harvests carried out at Zuchtgarten in the field experiments in 2000, 2001 and 2002.

Year	Growth stage	Harvested Area (m^2)	Days After Seeding	Date
2000	Beginning of shooting	1.0	212	22/03/00
	Beginning of flowering	1.0	241	17/04/00
	End of flowering	1.0	266	15/05/00
	Maturity	11.25	325	13/07/00
2001	Beginning of shooting	1.0	230	09/04/01
	Beginning of flowering	2.0	251	30/04/01
	End of flowering	1.0	274	23/05/01
	Maturity	11.25	332	20/07/01
2002	Beginning of flowering	2.0	244	24/04/02
	End of flowering	1.0	277	27/05/02
	Maturity	11.25	327	16/07/02

3.4.2 Nitrogen Analysis

The N concentration (mg N g^{-1}d.w.) for each plant fraction (leaf, stem, pod, and seed) was determined by a CNS analyzer (Vario EL Macro element-analyzer, Elementar Analysensysteme, Hanau). Dried and ground samples of 15-30 mg weight were placed in tin capsules (6 x 6 x 12 mm), which were carefully closed and pressed using a hand presser to bring the size fitting exactly to the CNS analyzer sample holder. As a standard, around 3-4 mg Sulfanilic acid (MERCK) (C: 41.6%, N: 8.1% and S: 18.5%) was weighed and placed in tin capsules.

3.4.3 Calculation of N efficiency Components

The nitrogen uptake of rape cultivars and DH lines was determined separately for each harvest date. N utilization, harvest index (HI) and N harvest index (NHI) was calculated from data taken at maturity. After analyzing the N concentration (mg N g^{-1}d.w.) in each plant fraction (leaf, stem, pod, and seed) separately, the N content of each fraction was derived by multiplying with the respective dry weight (t ha^{-1}). The sum of the N in each fraction was defined as the total N in the aboveground biomass (shoot N uptake kg N ha^{-1}). Nitrogen utilization was calculated as the ratio of seed yield to total N in the aboveground biomass (kg

seed yield kg^{-1} N). HI was calculated as the ratio of seed dry matter to total dry matter. NHI was calculated as the ratio of N in the seed to total N in the aboveground biomass. Biological production efficiency (BPE) was calculated as the ratio of total shoot dry matter to total N in the aboveground biomass (kg d.w. kg N^{-1}).

3.4.4 Determination of Seed Quality

The seed quality was determined using a Near Infrared Spectroscopy (NIRS) technique (AOCS, 1993) at the Institute of Agronomy and Plant Breeding, University of Göttingen. As seed quality components, the oil (%), the protein (%), the glucosinolat (GSL) (µmol g^{-1}) and three fatty acid (Oleic C18:1, Linolenic C18:3 and Erucic acid C22:1) contents were measured.

3.4.6 Determination of Yield Components

Yield components of rape cultivars were determined in the 2000 and 2001 field experiments at Zuchtgarten. In the first field experiment the yield components of eight rape cultivars were determined while in the second field experiments only two rape cultivars (Apex and Capitol) were examined. As the yield components plants per m^2, pod number per plant, seed number per pod and thousand grain weight were determined. Two weeks before maturity 1.0 m^2 plants were cut from each plot at the soil surface with the aid of a garden-scissor. Manually harvested plants were collected as a bunch and counted for the number of plant per m^2. From this bunch representative 20 plants were selected and the number of pods per plant was determined. The calculation of seed number per pod and thousand grain weight was carried out based on the seed yield attained at maturity.

3.5 Statistical Evaluation

Results were subjected to analyses of variance (ANOVA) using the SAS® statistics program version 8.1 Proc Mixed procedure (SAS, 2001 Inst., Inc. Cary, NC). Multiple comparisons of treatment means were made by the LSMEANS / PDIFF statement for N rate by cultivar interactions. In the tables and figures results of the F test (***, **, * and + indicate significance at the $p < 0.001$, 0.01, 0.05 and 0.1 level, respectively), are given. Letters for multiple comparisons were assigned using a SAS macro (Piepho, 2004). Simple correlation coefficients were attained seed yield combined analysis of years and sites.

PROC MIXED with N rate, cultivar and the N rate by cultivar interaction as fixed factors and year, site, year by site, year by site by block and year by site by block by N rate as random factor. Multiple comparisons were made between cultivars within each N rate using the Tukey adjustion. Letters were assigned by a SAS macro (Piepo, 2004). N efficiency parameters were analyzed separately for each year at Zuchtgarten. PROC MIXED with N rate, cultivar + interaction as fixed factors, and Block and Block by N rate as random factors. Multiple comparison: LSMEANS / PDIFF statement for the N rate by cultivar interactions. Letters were based on pair wise comparison between cultivars within N rates using a SAS Macro (Piepho 2004).

4. Results

4.1 Plant Development and Dry Matter Production

The shoot dry matter continuously increased from beginning of shooting up to end of flowering at all N rates (Fig. I-1). In contrast, during the seed filling phase, dry matter decreased at different levels of N supply in the 2000 (A) and 2002 (C) field experiments. This indicates 100% of the total biomass was attained when the flowering was completed and that substantial dry matter losses occurred until maturity. On the other hand, the dry matter accumulation after end of the flowering continuously increased at all levels of N supply up to maturity in the field experiment in 2001 (B).

Differences in dry matter production between N levels were usually small at the beginning of shooting whereas significant differences were found at later growth stages. From beginning of flowering until maturity the highest dry matter was produced at N2 supply. Dry matter production at N1 supply lay in between the values achieved at N0 and N2. Dry matter production of N1 and N2 supply did not significantly differ at the beginning of flowering in 2000 and 2001 and end of the flowering in 2002. On the other hand, dry matter production at N1 supply was significantly lower than N2 supply at maturity in all three field experiments. The lowest shoot dry matter was produced at N0 supply from beginning of shooting till maturity.

Attaining the 100% of the total biomass at the end of the flowering and substantial dry matter losses until maturity was invariable for each field experiment. Plants attained about 27%, 22% and 19% of their total biomass at the beginning of shooting and 61%, 59% and 55% at the beginning of flowering at N0, N1 and N2 supply, respectively in 2000. From end of the flowering up to maturity the dry matter losses were about 30% at N0, 10% at N1 and 11% at N2 supply. In the second field experiment (2001) plants produced about 28%, 25% and 22% of their total biomass at the beginning of shooting, 49%, 49% and 46% at the beginning of flowering and 100%, 92% and 89% at the end of the flowering at N0, N1 and N2 supply, respectively. No dry matter losses were found at three N rates in 2001, but the dry matter difference between two growth stages was negligible at N0 supply. Because of no dry matter losses after the end of flowering the growing period of the rape plants up to maturity was slightly prolonged and may be therefore the highest dry matter was shown in 2001 compared to other two field experiments (Fig. I-1).

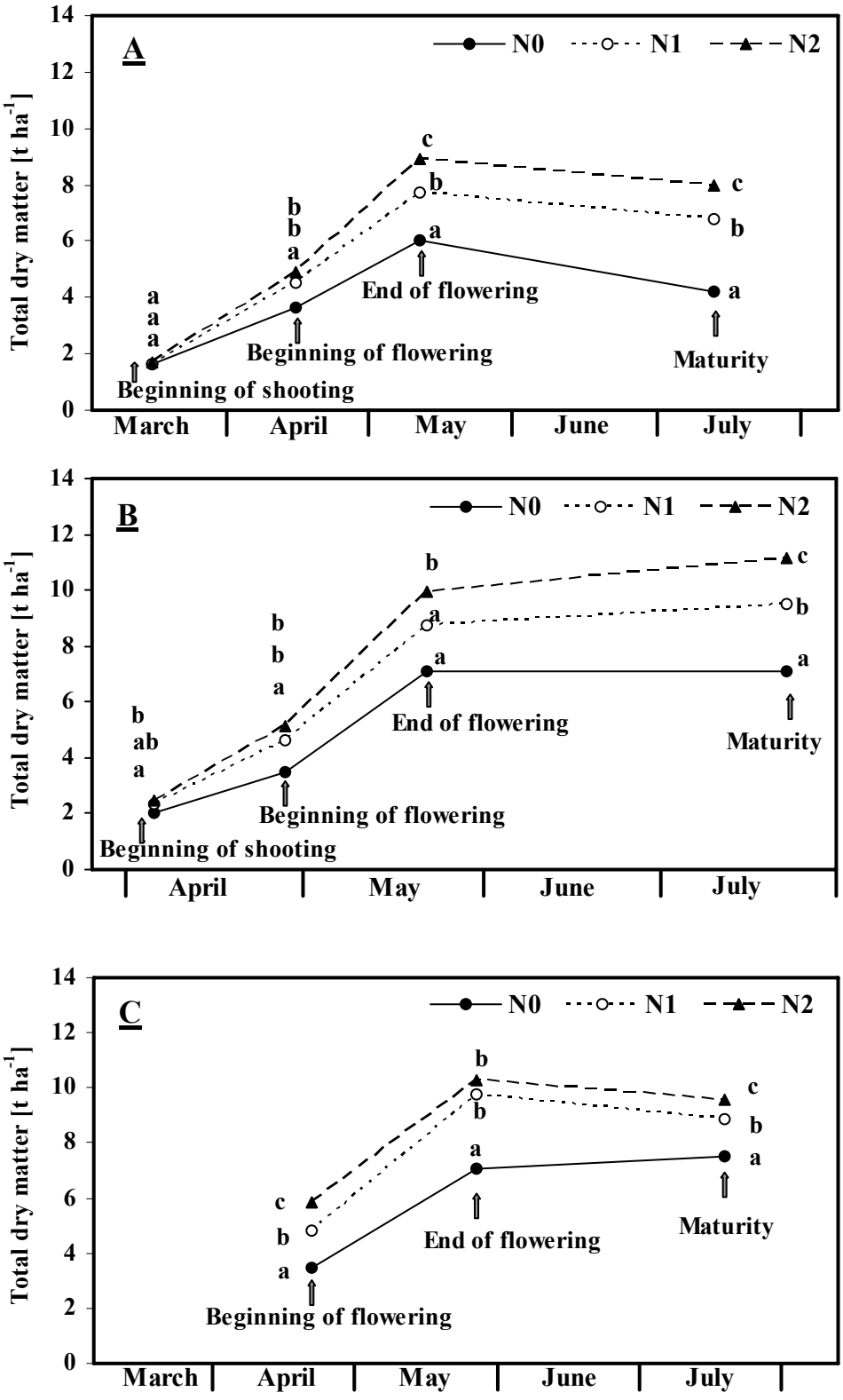


Figure I-1: Shoot dry matter of oilseed rape (means of 8, 5 and 6 cultivars, respectively) as affected by N supply (N0: soil mineral N supply, N1: 120 kg N ha^{-1}, N2: 240 kg N ha^{-1}) at different growth stages at Zuchtgarten in 2000 (A), 2001 (B), and 2002 (C). Statistics: Separate analysis of variance for different growth stages. Means with the same letter are not significantly different at $\alpha = 0.05$

In the last field experiment (2002) plants produced about 49%, 49% and 57% of their total biomass at the beginning of flowering at N0, N1 and N2 supply, respectively. The dry matter losses up to maturity were about and 9% at N1 and 8% at N2 supply in whereas no dry matter losses were found at N0 supply.

Eight rape cultivars differed significantly in shoot dry matter at four growth stages in the field experiment in 2000 (Tab. I-1). The interaction between N and cultivar for dry matter was significant at the beginning of flowering and end of the flowering. Shoot dry matter among cultivars varied in between 3.72 and 4.72 t ha^{-1} at N0, 5.98 and 7.57 t ha^{-1} at N1, and 7.24 and 8.46 t ha^{-1} at N2 supply at maturity. From beginning of shooting till end of flowering two cultivars, Lirajet and Prospa, constantly produced the lowest shoot dry matter at all N rates. However, at maturity, Prospa still had the lowest dry matter at three levels of N supply while Lirajet produced a significantly higher shoot dry matter at N2 supply. On the other hand, the higher shoot dry matter was produced by Mohican at the beginning of shooting at N0 and N2 supply. After shooting stage, the highest shoot dry matter was produced by Capitol at over all N rates at the beginning of flowering. At the end of the flowering this was still true for N0 supply. At the end of the flowering Bristol produced the highest shoot dry matter at N1 and N2 supply.

Until beginning of flowering significantly higher shoot dry matter was shown although, the dry matter production was significantly lowest at N0 supply by Capitol at the end of the flowering. A slight increase at maturity was shown at N0 supply while the low dry matter was accumulated at N1 and N2 supply. Contrast to Capitol, Apex accumulated lower shoot dry matter up to end of the flowering at N0 and N1 supply and then showed better performance under N0, N1 and N2 supply at maturity. Besides of Apex at maturity, Bristol and Express produced also significantly higher shoot dry matter at N0 supply.

Considerable shifts in the cultivar ranking of shoot dry matter production between the end of flowering and maturity, especially at N0. E.g., Capitol hand the highest shoot dry matter at the end of flowering, but at maturity it had a medium dry matter compared to the other cultivars. On the other hand, Apex had the lowest dry matter at the end of the flowering at N0, but a comparatively high shoot dry matter at maturity. Also for Bristol and Express shoot dry matter at N0 remained high until maturity, indicating lower dry matter losses of these cultivars.

Table I-1: Shoot dry matter of 8 oilseed rape cultivars as affected by N supply (N0: soil mineral N, N1: 120 kg N ha^{-1}, N2: 240 kg N ha^{-1}) at different growth stages at Zuchtgarten in 2000. Statistics: Separate analysis of variance for different growth stages. Means with the same letter are not significantly different at $\alpha = 0.05$ within each N rate.

Site: Zuchtgarten		**Shoot dry matter [t ha^{-1}]**				
Year: 2000		**Treatment**				
Growth stage	**Cultivar**	**N0**	**N1**	**N2**	**Mean**	**F test**
	Bristol	1.83 cd	1.84 bc	1.65 ab	1.78	N supply: n.s.
	Apex	1.69 cd	1.73 bc	1.61 ab	1.67	Cultivar: ***
	Express	1.60 bc	1.61 ab	1.53 a	1.58	N x Cult: n.s.
Beginning of	Mohican	1.87 d	1.81 bc	1.94 c	1.87	
shooting	Lirajet	1.27 a	1.38 a	1.48 a	1.38	
	Mansholt	1.60 bc	1.59 ab	1.73 abc	1.64	
	Capitol	1.71 cd	1.92 c	1.83 bc	1.82	
	Prospa	1.40 ab	1.36 a	1.62 ab	1.46	
	Mean	1.62	1.66	1.67		
	Bristol	4.21 cd	4.83 cde	4.71 b	4.58	N supply: **
	Apex	3.35 ab	4.53 bcd	5.44 c	4.44	Cultivar: ***
	Express	3.79 bc	4.86 de	4.98 bc	4.54	N x Cult: **
Beginning of	Mohican	3.60 ab	4.28 abc	4.73 b	4.20	
flowering	Lirajet	3.10 a	4.01 ab	4.94 bc	4.02	
	Mansholt	3.51 ab	4.62 cde	5.19 bc	4.44	
	Capitol	4.59 d	5.14 e	5.29 c	5.01	
	Prospa	3.22 a	3.93 a	4.00 a	3.72	
	Mean	3.67	4.52	4.91		
	Bristol	7.00 de	9.22 c	10.17 c	8.80	N supply: ***
	Apex	4.85 a	6.92 a	9.52 bc	7.10	Cultivar: ***
	Express	6.22 bcd	7.70 ab	8.42 a	7.44	N x Cult: *
End of	Mohican	6.73 cde	7.62 a	8.84 ab	7.73	
flowering	Lirajet	5.09 a	6.90 a	8.25 a	6.75	
	Mansholt	5.74 abc	6.94 a	8.67 ab	7.12	
	Capitol	7.27 e	8.74 bc	9.02 ab	8.34	
	Prospa	5.36 ab	7.75 ab	8.46 a	7.19	
	Mean	6.03	7.72	8.92		
	Bristol	4.48 bc	6.81 ab	8.46 b	6.58	N supply: ***
	Apex	4.56 bc	7.57 b	8.46 b	6.86	Cultivar: ***
	Express	4.72 c	7.42 b	8.00 ab	6.71	N x Cult: n.s.
Maturity	Mohican	4.28 abc	7.40 b	7.93 ab	6.54	
	Lirajet	4.10 abc	6.43 a	8.38 b	6.30	
	Mansholt	3.72 ab	5.98 a	7.45 a	5.72	
	Capitol	4.21 abc	6.44 a	7.24 a	5.96	
	Prospa	3.49 a	6.41 a	7.76 ab	5.89	
	Mean	4.19	6.81	7.96		

From eight rape cultivars five were selected and used in the second field experiment in 2001 (Table I-2). However, although the same cultivars were examined, differences among the cultivars were significant only at the beginning of shooting and beginning of flowering and a significant N x cultivar interaction was found only at maturity. Under N0 supply all cultivars produced similar shoot dry matter while cultivars varied in between 8.95 and 10.0 t ha^{-1} at N1 and 10.36 and 11.66 t ha^{-1} at N2 supply at maturity.

Similar as in the previous year Lirajet showed again lowest performance in dry matter production at the beginning of shooting flowering at three levels of N supply. Apex and Bristol showed a similarly low dry matter as Lirajet at the beginning of flowering at all N rates. On the other hand, the significantly highest dry matter at this stage was shown only by Capitol at all levels of N supply. At the end of flowering no significant differences among the cultivars were found, while highly significant differences existed in shoot dry matter at maturity. However, cultivars differed only at N1 and N2 supply at maturity. Opposite to flowering stage Apex and Bristol produced a significantly higher shoot dry matter than Capitol and Mohican at N2 supply. Moreover, as compared to other cultivars Apex showed best performance in dry matter accumulation at maturity at N1 supply.

Two rape cultivars and four double haploid (DH) lines differed significantly in shoot dry matter at the beginning of flowering, end of flowering and maturity in 2002 (Tab. I-3). An interaction between N and genotypes was not found at any growth stage. Among the cultivars and DH lines the shoot dry matter varied in between 6.98 and 8.42 t ha^{-1} at N0, 7.72 and 10.01 t ha^{-1} at N1, and 8.25 and 10.55 t ha^{-1} at N2 supply at maturity. At the beginning of flowering the significantly highest shoot dry matter was produced by Capitol at all levels of N supply whereas the lowest was shown by DH28. Also, Apex and DH15 produced a significantly low shoot dry matter at N0 supply. At the end of the flowering, either at N0 or at N2 supply no significant differences were found among six genotypes in terms of dry matter production. On the other hand, the best performance in dry matter was shown only by DH4 at N1 supply. The same DH line was superior also at maturity at N0 and N1 supply. At the same N supply (N0), the lowest dry matter was produced by DH28, DH15 and Capitol. However, Capitol produced significantly highest shoot dry matter when the N supply was increased from low (N0) to high (N2).

Table I-2: Shoot dry matter of 5 oilseed rape cultivars as affected by N supply (N0: soil mineral N, N1: 120 kg N ha^{-1}, N2: 240 kg N ha^{-1}) at different growth stages at Zuchtgarten in 2001. Statistics: Separate analysis of variance for different growth stages. Means with the same letter are not significantly different at $\alpha = 0.05$ within each N rate.

Site: Zuchtgarten		**Shoot dry matter [t ha^{-1}]**				
Year: 2001		**Treatment**				
Growth stage	**Cultivar**	**N0**	**N1**	**N2**	**Mean**	**F test**
Beginning of shooting	Apex	1.88 a	2.25 ab	2.41 a	2.18	N supply: n.s.
	Capitol	2.20 a	2.47 b	2.40 a	2.36	Cultivar: *
	Mohican	2.12 a	2.59 b	2.61 a	2.44	N x Cult: n.s.
	Lirajet	1.74 a	1.90 a	2.20 a	1.95	
	Bristol	2.13 a	2.43 b	2.67 a	2.41	
	Mean	2.01	2.33	2.46		
Beginning of flowering	Apex	3.02 a	4.62 ab	4.81 a	4.15	N supply: *
	Capitol	4.22 b	5.13 b	5.86 b	5.07	Cultivar: ***
	Mohican	3.89 ab	5.01 b	5.32 ab	4.74	N*Cult: n.s.
	Lirajet	3.07 a	4.50 ab	5.05 ab	4.21	
	Bristol	3.12 a	3.85 a	4.47 a	3.81	
	Mean	3.47	4.62	5.10		
End of flowering	Apex	6.77 n.s.	7.52 a	10.06 n.s.	8.12	N supply: **
	Capitol	7.19 n.s.	8.20 a	10.09 n.s.	8.49	Cultivar: n.s.
	Mohican	7.01 n.s.	8.54 ab	9.68 n.s.	8.41	N x Cult: n.s.
	Lirajet	7.23 n.s.	9.81 b	9.14 n.s.	8.73	
	Bristol	6.93 n.s.	8.84 ab	10.50 n.s.	8.76	
	Mean	7.03	8.58	9.89		
Maturity	Apex	7.02 a	10.00 b	11.66 c	9.56	N supply: ***
	Capitol	7.76 a	9.43 ab	10.36 a	9.18	Cultivar: n.s.
	Mohican	7.01 a	9.37 ab	10.57 ab	8.98	N x Cult: *
	Lirajet	6.89 a	8.95 a	11.54 bc	9.13	
	Bristol	6.81 a	9.78 ab	11.63 c	9.41	
	Mean	7.10	9.51	11.15		

Table I-3: Shoot dry matter of 6 oilseed rape cultivars as affected by N supply (N0: soil mineral N, N1: 120 kg N ha^{-1}, N2: 240 kg N ha^{-1}) at different growth stages at Zuchtgarten in 2002. Statistics: Separate analysis of variance for different growth stages. Means with the same letter are not significantly different at $\alpha = 0.05$ within each N rate.

Site: Zuchtgarten		**Shoot dry matter [t ha^{-1}]**				
Year: 2002		**Treatment**				
Growth stage	**Cultivar**	**N0**	**N1**	**N2**	**Mean**	**F test**
Beginning of flowering	DH4	3.58 ab	5.30 bc	6.23 bc	5.04	N supply: ***
	Apex	3.04 a	4.38 ab	5.69 ab	4.37	Cultivar: ***
	DH42	3.80 ab	4.76 ab	5.56 ab	4.71	N x Cult: n.s.
	DH28	2.92 a	3.99 a	5.19 a	4.03	
	DH15	3.01 a	4.53 ab	5.55 ab	4.36	
	Capitol	4.50 b	5.83 c	6.87 c	5.73	
	Mean	3.48	4.80	5.85		
End of flowering	DH4	7.58 a	11.92 b	10.77 a	10.09	N supply: ***
	Apex	6.93 a	8.83 a	10.02 a	8.59	Cultivar: *
	DH42	6.73 a	9.14 a	10.42 a	8.76	N x Cult: n.s.
	DH28	7.25 a	9.74 a	9.18 a	8.72	
	DH15	6.76 a	8.80 a	10.71 a	8.76	
	Capitol	7.25 a	10.30 ab	10.59 a	9.38	
	Mean	7.08	9.79	10.28		
Maturity	DH4	8.42 b	10.01 c	10.37 cd	9.60	N supply: ***
	Apex	7.54 ab	9.22 bc	9.37 b	8.71	Cultivar: ***
	DH42	7.78 ab	8.57 ab	9.40 bc	8.58	N x Cult: n.s.
	DH28	6.98 a	8.40 ab	8.25 a	7.88	
	DH15	7.07 a	7.72 a	9.69 bcd	8.16	
	Capitol	7.37 a	9.30 bc	10.55 d	9.07	
	Mean	7.53	8.87	9.60		

4.2 Seed Yield Formation

Averaged over experimental years and sites, the seed yield varied significantly (P<0.001) among cultivars and DH lines. Yield response to supplied N, i.e. the interaction between N and cultivar, was highly significant (P<0.001) (Tab. I-4). Under limiting N supply (N0) cultivars produced almost 70% of the seed yield produced at medium (N1) N and 63% of the seed yield produced at high (N2) N supply. At medium N supply almost 90% of the seed yield of N2 was produced. Among the cultivars and DH lines the seed yield varied in between 2.11 and 3.02 t ha^{-1} at N0, 3.14 and 4.23 t ha^{-1} at N1, and 3.68 and 4.54 t ha^{-1} at N2 supply at maturity. At N0 supply significantly highest seed yield was produced by DH4 and Apex. Thus, these cultivars can be classified as "N-efficient" genotypes. At the same N environment, the significantly lowest seed yields were produced by Prospa, Capitol and DH15 and therefore these three genotypes can be classified as "N-inefficient".

Table I-4: Mean seed yield of both experimental sites (Zuchtgarten and Dragoneranger) of 12 oilseed rape cultivars as affected by N supply (N0: soil mineral N, N1: 120 kg N ha^{-1}, N2: 240 kg N ha^{-1}) at maturity in 2000, 2001 and 2002. Statistics: Combined analysis of variance for all experimental years and sites. Means with the same letter are not significantly different at $\alpha = 0.05$ within each N rate.

		Seed yield [t ha^{-1}]				
	No. of Years	Treatment				
Cultivar	**Tested**	**N0**	**N1**	**N2**	**Mean**	**F test**
DH4	1	3.02 d	4.23 e	4.47 bc	3.91	N supply: ***.
Apex	3	2.75 cd	3.67 bcd	4.04 ab	3.48	Cultivar: ***
DH42	1	2.67 ad	3.51 acd	3.86 ac	3.35	N x Cult: ***
Express	1	2.64 ad	3.76 bce	4.19 ac	3.53	
Mohican	2	2.63 bcd	3.83 ce	3.99 ab	3.48	
DH28	1	2.50 ad	3.42 ac	3.80 a	3.24	
Mansholt	1	2.48 ad	3.34 ab	3.72 ab	3.18	
Bristol	2	2.46 ad	3.96 de	4.54 c	3.65	
Lirajet	2	2.44 ad	3.55 ac	4.00 ab	3.33	
Capitol	3	2.41 ab	3.50 ab	3.91 ab	3.28	
DH15	1	2.24 ac	3.14 a	3.68 a	3.02	
Prospa	1	2.11 a	3.33 ab	3.97 ac	3.14	
Mean		2.53	3.60	4.01		

The other cultivars and DH lines attained medium seed yield at N0 supply. Some of the cultivars still produced comparatively low seed yields when the N supply was increased from N0 to N1 or N2. Therefore, these genotypes (DH15 and DH28) can be classified as "non-responsive". By contrast, the N-efficient genotype DH4 produced the almost highest seed yields at N1 and N2 supply. Because of that DH4 can be characterized as an "efficient and responsive" genotype. Same response was not shown by the N-efficient genotype Apex. Since, a medium seed yield was produced at N1 supply while low seed yield was shown at N2 supply. Therefore Apex can be characterized as "efficient and non-responsive". On the other hand, although seed yield was rather low at N0, a high responsiveness in seed yield production was shown by Bristol at N1 and N2 supply. Thus, Bristol can be characterized as "inefficient and responsive" genotype (Tab. I-4).

In terms of N-efficiency, significant shifts in cultivars ranking were found at Zuchtgarten when the experimental years were separately evaluated (Tab. I-5). In 2000, cultivars at N0 supply produced almost 63% of the grain yield of N1 and 55% of the grain yield of N2 supply. At medium (N1) supply about 89% of the grain yield of N2 supply was produced. Among eight cultivars the seed yield varied in between 1.87 and 2.41 t ha^{-1} at N0, 3.08 and 3.92 t ha^{-1} at N1, and 3.43 and 4.36 t ha^{-1} at N2 supply. Under limiting (N0) N supply, the "N-efficient" classified cultivar Apex produced again highest seed yield at Zuchtgarten. At the same N environment, the "N-inefficient" defined cultivar Prospa showed once more lowest seed yield. All these indicate some of the cultivars can be differed similarly at both experimental sites at a certain N level.

On the other hand several cultivars (Bristol, Express and Mohican), which were not classified as N-efficient, showed a high N-efficiency in 2000 at N0 supply. As non-responsive defined cultivars Prospa and Apex showed also significant responses by producing higher seed yields at N1 and N2 supply, respectively. More interesting result was shown by the N-inefficient and non-responsive defined cultivar Mohican. This genotype responded significantly higher at N1 and N2 supply. On the other hand, Capitol and Mansholt could again be classified as N-inefficient and irresponsive cultivars due to producing lower seed yield at all levels of N supply.

Table I-5: Seed yield of oilseed rape cultivars (8, 5 and 6 cultivars) as affected by N supply (N0: soil mineral N, N1: 120 kg N ha^{-1}, N2: 240 kg N ha^{-1}) at Zuchtgarten in 2000 (A), 2001(B) and 2002 (C). Statistics: Separate analysis of variance for different experimental years. Means with the same letter are not significantly different at $\alpha = 0.05$ within each N rate.

Site: Zuchtgarten		**Seed yield [t ha^{-1}]**				
		Treatment				
Year	**Cultivar**	**N0**	**N1**	**N2**	**Mean**	**F test**
	Bristol	2.41 b	3.61 bcd	4.25 cd	3.42	N supply: **
	Apex	2.37 b	3.92 d	3.89 bc	3.39	Cultivar: ***
	Express	2.31 b	3.66 cd	4.18 bcd	3.38	N x Cult: n.s.
2000 (A)	Mohican	2.30 b	3.98 d	4.36 d	3.55	
	Lirajet	2.20 ab	3.37 abc	3.96 bcd	3.18	
	Mansholt	2.16 ab	3.08 a	3.79 ab	3.01	
	Capitol	2.14 ab	3.24 ab	3.43 a	2.94	
	Prospa	1.87 a	3.50 bc	4.20 cd	3.19	
	Mean	2.22	3.55	4.01		
	Apex	3.35 a	4.50 ab	5.02 a	4.29	N supply: ***
	Capitol	3.28 a	4.54 ab	5.05 a	4.29	Cultivar: n.s.
2001(B)	Mohican	3.21 a	4.61 ab	4.77 a	4.19	N x Cult: ***
	Lirajet	3.07 a	4.21 a	5.11 a	4.13	
	Bristol	2.86 a	4.76 b	5.72 b	4.45	
	Mean	3.15	4.52	5.13		
	DH4	3.27 c	4.43 d	4.57 c	4.09	N supply: ***
	Apex	3.06 bc	3.73 bc	4.16 b	3.65	Cultivar: *
2002 (C)	DH42	2.82 ab	3.57 b	3.75 a	3.38	N x Cult: n.s.
	DH28	2.82 ab	3.69 b	3.59 a	3.37	
	DH15	2.77 ab	3.14 a	3.81 a	3.24	
	Capitol	2.72 a	4.02 c	4.22 b	3.65	
	Mean	2.91	3.76	4.02		

Compared to the previous field experiment at Zuchtgarten, the grain yield was higher at all levels of N supply in 2001 (Tab. I-5 B). The cultivars produced at N0 supply almost 70% of the grain yield of N1 and 61% of the grain yield of N2 supply. About 88% of the grain yield of N2 supply was produced at N1 supply. Cultivars differed significantly in seed yield at N1 and N2 supply. The grain yield varied among five cultivars in between 4.21 and 4.76 t ha^{-1} at N1 and 5.11 and 5.72 t ha^{-1} at N2 supply. Significantly highest seed yield was produced by the responsive genotype Bristol at N1 and N2 supply. In contrast, the lowest grain yield at N1 and N2 was shown by the inefficient and non-responsive genotype Lirajet.

Seed yield slightly decreased in 2002 compared to the previous year at Zuchtgarten (Tab. I-5 C). The cultivars produced at N0 supply almost 77% of the grain yield of N1 and 72% of the grain yield of N2 supply. Considerably higher (94%) grain yield of N2 was produced at N1 supply. Genotypic variation among cultivars and DH lines were significant at all N rates. The grain yield varied in between 2.72 and 3.27 t ha^{-1} at N0, 3.14 and 4.43 t ha^{-1} at N1 and 3.59 and 4.57 t ha^{-1} at N2 supply. Highest seed yield was produced by the two N-efficient genotypes DH4 and Apex at N0 supply. At the same N rate the lowest seed yield was produced by the N-inefficient genotype Capitol. On the other hand, high responsiveness in grain yield was shown by DH4 at N1 and N2 supply. The lowest grain yield was produced by DH15 at N1 and DH28 at N2 supply. Grain yields of Apex and Capitol were not significantly different at N1 and N2 supply.

4.3. Harvest Index

The proportion of dry matter translocated to the grain, *i.e*. the harvest index, was determined in the field experiments at Zuchtgarten in 2000 (A), 2001 (B) and 2002 (C) (Tab. I-6). Averaged over cultivars, the harvest index was usually higher in 2000 compared to 2001 and 2002 at all N rates. Significant differences were found between N rates. Harvest index decreased when the N supply increased from low (N0) to high (N2) N in 2000. However opposite results were found in 2001 and 2002. The grain dry mater was slightly higher than straw dry matter at N0 in 2000. The higher harvest index at N0 compared to N1 and N2 supply could be the result of substantial dry matter losses (30%) that occurred from the end of the flowering till maturity in 2000 (Fig. I-1 A).

Table I-6: Harvest indices of oilseed rape cultivars (8, 5 and 6 cultivars) as affected by N supply (N0: soil mineral N, N1: 120 kg N ha^{-1}, N2: 240 kg N ha^{-1}) at Zuchtgarten in 2000 (A), 2001(B) and 2002 (C). Statistics: Separate analysis of variance for different experimental years. Means with the same letter are not significantly different at $\alpha = 0.05$ within each N rate.

Site: Zuchtgarten		**Harvest index**				
		Treatment				
Year	**Cultivar**	**N0**	**N1**	**N2**	**Mean**	**F test**
2000 (A)	Bristol	0.54 abc	0.53 ab	0.51 abc	0.52	N supply: *
	Apex	0.52 ab	0.52 ab	0.46 a	0.50	Cultivar: ***
	Express	0.49 a	0.49 a	0.52 c	0.50	N x Cult: n.s.
	Mohican	0.54 bc	0.54 ab	0.55 c	0.54	
	Lirajet	0.54 bc	0.53 ab	0.47 ab	0.51	
	Mansholt	0.58 c	0.52 ab	0.51 bc	0.53	
	Capitol	0.51 ab	0.51 ab	0.47 ab	0.50	
	Prospa	0.54 bc	0.55 b	0.54 c	0.54	
	Mean	0.53	0.52	0.50		
2001(B)	Apex	0.48 b	0.45 a	0.43 a	0.45	N supply: *
	Capitol	0.42 a	0.48 b	0.49 b	0.46	Cultivar: n.s.
	Mohican	0.46 b	0.49 b	0.45 a	0.47	N x Cult: ***
	Lirajet	0.45 ab	0.47 ab	0.44 a	0.45	
	Bristol	0.42 a	0.49 b	0.49 b	0.47	
	Mean	0.44	0.48	0.46		
2002 (C)	DH4	0.39 ab	0.45 b	0.44 bc	0.42 a	N supply: *
	Apex	0.41 b	0.40 a	0.44 c	0.42 a	Cultivar: *
	DH42	0.36 a	0.42 ab	0.40 ab	0.39 a	N x Cult: n.s.
	DH28	0.40 b	0.44 ab	0.44 bc	0.43 a	
	DH15	0.39 ab	0.41 a	0.39 a	0.40 a	
	Capitol	0.38 ab	0.43 ab	0.40 a	0.40 a	
	Mean	0.39	0.42	0.42		

Due to no dry matter losses in 2001 or an increase in dry matter in 2002 at N0 supply (Fig.I-1 B and C), opposite results were found and thus harvest index was lower at N0 than N1 and N2 supply in 2001 (B) and 2002 (C). Another reason for the higher harvest index at N0 in 2000 could be the result of continued vegetative growth in 2001 and 2002.

Harvest indices differed significantly among eight cultivars at all N rates in 2000 (Tab. I-6). The variation among genotypes was in the range of 49 and 58% at N0, 49 and 55% at N1 and 46 and 55% at N2 supply in 2000. The lowest harvest index was shown by Express at N0 supply. For this cultivar, the grain yield and especially shoot dry matter were high at maturity (Tab. I-1). On the other hand, due to low shoot dry matter (Tab. I-1) and average grain yield at maturity (Tab. I-5), significantly highest harvest index was shown by Mansholt at N0 supply (Tab. I-6). Similar results were shown by Express, Mohican and Prospa at N2 supply. These three genotypes were highly responsive in grain yield at N2 supply (Tab. I-6), whereas shoot dry matter production was low at the same N level.

Cultivars differed significantly for harvest indices at all N rates in 2001. A highly significant interaction between N and genotypes also occurred (Tab. I-6 B). The mean harvest index varied in between 42 and 48% at N0, 45 and 49% at N1 and 43 and 49% at N2 supply. The highest harvest indices were achieved by Apex and Mohican, while the lowest were shown by Capitol and Bristol at N0 supply. Since, there was no significant difference among cultivars in grain yield (Tab. I-5) and shoot dry matter (Tab. I-2) at N0 supply, significant difference in harvest index could be the result of slightly higher shoot dry matter of Capitol compared to Apex and Mohican and a slightly lower grain yield of Bristol at maturity. By contrast, Bristol and Capitol showed significantly higher harvest indices than Apex, Mohican and Lirajet at N2 supply (Tab. I-6 B).

The variation among six rapeseed genotypes for harvest index was significant at three levels of N supply in 2002 at Zuchtgarten (Tab. I-6 C). The harvest index among the genotypes varied in between 36 and 41% at N0 supply. At this N level, Apex and DH28 showed highest harvest indices while the lowest was shown by DH42 at N0. Actually, Apex and DH42 produced similar shoot dry matter (Tab. I-3) at maturity but Apex had a higher seed yield than DH42 (Tab. I-6 C). At medium N supply (N1), the mean harvest index among genotypes varied in between 40 and 45%. At this N rate, DH4 showed significantly highest harvest index due to the higher grain yield compared to other genotypes. Due to producing similar

shoot dry matter but oppositely lower seed yield than DH4, Apex showed the lowest harvest index. However, the same genotype (Apex) showed significantly highest harvest index at N2 supply. At this N level, the variation among genotypes was in between 40 and 44%. Despite its highest seed yield Capitol had the lowest harvest index at N2 supply. This was the result of significantly highest shoot dry matter at maturity (Tab. I-3).

4.4 Yield Components

The yield components of oilseed rape cultivars as affected by different levels of N supply were determined in the two field experiments conducted in 2000 (Tab. I-7) and 2001 (Tab. I-8) at Zuchtgarten. As yield components, i) number of plants per m^2 ii) number of pods per plant iii) number of seeds per pod and iv) thousand grain weight was calculated. Results indicated that, except number of plants per m^2, all yield components were significantly affected by N supply in 2000 (Tab. I-7). At seeding 80 kernels per m^2 were considered but between 61 and 65 plants per m^2 were grown at the different N levels. No significant differences between three N rates were found. However, Cultivars differed significantly in germination rates at all levels of N supply. Mansholt showed the highest plant density while the lowest was shown by Prospa at all N rates.

The number of pods per plant was significantly different between N rates and among cultivars at each N rate. Although it had the lowest plant number per m^2, the number of pods per plant was significantly highest for Prospa at N0, N1 and N2 supply. Opposite results were shown by Mansholt at all N rates. Although there were no overall cultivar differences or cultivar by N rate interactions in the number of seeds per pod, the cultivar comparison revealed some slight differences between individual cultivars. For instance, contrary to the significantly highest pod number, the seed number per pod was lower at N0 and N2 supply by Prospa. However, significantly lowest seed number per pod was shown by Capitol at N0 and N2 supply and the highest seed number per pod was shown by Bristol at N0 supply.

Contrasting relationship between number of seed per pod and thousand grain weight occurred at different levels of N supply. The seed number decreased when the N supply was increased from low (N0) to medium (N1) or high (N2) level. On the other hand thousand grain weights also increased with increasing N level. Cultivars differed significantly in thousand grain weight, and a significant interaction between N and cultivar was found.

Table I-7: Yield components of 8 rape cultivars as affected by N supply (N0: soil mineral N, N1: 120 kg N ha^{-1}, N2: 240 kg N ha^{-1}) at maturity at Zuchtgarten in 2000. Statistics: Separate analysis of variance. Means with the same letter are not significantly different at $\alpha = 0.05$ within each N rate.

Yield components	Cultivar	Treatment N0	N1	N2	Mean	F test
	Bristol	60 bcd	59 b	63 ab	61	N supply: n.s.
	Apex	55 ab	65 b	61 ab	60	Cultivar: ***
	Express	76 de	70 bc	71 bc	72	N x Cult: n.s.
Number of	Mohican	72 ce	53 ab	68 bc	65	
plants per m^2	Lirajet	56 ac	63 b	69 bc	63	
	Mansholt	81 e	82 c	84 c	82	
	Capitol	65 bce	60 b	60 ab	62	
	Prospa	41 a	39 a	47 a	43	
	Mean	63	61	65		
	Bristol	50 ab	105 cd	113 bc	89	N supply: ***
	Apex	57 ab	85 ac	94 ab	79	Cultivar: ***
	Express	44 ab	79 ab	91 ab	71	N x Cult: n.s.
Number of	Mohican	44 ab	99 bcd	88 a	77	
pods per plant	Lirajet	51 ab	71 a	79 a	67	
	Mansholt	42 a	75 ab	77 a	65	
	Capitol	46 ab	83 ac	95 ab	75	
	Prospa	67 b	113 d	121 c	101	
	Mean	50	89	95		
	Bristol	20 b	14 ab	14 ab	16	N supply: *
	Apex	18 ab	15 ab	17 b	17	Cultivar: n.s.
	Express	18 ab	16 ab	14 ab	16	N x Cult: n.s.
Number of	Mohican	16 ab	17 ab	15 ab	16	
seeds per pod	Lirajet	17 ab	16 ab	14 ab	16	
	Mansholt	16 ab	12 a	14 ab	14	
	Capitol	15 a	13 ab	12 a	13	
	Prospa	16 ab	17 b	16 ab	16	
	Mean	17	15	14		
	Bristol	4.14 b	4.25 ab	4.52 b	4.30	N supply: ***
	Apex	4.50 cd	4.58 c	4.89 cd	4.66	Cultivar: ***
	Express	4.13 b	4.39 b	4.74 c	4.42	N x Cult: **
Thousand	Mohican	4.59 d	4.70 cd	4.98 de	4.76	
grain weight	Lirajet	4.46 cd	4.68 cd	5.12 ef	4.75	
	Mansholt	3.93 a	4.11 a	4.29 a	4.11	
	Capitol	4.98 e	5.18 e	5.19 f	5.12	
	Prospa	4.37 c	4.76 d	5.17 f	4.77	
	Mean	4.39	4.58	4.86		

As a result of lowest seed number per pod, thousand grain weight was significantly highest by Capitol at N0, N1 and N2 supply. A similar result was also shown by Prospa at all N rates. However, Mansholt had the significantly lowest thousand grain weight at N0, N1 and N2.

In 2001, two contrasting cultivars were chosen for determinations of yield components, the N-efficient cultivar Apex and the N-inefficient cultivar Capitol. Yield components of these two cultivars were significantly different between N rates in the number of pod per plant and thousand grain weight (Tab. I-8). Both parameters increased with increasing N supply. Although, no significant differences existed between N rates, the number of plants per m^2 was considerably lower compared to the previous field experiment. Among two cultivars, the number of pod per plant differed significantly, but at N1. The number of seed per pod was also similar among two cultivars at all three N rates. This could be the result of similar grain yield production at all N rates in 2001 (Tab. I-5 C). Nevertheless thousand grain weight of Capitol was significantly higher than that of Apex at all N rates (Tab. I-8). The yield components of two field experiments clearly indicated that the grain size of the "N-efficient" cultivar Apex is smaller than the "N-inefficient" cultivar Capitol.

Table I-8: Yield components of 2 rape cultivars as affected by N supply (N0: soil mineral N, N1: 120 kg N ha^{-1}, N2: 240 kg N ha^{-1}) at maturity at Zuchtgarten in 2001. Statistics: Separate analysis of variance. Means with the same letter are not significantly different at $\alpha = 0.05$ within each N rate.

Yield		**Treatment**				
components	**Cultivar**	**N0**	**N1**	**N2**	**Mean**	**F test**
Number of plants per m^2	Apex	41	37	36	38	N supply: n.s.
	Capitol	35	35	32	34	Cultivar: n.s.
	Mean	38	36	34		N x Cult: n.s.
Number of pods per plant	Apex	94 a	159 b	165 a	139	N supply: *
	Capitol	83 a	120 a	186 a	130	Cultivar: n.s.
	Mean	88	139	176		N x Cult: n.s.
Number of seeds per pod	Apex	21	19	20	20	N supply: n.s.
	Capitol	25	26	18	23	Cultivar: n.s.
	Mean	23	22	19		N x Cult: n.s.
Thousand grain weight	Apex	4.27 a	4.33 a	4.53 a	4.38	N supply: *
	Capitol	4.96 b	5.10 b	5.21 b	5.09	Cultivar: ***
	Mean	4.61	4.72	4.87		N x Cult: n.s.

4.5 Shoot Nitrogen Concentration

In three field experiments the shoot N concentrations were determined at four growth stages; at the beginning of shooting (2000, 2001), beginning of flowering (2000, 2001, and 2002), end of flowering (2000, 2001, and 2002) and maturity (2000, 2001, and 2002) at Zuchtgarten (Fig. I-2). The shoot N concentration decreased sharply from beginning of shooting up to end of flowering at all N rates. During the seed filling phase, decline continued up to maturity only at N2 supply. By contrast, substantial increase in shoot N concentration occurred at N0 supply in 2000, 2001 and 2002. This could be the results of remained N uptake activity during the reproductive growth phase at N0 supply although no further growth occurred.

On the other hand a slight increase (2000) or a constant (2002) shoot N concentration was found at N1 supply from end of the flowering up to maturity. In the first field experiment shoot N concentration increased almost 52% at N0, 10% at N1 and 0.6% at N2 supply from end of flowering till maturity. In the second field experiment the increase was almost 19% at N0 and 0.4% at N1 supply and nearly 15% shoot N concentration declined at N2 supply at maturity. In the last field experiment the increase in shoot N concentration was about 21% at N0 and 3% at N1 supply whereas decline was almost 11% at N2 supply. Differences in shoot N concentration between N levels were usually significant from beginning of shooting up to maturity. In general significantly highest shoot N concentration was shown at N2 supply and the lowest at N0 supply. Shoot N concentration at N1 was significantly lower than at N2 and significantly higher than at N0 except at the beginning of shooting in 2000.

The shoot N concentration was 29 mg g^{-1} d.w. at N0, 30 mg g^{-1} d.w. at N1 and 33 mg g^{-1} d.w. at N2 supply at the beginning of shooting in 2000. Compared to previous field experiment, the shoot N concentration ranged in between 29 and 44 mg g^{-1} d.w. at the beginning of shooting in 2001, which means that considerably higher N concentrations were achieved for the higher N rates in 2001.

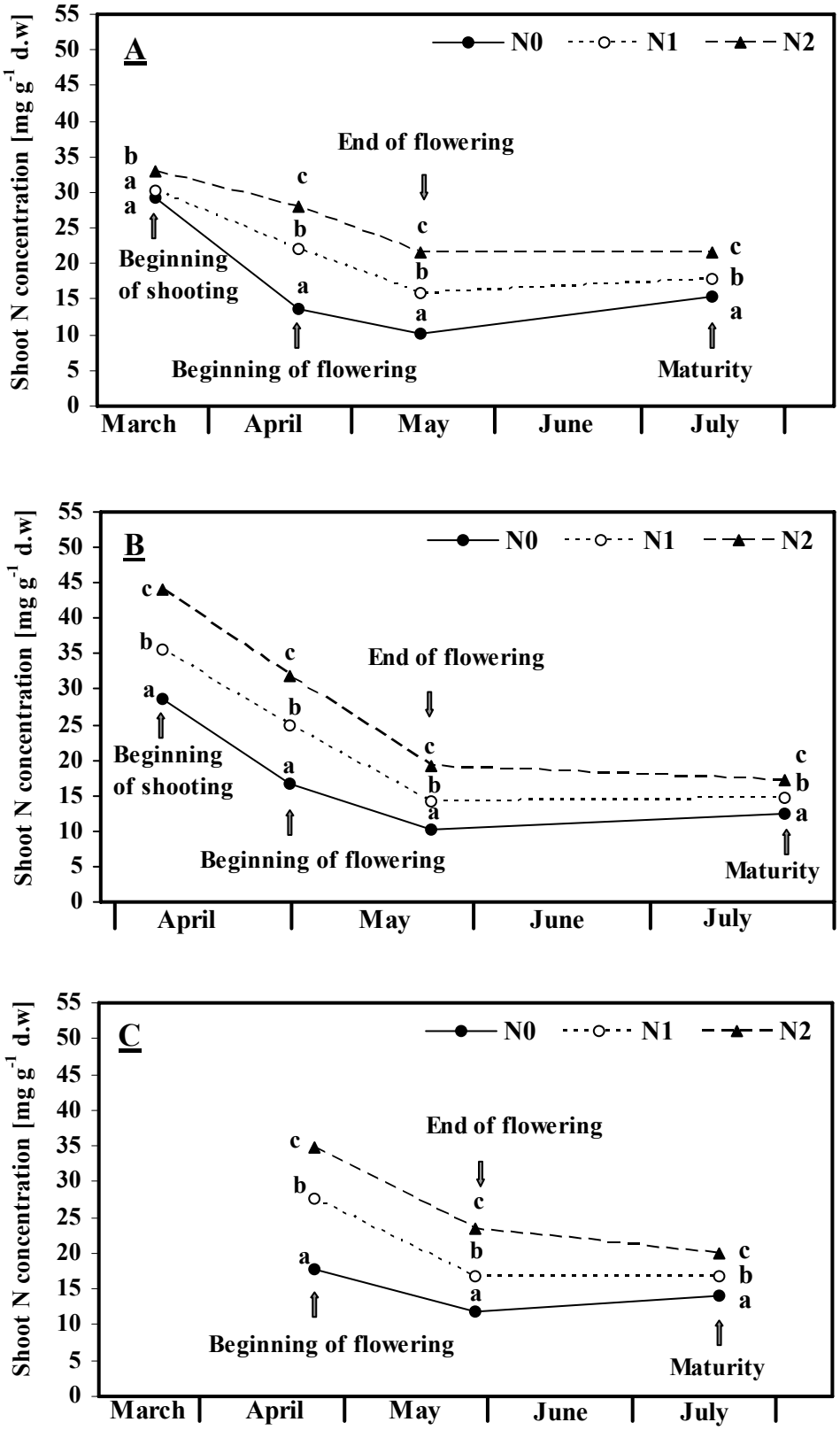


Figure I-2: Shoot N concentration of oilseed rape (means of 8, 5 and 6 cultivars, respectively) as affected by N supply (N0: soil mineral N supply, N1: 120 kg N ha^{-1}, N2: 240 kg N ha^{-1}) at different growth stages at Zuchtgarten in 2000 (A), 2001 (B), and 2002 (C). Statistics: Separate analysis of variance for different growth stages. Means with the same letter are not significantly different at $\alpha = 0.05$

Among eight rape cultivars highly significant differences in shoot N concentration were found at the beginning of shooting, beginning of flowering, end of flowering and maturity in 2000 (Tab. I-9). A significant interaction between N and genotype occurred only at the beginning of flowering. At the beginning of shooting the shoot N concentration among cultivars varied in between 25.61 and 32.94 mg g^{-1} d.w. at N0, 27.12 and 33.96 mg g^{-1} d.w. at N1 and 29.86 and 35.23 mg g^{-1} d.w. at N2 supply. Significantly highest shoot N concentration was shown by Lirajet at N0 and N1 supply whereas the lowest was shown by Bristol at all N rates. This might be the result of the significantly lowest shoot dry matter by Lirajet at all N rates (Tab. I-1). On the other hand, some of the cultivars (Mohican and Capitol) which produced a high shoot dry matter at all N rates (Tab. I-1) showed lower shoot N concentration only at N0 and N1 supply (Tab. I-9).

At the beginning of flowering, the shoot N concentration among cultivars ranged in between 12.52 and 15.83 mg g^{-1} d.w. at N0 and 18.27 and 25.77 mg g^{-1} d.w. at N1 supply. Propsa which produced a low shoot dry matter (Tab. I-1) had the significantly highest N concentration at N0 supply (Tab. I-9). Bristol and Capitol which produced highest shoot dry matter at N0 and N1 supply showed the lowest N concentration at the same N rates. On the other hand, irrespective of the dry matter produced, a lower shoot N concentration was shown again by Bristol and Capitol at N2 supply. The decline in shoot N concentration continued until end of the flowering. At this stage no significant differences among cultivars were found at N0 supply. However, cultivars differed significantly at N1 and N2 supply. The shoot N concentration ranged in between 14.12 and 17.73 mg g^{-1} d.w. at N1 and 19.76 and 22.77 mg g^{-1} d.w. at N2 supply. Express, Mansholt and Prospa showed significantly higher shoot N concentration than Bristol, Mohican and Capitol at N1 supply. Again Express had the highest shoot N concentration at N2 supply while the lowest was shown by Capitol.

At maturity cultivars accumulated almost 50% more N concentration than at the end of flowering at N0 supply. Cultivars varied significantly at all N rates. The shoot N concentration among cultivars varied in between 14.31 and 17.63 mg g^{-1} d.w. at N0, 16.42 and 18.85 mg g^{-1} d.w. at N1 and 19.89 and 24.10 mg g^{-1} d.w. at N2 supply.

Table I-9: Shoot N concentration of 8 oilseed rape cultivars as affected by N supply (N0: soil mineral N, N1: 120 kg N ha^{-1}, N2: 240 kg N ha^{-1}) at different growth stages at Zuchtgarten in 2000. Statistics: Separate analysis of variance for different growth stages. Means with the same letter are not significantly different at $\alpha = 0.05$ within each N rate.

Site: Zuchtgarten		**Shoot N concentration [mg g^{-1} d.w.]**				
Year: 2000		**Treatment**				
Growth stage	**Cultivar**	**N0**	**N1**	**N2**	**Mean**	**F test**
	Bristol	25.61 a	27.12 a	29.86 a	27.53	N supply: **
	Apex	28.73 bc	31.21 cd	31.55 ab	30.49	Cultivar: ***
	Express	29.13 ab	30.42 bc	32.25 abc	30.60	N x Cult: n.s.
Beginning of	Mohican	27.51 ab	28.02 ab	35.23 d	30.25	
shooting	Lirajet	32.94 d	33.96 d	34.07 bcd	33.66	
	Mansholt	31.47 cd	31.65 cd	33.60 bcd	32.24	
	Capitol	27.95 ab	28.15 ab	33.23 bcd	29.77	
	Prospa	29.81 bc	31.84 cd	34.67 cd	32.10	
	Mean	29.14	30.29	33.06		
	Bristol	12.52 a	18.27 a	23.12 a	17.97	N supply: ***
	Apex	13.77 ab	24.02 cde	29.49 c	22.43	Cultivar: ***
	Express	12.72 a	24.67 de	28.11 bc	21.83	N x Cult: ***
Beginning of	Mohican	13.38 ab	23.17 cd	29.27 c	21.94	
flowering	Lirajet	14.61 ab	25.77 e	29.72 c	23.36	
	Mansholt	14.04 ab	20.40 ab	29.05 c	21.16	
	Capitol	12.98 a	18.66 a	26.26 b	19.30	
	Prospa	15.83 b	21.63 bc	28.45 bc	21.97	
	Mean	13.73	22.07	27.93		
	Bristol	9.63 a	14.12 a	20.43 ab	14.73	N supply: ***
	Apex	10.27 a	15.63 ab	21.00 ab	15.63	Cultivar: **
	Express	10.71 a	17.73 b	22.77 b	17.07	N x Cult: n.s.
End of	Mohican	10.23 a	14.66 a	21.74 ab	15.54	
flowering	Lirajet	10.03 a	16.06 ab	21.85 ab	15.98	
	Mansholt	10.48 a	17.66 b	22.62 b	16.92	
	Capitol	9.38 a	14.35 a	19.76 a	14.50	
	Prospa	10.25 a	17.36 b	21.93 ab	16.51	
	Mean	10.12	15.95	21.51		
	Bristol	14.31 a	16.90 a	20.35 ab	17.18	N supply: ***
	Apex	14.80 ab	17.56 ab	21.19 abc	17.85	Cultivar: ***
	Express	14.93 ab	17.66 ab	21.64 bcd	18.07	N x Cult: n.s.
Maturity	Mohican	15.36 ab	17.53 ab	22.36 cd	18.41	
	Lirajet	15.20 ab	17.79 ab	20.71 abc	17.90	
	Mansholt	17.63 c	18.85 b	22.93 de	19.80	
	Capitol	14.57 a	16.42 a	19.89 a	16.96	
	Prospa	16.40 bc	19.03 b	24.10 e	19.84	
	Mean	15.40	17.72	21.64		

Significantly higher shoot N concentrations were shown by Mansholt and Prospa at three levels of N supply. In contrast, Bristol and Capitol showed a significantly lower shoot N concentration than Mansholt and Prospa at all N rates. The high shoot N concentration of Mansholt and Prospa was due to their low shoot dry matter production at maturity (Tab. I-1). However, the low shoot N concentration of Capitol and Bristol was not the result of a higher shoot dry matter at maturity (Tab. I-1).

Table I-10 shows the shoot N concentration of five rape cultivars as affected by N supply in the second field experiment in 2001. At the beginning of shooting cultivars varied significantly at all N rates. However, at the beginning of flowering and end of the flowering stages significant variation occurred among cultivars only at medium (N1) N supply. Furthermore, at maturity cultivars differed only at N0 and N1 supply.

At the beginning of shooting, the N concentration among five cultivars varied in between 27.30 and 31.13 mg g^{-1} d.w. at N0, 32.25 and 39.87 mg g^{-1} d.w. at N1 and 40.77 and 47.06 mg g^{-1} d.w. at N2 supply. Similar to previous field experiment, shoot N concentration was significantly highest for Lirajet and lowest for Bristol at N0 and N1 supply. Opposite to the previous year, Mohican had the lowest shoot N concentration at N2 supply.

Under medium (N1) N supply, cultivars differed significantly with in the range of 22.55 - 27.54 mg g^{-1} d.w. and 13.48 – 16.03 mg g^{-1} d.w. at the beginning of flowering and end of the flowering, respectively (Tab. I-10). Significantly higher shoot N concentration was shown by Bristol at the beginning of flowering while Apex showed a higher shoot N concentration at the end of the flowering at N1 supply. At both growth stages the significantly lowest shoot N concentrations were shown by Capitol and Mohican.

The five rape cultivars varied significantly at all N rates in shoot N concentration at maturity (Tab. I-10). Apex, Mohican and Lirajet similarly showed higher shoot N concentrations than other cultivars at N0 supply. Differences among cultivars ranged in between 11.59 and 13.03 mg g^{-1} d.w.. Mohican still had high shoot N concentration at N1, while Bristol again showed the lowest N concentration in the shoot. At N2, no significant differences among cultivars were found.

Table I-10: Shoot N concentration of 5 oilseed rape cultivars as affected by N supply (N0: soil mineral N, N1: 120 kg N ha^{-1}, N2: 240 kg N ha^{-1}) at different growth stages at Zuchtgarten in 2001. Statistics: Separate analysis of variance for different growth stages. Means with the same letter are not significantly different at $\alpha = 0.05$ within each N rate.

Site: Zuchtgarten		**Shoot N concentration [mg g d.w.$^{-1}$]**				
Year: 2001		**Treatment**				
Growth stage	**Cultivar**	**N0**	**N1**	**N2**	**Mean**	**F test**
	Apex	28.17 ab	35.76 ab	45.63 bc	36.52	N supply: ***
	Capitol	28.39 ab	36.68 bc	43.24 ab	36.10	Cultivar: ***
Begining of	Mohican	27.74 ab	33.09 ab	40.77 a	33.86	N x Cult: n.s.
shooting	Lirajet	31.13 b	39.87 c	47.06 c	39.35	
	Bristol	27.30 a	32.25 a	42.99 b	34.18	
	Mean	28.54	35.53	43.94		
	Apex	15.87 a	25.68 ab	33.48 a	25.01	N supply: ***
	Capitol	16.03 a	22.55 a	30.76 a	23.11	Cultivar: **
Begining of	Mohican	14.82 a	22.90 a	29.59 a	22.44	N x Cult: n.s.
flowering	Lirajet	18.37 a	25.67 ab	32.67 a	25.57	
	Bristol	18.16 a	27.54 b	33.32 a	26.34	
	Mean	16.65	24.87	31.96		
	Apex	10.03 a	16.03 b	19.69 a	15.25	N supply: ***
	Capitol	9.35 a	13.48 a	18.10 a	13.64	Cultivar: n.s.
End of	Mohican	10.61 a	13.70 a	19.55 a	14.62	N x Cult: n.s.
flowering	Lirajet	10.17 a	14.19 ab	19.95 a	14.77	
	Bristol	11.30 a	13.95 ab	19.09 a	14.78	
	Mean	10.29	14.27	19.28		
	Apex	13.03 b	14.65 ab	18.48 a	15.39	N supply: ***
	Capitol	12.05 ab	14.64 ab	18.04 a	14.91	Cultivar: *
Maturity	Mohican	12.91 b	15.66 b	17.82 a	15.46	N x Cult: n.s.
	Lirajet	12.79 b	14.75 ab	13.51 a	13.68	
	Bristol	11.59 a	13.85 a	17.92 a	14.45	
	Mean	12.47	14.71	17.15		

In the last field experiment, except at the end of flowering at N0 and at maturity at N2 supply, cultivars and DH lines differed significantly in shoot N concentration at all growth stages at all N rates (Tab. I-11). The mean shoot N concentration at the beginning of flowering varied in between 15.05 and 20.83 mg g^{-1} d.w. at N0, 22.55 and 31.68 mg g^{-1} d.w. at N1 and 30.79 and 37.11 mg g^{-1} d.w. at N2 supply. The N-inefficient cultivar Capitol had the lowest shoot N concentration at all levels of N supply. On the other hand another N-inefficient genotype DH28 showed significantly highest shoot N concentration at N0 and N1 supply. The N-efficient cultivar Apex showed had a comparatively high N concentration only at N1 supply. Moreover, similar high N concentrations were shown by Apex, DH42, DH28 and DH15 at N2 supply.

At the end of flowering, the significantly highest shoot N concentration was shown again by DH28 at N1 supply. At N2 however, the same genotype had a lower N concentration as Capitol. The efficient and responsive genotype DH4 showed the highest shoot N concentration at N2 supply. Among genotypes the shoot N concentration varied in between 15.79 and 18.67 mg g^{-1} d.w. at N1 and 21.55 and 25.42 mg g^{-1} d.w. at N2 supply.

At maturity, Apex, DH42, DH28 and DH15 had highest shoot N concentration at N0 supply (Tab. I-11). On the other hand, at the same N rate significantly lower shoot N concentrations were shown by the N-efficient genotype DH4 and the N-inefficient genotype Capitol. At medium N (N1) supply, DH42 showed the significantly highest shoot N concentration and Apex the lowest. Among genotypes the shoot N concentration varied in between 12.53 and 14.95 mg g^{-1} d.w. at N0 and 15.66 and 17.81 mg^{-1} d.w. at N1 supply.

Table I-11: Shoot N concentration of 6 oilseed rape cultivars as affected by N supply (N0: soil mineral N, N1: 120 kg N ha^{-1}, N2: 240 kg N ha^{-1}) at different growth stages at Zuchtgarten in 2002. Statistics: Separate analysis of variance for different growth stages. Means with the same letter are not significantly different at $\alpha = 0.05$ within each N rate.

Site: Zuchtgarten		**Shoot N concentration [mg g^{-1} d.w.]**				
Year: 2002		**Treatment**				
Growth stage	**Cultivar**	**N0**	**N1**	**N2**	**Mean**	**F test**
Beginning of flowering	DH4	19.43 bc	25.90 ab	33.43 ab	26.25	N supply: ***
	Apex	16.93 ab	31.22 c	35.26 b	27.80	Cultivar: ***
	DH42	15.21 a	26.65 b	36.20 b	26.02	N x Cult: n.s.
	DH28	20.83 c	31.68 c	37.11 b	29.87	
	DH15	19.71 bc	28.35 bc	35.84 b	27.97	
	Capitol	15.05 a	22.55 a	30.79 a	22.80	
	Mean	17.86	27.73	34.77		
End of flowering	DH4	11.89 a	16.07 a	25.42 c	17.79	N supply: ***
	Apex	11.35 a	15.82 a	23.60 abc	16.92	Cultivar: *
	DH42	12.26 a	17.73 ab	23.77 bc	17.92	N x Cult: n.s.
	DH28	12.58 a	18.67 b	22.04 ab	17.76	
	DH15	12.27 a	16.34 a	24.44 c	17.68	
	Capitol	10.78 a	15.79 a	21.55 a	16.04	
	Mean	11.85	16.74	23.47		
Maturity	DH4	12.53 a	16.28 ab	20.29 a	16.37	N supply: ***
	Apex	14.30 b	15.66 a	19.27 a	16.41	Cultivar: *
	DH42	14.50 b	17.81 b	19.90 a	17.40	N x Cult: n.s.
	DH28	14.73 b	17.17 ab	20.62 a	17.51	
	DH15	14.95 b	17.13 ab	19.86 a	17.31	
	Capitol	13.39 ab	16.78 ab	19.20 a	16.46	
	Mean	14.07	16.81	19.86 a		

4.6 Shoot Nitrogen Uptake

The total shoot N uptake continuously increased from beginning of shooting up to end of flowering at all N rates in the field experiments 2000 (A), 2001 (B), and 2002 (C) (Fig. I-3). In contrast, during the seed filling phase, shoot N uptake decreased particularly at medium (N1) and high (N2) N supply in the 2000 (A) and 2002 (C) field experiments. This indicates that 100% of the total shoot N uptake was attained when the flowering was completed and that substantial N losses occurred until maturity. On the other hand the N uptake still increased from the end of flowering till maturity under limiting (N0) N supply in the three field experiments.

The differences in shoot N uptake between N levels were usually small but significant at the beginning of shooting. At later growth stages the differences were significantly higher between three N rates. From beginning of shooting until maturity plants showed significantly highest shoot N uptake at N2 supply whereas the lowest was shown at N0 supply. A medium N uptake was shown at N1 supply at all growth stages. Plants accumulated about 47, 50 and 55 kg N ha^{-1} at the beginning of shooting, 50, 100 and 137 kg N ha^{-1} at the beginning of flowering and 61, 123 and 190 kg N ha^{-1} at the end of the flowering at N0, N1 and N2 supply, respectively in 2000.

This revealed that the plants accumulated about 73%, 41% and 29% of their total shoot N (at the end of the flowering) at the beginning of shooting and 77%, 81% and 72% at the beginning of flowering at N0, N1 and N2 supply, respectively. On the other hand, the N losses from end of the flowering up to maturity amounted to about 2% at N1 and 10% at N2 supply. In spite of substantial dry matter losses (30%) at N0 supply (Fig. I-1 A), total shoot N uptake increased by almost 5% from the end of flowering till maturity in 2000 (Fig. I-3 A). This clearly indicates that N uptake activity remained high during the reproductive growth phase under limiting (N0) N supply.

In the second field experiment (2001), plants accumulated about 57, 82 and 107 kg N ha^{-1} in the shoot at the beginning of shooting, 57, 113 and 163 kg N ha^{-1} at the beginning of flowering and 70, 114 and 185 kg N ha^{-1} at the end of the flowering at N0, N1 and N2 supply, respectively. The considerably high variations in N uptake between the N rates, particularly at the beginning of shooting, could be the result of the delayed shooting date in 2001 (Tab. 3).

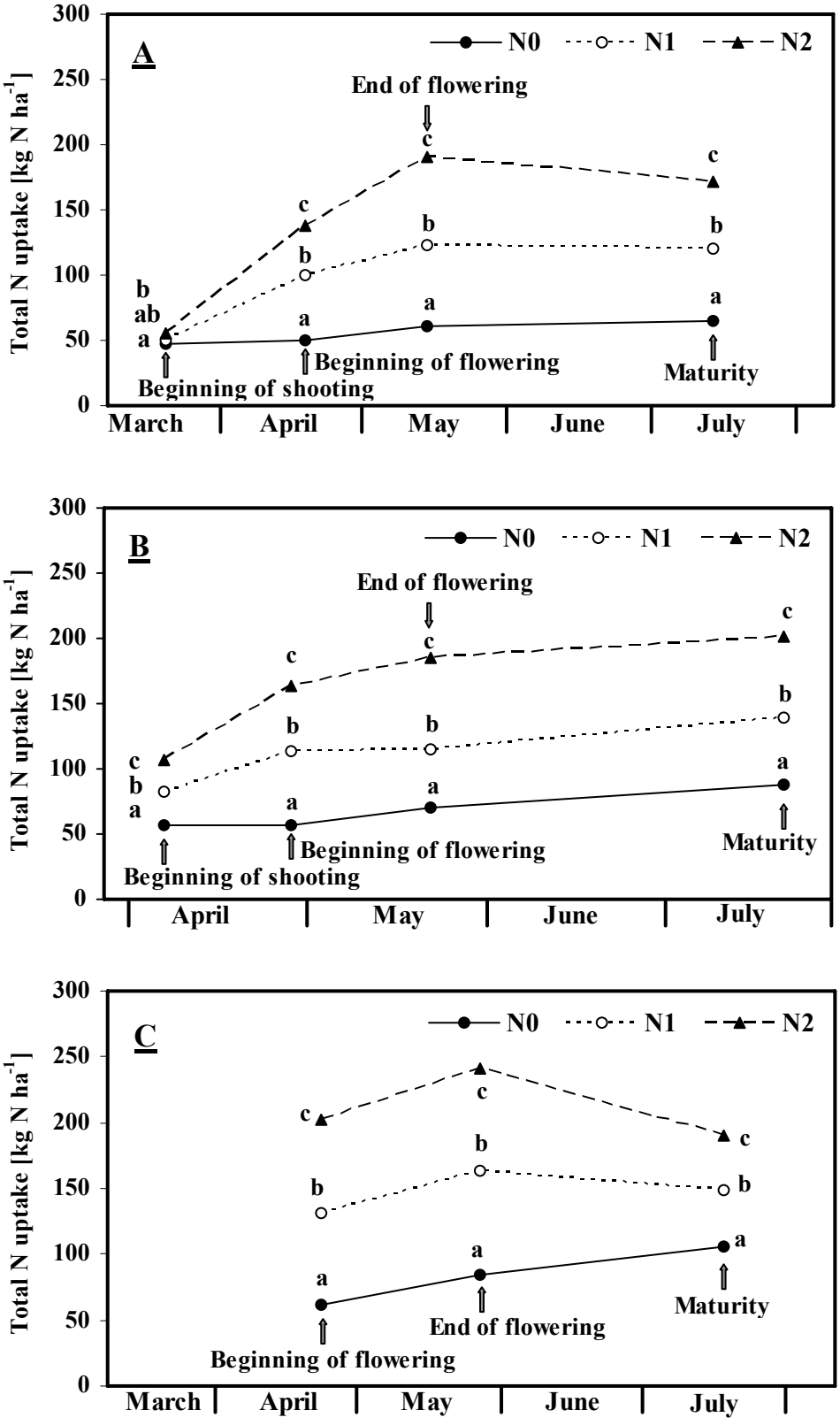


Figure I-3: Total N uptake of oilseed rape (means of 8, 5 and 6 cultivars, respectively) as affected by N supply (N0: soil mineral N, N1: 120 kg N ha^{-1}, N2: 240 kg N ha^{-1}) at different growth stages at Zuchtgarten in 2000 (A), 2001 (B), and 2002 (C). Statistics: Separate analysis of variance for different growth stages. Means with the same letter are not significantly different at $\alpha = 0.05$.

Since no dry matter losses occurred at all N rates (Fig. I-1 B), shoot N uptake increased at maturity by almost 26% at N0, 22% at N1 and 9% at N2 supply compared to the N uptake at the end of flowering.

When flowering started, the shoot N uptake amounted to 61, 131 and 202 kg N ha^{-1} at N0, N1 and N2 supply, respectively in 2002 (Fig. I-3 C). N uptake continued by almost 23 kg N ha^{-1} at N0, 32 kg N ha^{-1} at N1 and 40 kg N ha^{-1} at N2 supply until end of the flowering. However, up to maturity about 21 kg N ha^{-1} was taken up at N0 supply whereas 14 kg N ha^{-1} (9%) at N1 and 52 kg N ha^{-1} (22%) at N2 were lost. High N losses at N1 and N2 supply were the results of the substantial dry matter losses that occurred after end of flowering till maturity (Fig. I-1 C).

In terms of shoot N uptake highly significant differences among eight rape cultivars were found at the beginning of shooting, beginning of flowering, end of flowering and maturity at different levels of N supply in 2000 (Tab. I-12). A highly significant interaction between N and genotype occurred only at the beginning of flowering. At the beginning of shooting the shoot N uptake among cultivars varied in between 42 and 51 kg N ha^{-1} at N0, 44 and 54 kg N ha^{-1} at N1 and 49 and 68 kg N ha^{-1} at N2 supply. At this stage the highest shoot N uptake was shown by Mohican at N0 and N2 supply, whereas the lowest shoot N uptake was shown by Prospa at N0 and N1 supply. At the beginning of flowering, end of the flowering and maturity no significant differences were found among cultivars at N0 supply. On the other hand, significantly highest variation among genotypes was almost 35 kg N ha^{-1} at N1 and 53 kg N ha^{-1} at N2 supply at the beginning of flowering. Express at N1 and Apex at N2 supply showed the best performance in N accumulation at this growth stage, while Prospa and Bristol had the lowest N uptake at N1 and N2.

At the end of the flowering uptake differences among genotypes varied in between 108 and 137 kg N ha^{-1} at N1 and 179 and 208 kg N ha^{-1} at N2 supply. Prospa and Express showed significantly highest N uptake at N1 supply whereas Apex showed the lowest N uptake at the same N rate. At N2 supply, Bristol showed the significantly best performance in N uptake compared to other cultivars. At maturity, the N uptake differences among genotypes varied in between 105 and 133 kg N ha^{-1} at N1 and 144 and 187 kg N ha^{-1} at N2 supply.

Table I-12: Total N uptake of 8 oilseed rape cultivars as affected by N supply (N0: soil mineral N, N1: 120 kg N ha^{-1}, N2: 240 kg N ha^{-1}) at different growth stages at Zuchtgarten in 2000. Statistics: Separate analysis of variance for different growth stages. Means with the same letter are not significantly different at $\alpha = 0.05$ within each N rate.

Site: Zuchtgarten		**Total N uptake [kg ha^{-1}]**				
Year: 2000		**Treatment**				
Growth stage	**Cultivar**	**N0**	**N1**	**N2**	**Mean**	**F test**
Beginning of shooting	Bristol	46.96 ab	49.94 ab	49.11 a	48.67	N supply: *
	Apex	48.61 ab	54.21 b	50.58 ab	51.14	Cultivar: ***
	Express	46.44 ab	48.86 ab	49.43 a	48.24	N x Cult: n.s.
	Mohican	51.20 b	50.80 ab	67.85 d	56.61	
	Lirajet	41.79 a	46.60 ab	50.02 ab	46.14	
	Mansholt	50.54 b	50.05 ab	58.30 bc	52.97	
	Capitol	47.72 ab	54.07 b	61.15 cd	54.31	
	Prospa	41.64 a	43.47 a	55.42 abc	46.84	
	Mean	46.86	49.75	55.23		
Beginning of flowering	Bristol	52.85 a	87.63 a	108.80 a	83.09	N supply: ***
	Apex	46.06 a	108.84 bc	160.93 c	105.28	Cultivar: ***
	Express	48.48 a	119.79 c	139.88 b	102.72	N x Cult: ***
	Mohican	48.14 a	100.14 ab	138.88 b	95.72	
	Lirajet	45.16 a	102.91 abc	146.70 bc	98.25	
	Mansholt	49.47 a	94.79 ab	150.74 bc	98.34	
	Capitol	59.53 a	96.73 ab	138.86 b	98.37	
	Prospa	51.25 a	84.96 a	113.46 a	83.22	
	Mean	50.12	99.47	137.28		
End of flowering	Bristol	67.15 a	130.33 bc	207.45 b	134.97	N supply: ***
	Apex	49.84 a	108.06 a	190.48 ab	116.13	Cultivar: *
	Express	66.78 a	136.49 c	191.66 ab	131.64	N x Cult: n.s.
	Mohican	68.92 a	111.53 ab	190.79 ab	123.75	
	Lirajet	51.02 a	111.03 ab	180.74 a	114.26	
	Mansholt	60.30 a	123.28 abc	196.34 ab	126.64	
	Capitol	68.29 a	125.34 abc	178.94 a	124.19	
	Prospa	55.34 a	133.79 c	185.48 ab	124.87	
	Mean	60.95	122.48	190.24		
Maturity	Bristol	64.32 a	114.76 abcd	170.94 bc	116.67	N supply: ***
	Apex	67.44 a	132.51 e	179.14 bc	126.37	Cultivar: ***
	Express	70.44 a	130.85 de	173.01 bc	124.77	N x Cult: n.s.
	Mohican	65.53 a	130.05 cde	177.24 bc	124.27	
	Lirajet	62.39 a	113.94 abc	173.41 bc	116.58	
	Mansholt	65.71 a	112.87 ab	170.63 b	116.40	
	Capitol	61.18 a	105.09 a	143.94 a	103.40	
	Prospa	57.07 a	122.23 bcde	187.01 c	122.10	
	Mean	64.26	120.29	171.92		

Opposite to end of the flowering, Apex showed significantly highest shoot N uptake at this stage while the lowest was shown by Capitol at N1 supply. At N2 supply most N was taken up by Prospa whereas the lowest N uptake was shown again by Capitol.

In the second field experiment total shoot N uptake of five rape genotypes varied significantly at the beginning of shooting, beginning of flowering and maturity between N rates (Tab. I-13). No significant differences among genotypes in total N uptake were found at N0. This might be the result of a similar shoot dry matter production among genotypes at the beginning of flowering, end of the flowering and maturity in 2001 (Tab. I-2). At the beginning of shooting genotypes varied in between 75 and 91 kg N ha^{-1} at N1 supply in 2001 (Tab. I-13). At this stage Capitol showed a higher total N uptake than Lirajet. Differences in N uptake were found only at N2 supply at the beginning of flowering. Here Capitol showed a higher N uptake than Bristol. The difference in N uptake between these two genotypes amounted to almost 30 kg N ha^{-1}. A similar difference in N uptake (29 kg N ha^{-1}) was found between genotypes at N2 supply at maturity. The best performance was shown by Apex, whereas Capitol had a significantly lower N uptake.

In the last field experiment (2002) no significant differences among cultivars and DH lines were found at the beginning of flowering at all N rates (Tab. I-14). However, genotypes differed significantly and the interaction between N and genotype was also significant at the end of the flowering and at maturity. The total shoot N uptake varied in between 140 and 190 kg N ha^{-1} at N1 and 204 and 274 kg N ha^{-1} at N2 supply at the end of the flowering. At this stage, DH4 consistently accumulated highest N in the shoot at N1 and N2 supply. A significantly lower shoot N uptake was shown by Apex and DH15 at N1 and by DH28 at N2 supply. At maturity, the highest N uptake differences among the genotypes were about 30 kg N ha^{-1} at N1 and 40 kg N ha^{-1} at N2 supply. Significantly highest shoot N uptake was shown again by DH4 at both N rates. The genotypes DH15 at N1 and DH28 at N2 supply accumulated the lowest N in the shoot at maturity.

Table I-13: Total N uptake of 5 oilseed rape cultivars as affected by N supply (N0: soil mineral N, N1: 120 kg N ha^{-1}, N2: 240 kg N ha^{-1}) at different growth stages at Zuchtgarten in 2001. Statistics: Separate analysis of variance for different growth stages. Means with the same letter are not significantly different at $\alpha = 0.05$ within each N rate.

Site: Zuchtgarten		**Total N uptake [kg ha^{-1}]**				
Year: 2001		**Treatment**				
Growth stage	**Cultivar**	**N0**	**N1**	**N2**	**Mean**	**F test**
	Apex	52.98 a	80.35 ab	108.14 a	80.49	N supply: ***
	Capitol	60.58 a	90.67 b	103.44 a	84.90	Cultivar: n.s.
Beginning of	Mohican	58.78 a	85.07 ab	105.72 a	83.19	N x Cult: n.s.
shooting	Lirajet	54.22 a	75.23 a	103.13 a	77.53	
	Bristol	57.76 a	78.71 ab	114.55 a	83.67	
	Mean	56.86	82.01	107.00		
	Apex	47.96 a	118.42 a	165.29 ab	110.56	N supply: ***
	Capitol	67.53 a	112.62 a	179.73 b	119.96	Cultivar: n.s.
Beginning of	Mohican	57.76 a	114.80 a	156.30 ab	109.62	N x Cult: n.s.
flowering	Lirajet	56.19 a	114.45 a	164.42 ab	111.68	
	Bristol	56.32 a	106.54 a	149.60 a	104.16	
	Mean	57.15	113.37	163.07		
	Apex	68.18	120.35	197.34	128.62	N supply: ***
	Capitol	67.04	110.39	183.06	120.16	Cultivar: n.s.
End of	Mohican	74.46	117.28	189.95	127.23	N x Cult: n.s.
flowering	Lirajet	73.57	120.54	182.99	125.70	
	Bristol	78.25	123.30	200.53	134.03	
	Mean	72.30	118.37	190.77		
	Apex	91.83 a	147.03 a	215.78 b	151.55	N supply: ***
	Capitol	93.64 a	138.12 a	187.07 a	139.61	Cultivar: n.s.
Maturity	Mohican	90.23 a	146.23 a	188.36 a	141.61	N x Cult: n.s.
	Lirajet	88.23 a	132.06 a	207.91 b	142.73	
	Bristol	78.32 a	135.58 a	208.59 b	140.83	
	Mean	88.45	139.80	201.54		

Table I-14: Total N uptake of 6 oilseed rape cultivars as affected by N supply (N0: soil mineral N, N1: 120 kg N ha^{-1}, N2: 240 kg N ha^{-1}) at different growth stages at Zuchtgarten in 2002. Statistics: Separate analysis of variance for different growth stages. Means with the same letter are not significantly different at $\alpha = 0.05$ within each N rate.

Site: Zuchtgarten		**Total N uptake [kg ha^{-1}]**				
Year: 2002		**Treatment**				
Growth stage	**Cultivar**	**N0**	**N1**	**N2**	**Mean**	**F test**
	DH4	70.16	135.95	207.95	138.02	N supply: ***
	Apex	50.55	137.47	198.98	129.00	Cultivar: n.s.
Beginning of	DH42	57.89	126.64	201.05	128.53	N x Cult: n.s.
flowering	DH28	60.90	126.53	193.10	126.85	
	DH15	59.40	127.21	198.77	128.46	
	Capitol	67.92	131.11	211.66	136.90	
	Mean	61.14	130.82	201.92		
	DH4	90.50 a	190.28 b	273.88 d	184.89	N supply: ***
	Apex	78.66 a	139.51 a	236.29 bc	151.48	Cultivar: *
End of	DH42	82.61 a	161.12 ab	246.97 bcd	163.57	N x Cult: *
flowering	DH28	91.68 a	181.09 b	203.45 a	158.74	
	DH15	82.95 a	144.19 a	261.54 cd	162.89	
	Capitol	78.60 a	162.54 ab	227.81 ab	156.32	
	Mean	84.17	163.12	241.66		
	DH4	105.29 a	162.14 b	210.14 d	159.19	N supply: ***
	Apex	107.75 a	144.57 ab	180.02 ab	144.11	Cultivar: **
	DH42	113.01 a	152.14 b	185.74 abc	150.30	N x Cult: *
Maturity	DH28	102.79 a	144.26 ab	170.19 a	139.08	
	DH15	105.52 a	132.29 a	192.25 bcd	143.35	
	Capitol	97.37 a	156.10 b	202.87 cd	152.11	
	Mean	105.29	148.58	190.20		

4.7 Nitrogen Utilization Efficiency and Its Components (Partitioning of Nitrogen within the Plant)

4.7.1 Nitrogen Utilization Efficiency

The seed yield per unit N taken up by the plant, *i.e*. the nitrogen utilization efficiency, was determined in the field experiments at Zuchtgarten in 2000 (A), 2001 (B) and 2002 (C) (Tab. I-15). The N utilization efficiency was significantly different between the N rates and among the cultivars in all three field experiments. A significant interaction between N and genotype was found in 2001. In general, the N utilization decreased when the N supply was increased from N0 to N1 or N2 supply in all three field experiments. Averaged over cultivars the decline in N utilization was about 15% at N1 and 33% at N2 in 2000, 10% at N1 and 28% at N2 in 2001 and 9% at N1 and 24% at N2 in 2002.

Among eight rape cultivars the N utilization varied in between 33 and 38 kg kg^{-1} at N0, 27 and 32 kg kg^{-1} at N1 and 22 and 25 kg kg^{-1} at N2 supply in 2000 (A). Under low (N0) N supply, the lowest N utilization was shown by Express and Mansholt. Both cultivars showed a low N utilization also at N1 supply. On the other hand, significantly highest N utilization was shown by Bristol at N0, N1 and N2 supply. Actually, Bristol and Express produced a similarly high grain yield (Tab. I-5 A) and the highest shoot dry matter (Tab. I-1) at maturity at N0 supply (Tab. I-5 A). Thus, the lowest N utilization of Express can be explained by a high N uptake efficiency that contributed to the high seed yield.

In the second field experiment (2001) cultivars did not differ significantly in N utilization at N0 supply (Tab. I-15). However, significant differences among cultivars were found at N1 and N2 supply. In terms of N utilization cultivars varied in between 31 and 35 kg kg^{-1} at N1 and 23 and 28 kg kg^{-1} at N2. Apex showed the lowest N utilization efficiency both at N1 and N2 supply. In contrast, Bristol had the highest showed highest N utilization efficiency at the same N levels. A medium N utilization at N1 and an almost similarly high N utilization as compared to Bristol at N2, was shown by Capitol.

Table I-15: N utilization efficiency of oilseed rape cultivars (8, 5 and 6 cultivars) as affected by N supply (N0: soil mineral N, N1: 120 kg N ha^{-1}, N2: 240 kg N ha^{-1}) at Zuchtgarten in 2000 (A), 2001(B) and 2002 (C). Statistics: Separate analysis of variance for different experimental years. Means with the same letter are not significantly different at $\alpha = 0.05$ within each N rate.

Site: Zuchtgarten		**N utilization efficiency [kg grain kg N $^{-1}$]**				
		Treatment				
Year	**Cultivar**	**N0**	**N1**	**N2**	**Mean**	**F test**
	Bristol	37.50 d	31.46 c	24.86 d	31.27	N supply: ***
	Apex	35.08 bc	29.63 bc	21.75 a	28.82	Cultivar: ***
	Express	32.90 a	27.99 ab	24.15 bcd	28.35	N x Cult: n.s.
2000 (A)	Mohican	35.11 c	30.91 c	24.67 cd	30.23	
	Lirajet	35.33 c	29.65 bc	22.80 abc	29.26	
	Mansholt	32.82 a	27.44 a	22.25 ab	27.50	
	Capitol	34.94 bc	30.85 c	23.81 bcd	29.87	
	Prospa	33.11 ab	28.73 ab	22.53 ab	28.12	
	Mean	34.60	29.58	23.35		
	Apex	36.48 a	30.75 a	23.37 a	30.20	N supply: ***
	Capitol	34.97 a	32.85 b	26.99 cd	31.60	Cultivar: ***
2001(B)	Mohican	35.55 a	31.54 ab	25.34 bc	30.81	N x Cult: *
	Lirajet	34.85 a	32.13 ab	24.57 ab	30.52	
	Bristol	36.60 a	35.12 c	27.48 d	33.07	
	Mean	35.69	32.48	25.55		
	DH4	31.09 d	27.46 c	21.74 bc	26.76	N supply: ***
	Apex	28.37 c	25.86 bc	23.08 c	25.77	Cultivar: ***
2002 (C)	DH42	25.24 a	23.49 a	20.21 ab	22.98	N x Cult: n.s.
	DH28	27.50 bc	25.59 b	21.20 ab	24.76	
	DH15	26.19 ab	23.85 a	19.84 a	23.29	
	Capitol	27.99 c	25.74 b	20.87 ab	24.87	
	Mean	27.73	25.33	21.16		

Six rape genotypes differed significantly in N utilization efficiency at all three N rates in 2002 (C). Under limiting N supply (N0) the N utilization varied in between 25 and 31 kg kg^{-1} among genotypes. At this N level, the most efficient genotype was DH4 and the least efficient was DH42. Although similarly high grain yields were produced by Apex and DH4 at N0 (Tab. I-5 C), Apex had a significantly lower N utilization than DH4 (Tab. I-15).

This clearly indicated that both N-efficient genotypes (DH4 and Apex) achieved their high seed yields through different N efficiency components at N0 supply. The N utilization varied in between 24 and 28 kg kg^{-1} at medium N (N1) and 20 and 23 kg kg^{-1} at high N (N2) supply among six genotypes. At both N levels, highest N utilization efficiencies were shown by DH4 and Apex and the lowest by DH15.

4.7.2 Biological Production Efficiency

The shoot dry matter per unit N taken up by the plant, *i.e*. the biological production efficiency (BPE), was determined in the field experiments at Zuchtgarten in 2000 (A), 2001 (B) and 2002 (C) (Tab. I-16). Highly significant differences in BPE were found between the N rates and among cultivars in all three field experiments. In general, the BPE decreased when the N supply was increased from N0 to N1 or N2 supply in 2000, 2001 and 2002. Averaged over cultivars the BPE decreased by almost 13% at N1 and 29% at N2 in 2000, 15% at N1 and 31% at N2 in 2001 and 17% at N1 and 30% at N2 in 2002. On the other hand, the BPE was usually higher in 2001 and 2002 compared to 2000 at all N rates. Particularly at limiting (N0) N supply, the BPE was increased about 23% in 2001 and 10% in 2002 compared to 2000. The lower BPE at N0 in 2000 could be the result of substantial dry matter losses (30%) that occurred from the end of the flowering till maturity at N0 supply in 2000 (Fig. I-1 A).

BPE differed significantly among eight cultivars at all N rates in 2000 (Tab. I-16). The variation among genotypes was in the range of 57 and 71 kg kg N^{-1} N0, 52 and 61 kg kg N^{-1} at N1 and 42 and 51 kg kg N^{-1} at N2 supply in 2000. The lowest BPE was shown by Mansholt and Prospa while the significantly highest BPE was shown by Express, Capitol, Apex and Bristol at N0 supply. The differences were related to differences in shoot dry matter production among cultivars (Tab. I-1), whereas no genotypic differences in N uptake were found at N0 (Tab. I-12). Mansholt and Prospa still had the lowest BPE at N1 and N2 supply (Tab. I-16). However, at the both N rates, significantly highest BPE was shown by Bristol and Capitol.

Table I-16: Biological production efficiency (BPE) of oilseed rape cultivars (8, 5 and 6 cultivars) as affected by N supply (N0: soil mineral N, N1: 120 kg N ha^{-1}, N2: 240 kg N ha^{-1}) at Zuchtgarten in 2000 (A), 2001(B) and 2002 (C). Statistics: Separate analysis of variance for different experimental years. Means with the same letter are not significantly different at $\alpha = 0.05$ within each N rate.

Site: Zuchtgarten		**BPE [kg d.w. kg N^{-1}]**				
		Treatment				
Year	**Cultivar**	**N0**	**N1**	**N2**	**Mean**	**F test**
2000 (A)	Bristol	66.04 c	59.05 b	47.77 c	57.62	N supply: ***
	Apex	66.80 c	57.82 ab	47.23 ac	57.28	Cultivar: ***
	Express	70.91 c	56.74 ab	46.22 ac	57.96	N x Cult: n.s.
	Mohican	65.02 bc	56.99 ab	46.64 ac	56.22	
	Lirajet	67.80 bc	55.39 ab	48.28 bc	57.16	
	Mansholt	56.53 a	54.02 a	44.06 ab	51.54	
	Capitol	68.19 c	61.08 b	50.75 c	60.00	
	Prospa	61.91 ab	52.39 a	42.11 a	52.14	
	Mean	65.40	56.69	46.63		
2001(B)	Apex	76.94 a	68.36 ab	54.24 a	66.52	N supply: ***
	Capitol	83.18 bc	68.36 ab	55.58 a	69.04	Cultivar: **
	Mohican	77.59 a	64.05 a	56.19 a	65.94	N x Cult: n.s.
	Lirajet	78.35 ab	68.01 ab	55.51 a	67.29	
	Bristol	86.70 c	72.45 b	56.04 a	71.73	
	Mean	80.55	68.25	55.51		
2002 (C)	DH4	80.10 c	61.96 ab	49.45 a	63.84	N supply: ***
	Apex	69.96 ab	63.89 b	52.09 a	61.98	Cultivar: **
	DH42	69.65 ab	56.29 a	50.69 a	58.88	N x Cult: n.s.
	DH28	68.04 a	58.31 ab	48.53 a	58.30	
	DH15	67.01 a	58.53 ab	50.45 a	58.66	
	Capitol	75.71 bc	59.61 ab	52.18 a	62.50	
	Mean	71.74	59.77	50.57		

Since Capitol had a low shoot dry matter and grain yield (I-5 A), the high BPE of Capitol at N1 and N2 (Tab. I-16 A) could be the result of the lowest total N uptake at maturity in 2000 (Tab. I-12).

Cultivars differed significantly for BPE only at low (N0) and medium (N1) N rates in 2001 (Tab. I-16 B). The mean BPE varied in between 77 and 87 kg kg N^{-1} at N0 and 64 and 73 kg kg N^{-1} at N1 supply. The highest BPE was achieved by Bristol and Capitol at N0 supply. At the same N rate, Apex and Mohican showed the lowest BPE. Bristol still had the highest BPE at N1 while the lowest was still shown by Mohican at the same N level. The high BPE of Bristol, particularly at N1, was related to both, a comparatively low total N uptake (Tab. I-13), and a comparatively high shoot dry matter (Tab. 1-2).

The variation among six rapeseed genotypes for BPE was significant at N0 and N1 supply in 2002 at Zuchtgarten (Tab. I-16 C). The BPE among the genotypes varied in between 67 and 80 kg kg N^{-1} at N0 and 56 and 64 kg kg N^{-1} at N1 supply. At low (N0) N supply, highest BPE was shown by DH4 due to its highest shoot dry matter production (Tab. I-3) combined with an only medium total N uptake at maturity (Tab. I-14). At the same N rate, the significantly lowest BPE was shown by DH28 and DH15 (Tab. I-16 C) due to this low shoot dry matter productions (Tab. I-3). At medium (N1) N supply, Apex had the highest BPE and the lowest was shown by DH42 (Tab. I-16 C). This was due to the fact that Apex had a slightly higher shoot dry mater production than DH42 (Tab. I-3) and a slightly lower N uptake (Tab. I-14).

4.7.3 Nitrogen Harvest Index

The proportion of total dry matter N translocated to the grain, *i.e*. the N harvest index, was determined in the field experiments at Zuchtgarten in 2000 (A), 2001 (B) and 2002 (C) (Tab. I-17). Highly significant differences in N harvest index were found between N rates and among cultivars in all three field experiments. The interaction between N and genotype was highly significant in 2000, 2001 and 2002. N harvest index usually decreased (except in 2001 at N1) when the N supply was increased from N0 to N1 or N2 supply in all three field experiments. Averaged over cultivars the N-harvest index decreased by almost 3% at N1 and 11% at N2 in 2000, 7% at N2 in 2001, and 3% at N1 and 10% at N2 in 2002. On the other hand, the N harvest indices were lower in 2001 and 2002 compared to 2000 at all N rates.

Table I-17: N Harvest index of oilseed rape cultivars (8, 5 and 6 cultivars) as affected by N supply (N0: soil mineral N, N1: 120 kg N ha^{-1}, N2: 240 kg N ha^{-1}) at Zuchtgarten in 2000 (A), 2001(B) and 2002 (C). Statistics: Separate analysis of variance for different experimental years. Means with the same letter are not significantly different at $\alpha = 0.05$ within each N rate.

		N-Harvest index				
Site: Zuchtgarten		**Treatment**				
Year	**Cultivar**	**N0**	**N1**	**N2**	**Mean**	**F test**
2000 (A)	Bristol	0.90 ab	0.87 a	0.81 bc	0.86	N supply: ***
	Apex	0.86 a	0.89 a	0.72 a	0.82	Cultivar: ***
	Express	0.89 ab	0.86 a	0.83 c	0.86	N x Cult: **
	Mohican	0.90 ab	0.85 a	0.80 bc	0.85	
	Lirajet	0.90 ab	0.86 a	0.78 b	0.85	
	Mansholt	0.93 b	0.88 a	0.83 c	0.88	
	Capitol	0.90 ab	0.87 a	0.82 c	0.86	
	Prospa	0.90 ab	0.89 a	0.83 c	0.87	
	Mean	0.90	0.87	0.80		
2001(B)	Apex	0.85 ab	0.81 a	0.74 a	0.80	N supply: ***
	Capitol	0.82 a	0.85 bc	0.82 b	0.83	Cultivar: ***
	Mohican	0.84 ab	0.84 bc	0.76 a	0.82	N x Cult: ***
	Lirajet	0.83 a	0.83 ab	0.75 a	0.80	
	Bristol	0.86 b	0.86 c	0.81 b	0.84	
	Mean	0.84	0.84	0.78		
2002 (C)	DH4	0.80 ab	0.78 ab	0.69 a	0.76	N supply: ***
	Apex	0.79 a	0.77 a	0.75 bc	0.77	Cultivar: ***
	DH42	0.78 a	0.79 ab	0.72 b	0.77	N x Cult: *
	DH28	0.83 c	0.81 b	0.77 c	0.80	
	DH15	0.82 bc	0.79 ab	0.73 b	0.78	
	Capitol	0.81 abc	0.81 b	0.73 b	0.78	
	Mean	0.81	0.79	0.73		

Particularly at limiting N supply (N0), the N harvest index declined about 7% in 2001 and 10% in 2002 compared to 2000. The higher N harvest index at N0 in 2000 could be the result of substantial dry matter losses (30%) that occurred from the end of the flowering till maturity at N0 supply in 2000 (Fig. I-1 A). Another reason for the higher N harvest index at N0 in 2000 could be the result of continued vegetative growth in 2001 and 2002.

N harvest indices differed significantly among eight cultivars only at N0 and N2 supply in 2000 (Tab. I-17). The variation among genotypes was in the range of 86 and 93% at N0 and 72 and 83% at N2 in 2000. At N0, the N-efficient cultivar Apex had a significantly lower N harvest index than Mansholt. These two genotypes also differed in their N harvest index at high N supply (N2), however, besides Mansholt also Express, Capitol and Prospa had very high N harvest indices at high N supply.

In the second field experiment (2001), the cultivars differed significantly in their N harvest indices at all N rates (Tab. I-17 B). The mean harvest index varied in between 82 and 86% at N0, 81 and 86% at N1 and 74 and 82% at N2 supply. The highest N-harvest index was achieved by Bristol at N0. At the same N supply Capitol and Lirajet had the lowest N-harvest indices. At medium N supply (N1), Bristol still had highest N harvest index while the lowest was shown by Apex. At high N supply Brsitol and Capitol showed significantly highest N harvest indices compared to other cultivars.

The variation among six rapeseed genotypes for N harvest index was significant at three levels of N supply in 2002 (Tab. I-17 C). The N harvest index among the genotypes varied in between 78 and 83% at N0, 77 and 81% at N1 and 69 and 77% at N2 supply. At N0, the highest N harvest index was shown by DH28 and the lowest by Apex and DH42. At medium (N1) N supply, Apex still had the lowest N-harvest index while DH28 and Capitol showed the highest N harvest indices. The lowest N harvest index was shown by DH4 at N2 supply. At the same N rate the highest N harvest index was shown again by DH28.

4.7.4 Seed Nitrogen Concentration

The seed N concentration of the oilseed rape cultivars was determined in the field experiment in 2000 (A), 2001 (B) and 2002 (C) at Zuchtgarten (Tab. I-18). The seed N concentration was significantly different between the N rates and among the cultivars in all three field experiments. The seed N concentration increased when the N supply was increased from N0 to N1 or N2 supply in all field experiments. Averaged over cultivars the seed N concentration was increased by almost 14% at N1 and 32% at N2 in 2000, 10% at N1 and 30% at N2 in 2001 and 7% at N1 and 19% at N2 in 2002.

In the first field experiment (2000), the N concentration differed significantly among eight cultivars at all N rates. The variation among the genotypes was in the range of 24 – 28 mg g^{-1} d.w. at N0, 28 – 32 mg g^{-1} d.w. at N1 and 33 – 37 mg g^{-1} d.w. at N2 in 2000. Constantly the highest seed N concentrations were shown by Mansholt at all levels of N supply. In contrast, Bristol had the lowest seed N concentrations at all N rates. Furthermore, Apex had similarly low seed N concentration as Bristol at N0 supply. At N1 and N2 supply Mohican had similarly low seed N concentration as Bristol. The high N harvest index of Mansholt (Tab. I-17 A) was thus related to high seed N concentrations while the low N harvest index of Apex was related to a low seed N concentration (Tab. I-18 A)

Although no significant differences in seed N concentration at N0 were found in the second field experiment (2001), the five rape cultivars differed significantly at N1 and N2 supply (Tab. I-18 B). Under medium N supply (N1), the mean seed N concentration varied in between 25 and 27 mg g^{-1} d.w.. At this N rate, the significantly highest seed N concentrations were shown by Mohican, Apex and Lirajet as compared to Bristol, having the lowest seed N concentration. At high N supply (N2) the highest seed N concentration was shown by Apex. The significantly lowest seed N concentrations were shown by Capitol, Mohican and Bristol.

The variation among six rapeseed genotypes for seed N concentration was significant for all three levels of N supply in 2002. The seed N concentration among the genotypes varied in between 26 – 32 mg g^{-1} d.w. at N0, 29 – 34 mg g^{-1} d.w. at N1 and 32 – 35 mg g^{-1} d.w. at N2. Under low N supply (N0), the significantly highest seed N concentrations were shown by DH15 and DH42 whereas the significantly lowest N concentrations were shown by DH4 and Apex.

Table I-18: Seed N concentration of oilseed rape cultivars (8, 5 and 6 cultivars) at maturity as affected by N supply (N0: soil mineral N, N1: 120 kg N ha^{-1}, N2: 240 kg N ha^{-1}) at Zuchtgarten in 2000 (A), 2001(B) and 2002 (C). Statistics: Separate analysis of variance for different experimental years. Means with the same letter are not significantly different at $\alpha = 0.05$ within each N rate.

Site: Zuchtgarten		**Seed N concentration [mg g^{-1} d.w.]**				
		Treatment				
Year	**Cultivar**	**N0**	**N1**	**N2**	**Mean**	**F test**
	Bristol	24.14 a	27.53 a	32.46 a	28.04	N supply: ***
	Apex	24.68 a	29.73 bcd	33.18 ab	29.19	Cultivar: ***
	Express	27.13 bd	30.72 ce	34.54 b	30.79	N x Cult:
2000 (A)	Mohican	25.69 abc	27.66 a	32.49 a	28.61	
	Lirajet	25.48 ab	29.19 ac	34.11 ab	29.59	
	Mansholt	28.26 d	32.03 e	37.16 c	32.48	
	Capitol	25.68 abc	28.54 ab	34.28 b	29.50	
	Prospa	27.19 cd	31.00 de	36.74 c	31.65	
	Mean	26.03	29.55	34.37		
	Apex	23.23 a	26.33 b	31.88 b	27.15	N supply: ***
	Capitol	23.57 a	25.81 ab	30.26 a	26.55	Cultivar: *
2001(B)	Mohican	23.71 a	26.64 b	30.20 a	26.85	N x Cult: n.s.
	Lirajet	23.75 a	25.89 b	30.99 ab	26.88	
	Bristol	23.43 a	24.46 a	29.63 a	25.84	
	Mean	23.54	25.83	30.59		
	DH4	25.86 a	28.58 a	31.83 a	28.75	N supply: ***
	Apex	27.82 ab	29.74 ab	32.60 a	30.06	Cultivar: ***
2002 (C)	DH42	31.36 d	33.78 d	35.65 b	33.60	N x Cult: n.s.
	DH28	30.30 cd	31.49 bc	36.54 b	32.78	
	DH15	31.49 d	33.09 cd	37.01 b	33.86	
	Capitol	28.96 bc	31.32 bc	34.96 b	31.75	
	Mean	29.30	31.33	34.76		

These N-efficient genotypes (DH4 and Apex) still had the significantly lowest seed N concentrations at medium (N1) and high (N2) N rates. These results clearly explain why the N-harvest indices of Apex at N0 and N1 and DH4 at all N rates were low (Tab. I-17) although they achieved a high grain yield (Tab. I-5 C). At N1 and N2, the highest seed N concentrations were again shown by DH42 (Tab. I-18). However, besides DH42, also DH28, DH15 and Capitol also had significantly higher seed N concentrations at N2 supply than DH4 and Apex.

4.8 Seed Quality

Several seed quality components as oil, protein, and glucosinolate (GSL) content and the fatty acid composition (oleic, linolenic and erucic acid) of the oilseed rape cultivars were determined in the field experiment in 2000 (Tab. I-19), 2001 (Tab. I-20) and 2002 (Tab. I-21) at Zuchtgarten. The oil and protein contents were significantly different between the N rates and among the genotypes in all three field experiments. Significant interaction between N and genotype was found only in oil content in 2001 (Tab. I-20). In general the oil content decreased whereas protein content increased when the N supply was increased from N0 to N1 or N2 supply in all field experiments. The correlations between oil and protein were significantly negative particularly in 2001 (Tab. I-19) and 2002 (Tab. I-21) at limiting (N0) and high (N2) N supply. Averaged over cultivars decline in oil content was by almost 4% at N1 and 8% at N2 and increase in protein content was by almost 15% at N1 and 28% at N2 in 2000. In the second field trail (2001) the reduction in oil content was almost similar as previous year and ranged about by 3% at N1 and 8% at N2. However, protein content was increased by almost 11% at N1 and 34% at N2. In the last field experiment (2002) the oil content reduced by almost 2% at N1 and 6% at N2 while protein content increased by almost 5% at N1 and 19% at N2.

Among eight rape cultivars the oil content varied in between 46 and 49% at N0, 43 and 47% at N1 and 41 and 44% at N2 supply (Tab. I-19). Mansholt had the highest oil content at N0 and N1 supply. At the same N rates the significantly lowest oil contents were shown by Lirajet, Apex and Capitol. At high N supply (N2) Mohican accumulated the highest oil content whereas the lowest was shown once more by Lirajet. The protein content differed in the range of 16 and 18% at N0, 18 and 20% at N1 and 20 and 23% at N2 supply.

Table I-19: Seed quality parameters of 8 rape cultivars as affected by N supply (N0: soil mineral N, N1: 120 kg N ha^{-1}, N2: 240 kg N ha^{-1}) at maturity at Zuchtgarten in 2000. Statistics: Separate analysis of variance. Means with the same letter are not significantly different. ***, **, *, and + indicate significance at $p < 0.001$, 0.01, 0.05, and 0.1

Site: Zuchtgarten		**Seed quality**					
Year: 2000		**Oil**	**Protein**	**GSL**	**Fatty acid composition [%]**		
		content	**content**	**content**	**Oleic**	**Linolenic**	**Erucic**
Treatment	**Cultivar**	**[%]**	**[%]**	**[µmol g^{-1}]**	**C18:1**	**C18:3**	**C22:1**
	Bristol	47.85 de	15.47 a	14.98 a	58.81 b	7.07 b	1.30 a
	Apex	45.88 ab	16.65 bcd	19.24 a	53.93 b	6.98 ab	4.02 b
	Express	46.94 cd	17.66 de	16.28 a	53.90 b	6.17 a	3.63 b
N0	Mohican	47.90 e	15.92 ab	17.95 a	56.71 b	6.93 ab	3.97 b
	Lirajet	45.68 a	15.99abc	13.33 a	56.71 b	7.42 b	3.73 b
	Mansholt	49.09 f	17.94 e	60.33 b	9.09 a	6.19 a	4.47 b
	Capitol	45.91 ab	16.25 abc	16.98 a	53.53 b	7.21 b	4.04 b
	Prospa	46.77 bc	16.97 cde	19.78 a	52.86 b	7.02 ab	4.64 b
	Mean	47.00	16.60	22.36	49.44	6.87	3.72
	Bristol	45.65 c	17.80 a	15.68 a	58.22 cd	8.19 bcd	0.71 a
	Apex	43.42 a	20.07 c	21.22 a	50.81 bc	8.26 cd	3.55 b
	Express	45.62 c	19.60 bc	29.64 b	43.43 b	7.60 bc	2.60 ab
N1	Mohican	46.10 cd	17.81 a	17.57 a	58.79 d	7.36 ab	3.34 b
	Lirajet	43.57 a	18.23 a	15.02 a	52.73 cd	7.56 bc	3.37 b
	Mansholt	46.82 d	20.35 c	62.91 c	6.01 a	6.64 a	4.47 b
	Capitol	44.18 ab	18.58 ab	18.10 a	51.29 c	7.36 ab	3.05 b
	Prospa	44.60 b	19.65 c	22.29 ab	52.60 cd	8.80 d	2.86 b
	Mean	44.99	19.01	25.30	46.73	7.72	2.99 b
	Bristol	43.61 de	20.44 ab	18.72 a	56.70 b	8.45 de	4.62 b
	Apex	42.88 bcd	20.72 b	21.39 a	49.89 b	8.25 cde	3.98 ab
	Express	43.44 cde	21.87 cd	19.96 a	53.29 b	7.40 bc	4.13 ab
N2	Mohican	44.35 e	19.56 a	19.96 a	51.67 b	6.71 ab	2.20 a
	Lirajet	41.30 a	20.76 b	15.89 a	52.72 b	7.64 cd	2.90 ab
	Mansholt	43.78 de	23.20 e	63.51 b	10.20 a	6.43 a	4.27 b
	Capitol	42.35 b	21.00 bc	17.99 a	53.42 b	7.38 bc	3.02 ab
	Prospa	42.64 bc	22.11 d	22.58 a	52.12 b	8.83 e	3.45 ab
	Mean	43.05	21.21	25.00	47.50	7.64	3.57
	Bristol	45.70	17.90	16.46	57.91	7.90	2.21
	Apex	44.06	19.15c	20.62	51.54	7.83	3.85
	Express	45.33	19.71	21.96	50.21	7.06	3.45
Mean	Mohican	46.12	17.76	18.49	55.72	7.00	3.17
	Lirajet	43.52	18.33	14.75	54.05	7.54	3.33
	Mansholt	46.56	20.50	62.25	8.43	6.42	4.40
	Capitol	44.15	18.61	17.69	52.75	7.32	3.37
	Prospa	44.67	19.58	21.55	52.53	8.22	3.65
F test	N supply:	***	***	n.s.	n.s.	**	n.s.
	Cultivar:	***	***	***	***	***	*
	N x Cult:	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Oil-Protein correlation			**N0**: 0.30 n.s.		**N1**: 0.026 n.s.		**N2**: - 0.028 n.s.

As similar as oil content, constantly highest protein contents were shown by Mansholt at all N rates. The significantly lowest protein contents were shown by Bristol (N0 and N1), Mohican (N1 and N2) and Lirajet (N1) at different levels of N supply.

In the second field experiment (2001) the oil content among five genotypes varied in between 52 and 55% at N0, 50 and 54% at N1 and 47 and 51% at N2 supply (Tab. I-20). Constantly the highest oil content was produced by Mohican at all N rates. In contrast, Capitol at N0, Apex, Capitol and Lirajet, at N1 and Lirajet at N2 was shown the significantly lowest oil content. The variation among same genotypes in the protein content was in the rage of 14 and 15% at N0, 15 and 16% at N1 and 18 and 20% at N2 supply. Under low (N0) N supply, as a result of lowest oil content, Capitol had the highest protein content in the seed. At N1 and N2 supply the highest protein content was shown by Apex. On the other hand Mohican showed the lowest protein content at all N rates due to high oil accumulation in the seed.

The oil content among six genotypes varied in between 48 and 53% at N0, 47 and 51% at N1 and 45 and 49% at N2 supply in the last field experiment (2002) (Tab. I-21). The highest seed oil content was shown by DH4 at all N rates. At the same N levels, DH28 had the lowest oil content in the seed. Genotypic variation among same genotypes in protein content was in between 14 and 19% at N0, 16 and 20% at N1 and 19 and 23% at N2 supply. Corresponding to the highest oil content, the protein content was in the lowest amount by DH4 at three N rates. However, DH15 showed the highest protein contents in the seeds at the same N rates.

The other quality parameters i.e. glucosinolate (GSL) content (except in 2000) and fatty acid compositions (oleic, linolenic and erucic acid) were significantly different between N rates and among the genotypes in all three field experiments at Zuchtgarten (Tab. I-19, I-20, I-21). Significant interaction between N and genotype was found only in GSL content in 2001 (Tab. I-20) and linolenic acid content in 2002 (Tab. I-21). In the first field trail (2000) the mean GSL content among genotypes varied in between 15 and 60 µmol g^{-1} at N0 and 15 and 63 µmol g^{-1} at N1 and 16 and 64 µmol g^{-1} at N2 supply. Compared to other cultivars an extremely highest GSL contents were shown by Mansholt at all N rates which could be explain by that Mansholt is a very old variety. This genotype also produced the lowest seed yield at all N rates in 2000 (Tab. I-5). In spite of highest oil content, the oleic and linolenic acids contents of Mansholt were the lowest at all N rates compared to the other cultivars in 2000 (Tab. I-19).

Table I-20: Seed quality parameters of 5 rape cultivars as affected by N supply (N0: soil mineral N, N1: 120 kg N ha^{-1}, N2: 240 kg N ha^{-1}) at maturity at Zuchtgarten in 2001. Statistics: Separate analysis of variance. Means with the same letter are not significantly different. ***, **, *, and + indicate significance at $p < 0.001$, 0.01, 0.05, and 0.1

Site: Zuchtgarten **Year: 2001**		**Seed quality**					
		Oil	**Protein**	**GSL**	**Fatty acid composition [%]**		
		content	**content**	**content**	**Oleic**	**Linolenic**	**Erucic**
Treatment	**Cultivar**	**[%]**	**[%]**	**[µmol g^{-1}]**	**C18:1**	**C18:3**	**C22:1**
	Apex	53.24 bc	14.46 ab	14.81 c	65.44 a	9.69 b	5.62 c
	Capitol	51.99 a	15.04 b	11.56 b	66.21 a	10.50 c	2.66 a
N0	Mohican	54.82 d	13.87 a	11.10 b	66.07 a	9.89 b	3.25 ab
	Lirajet	52.61 ab	13.99 a	8.45 a	67.20 a	9.53 b	5.12 bc
	Bristol	54.24 cd	14.25 ab	9.33 a	66.78 a	8.42 a	3.89 abc
	Mean	53.38	14.32	11.05	66.34	9.61	4.11
	Apex	51.29 a	16.39 b	15.56 c	63.36 a	10.16 cd	7.00 b
	Capitol	51.00 a	16.06 ab	11.77 b	65.42 ab	10.58 d	4.09 a
N1	Mohican	54.07 b	15.14 a	11.92 b	68.25 c	9.25 b	3.92 a
	Lirajet	50.33 a	16.33 b	10.26 a	66.14 bc	9.88 c	4.46 a
	Bristol	53.36 b	15.29 a	10.07 a	65.79 abc	8.56 a	4.69 a
	Mean	52.01	15.84	11.91	65.79	9.69	4.83
	Apex	47.88 ab	20.44 c	20.33 c	63.95 abc	10.07 b	8.05 c
	Capitol	48.85 b	19.30 b	13.87 b	61.71 a	11.15 c	5.70 ab
N2	Mohican	50.82 c	18.26 a	14.29 b	65.06 bc	9.71 ab	4.82 a
	Lirajet	47.11 a	19.71 bc	14.56 b	66.30 c	9.74 ab	7.69 bc
	Bristol	51.26 c	18.27 a	11.72 a	62.70 ab	9.36 a	6.88 abc
	Mean	49.19	19.20	14.95	63.94	10.01	6.63
	Apex	50.80	17.10	16.90	64.25	9.97	6.89
	Capitol	50.61	16.80	12.40	64.45	10.74	4.15
Mean	Mohican	53.24	15.76	12.44	66.46	9.62	4.00
	Lirajet	50.02	16.68	11.09	66.55	9.72	5.76
	Bristol	52.95	15.94	10.37	65.09	8.78	5.15
F test	N supply:	***	***	***	**	n.s.	**
	Cultivar:	***	***	***	**	***	***
	N x Cult:	*	n.s	**	n.s.	n.s.	n.s.
Oil-Protein correlation			**N0**: - 0.69		**N1**: - 0.95 **	**N2**: - 0.90 *	

Table I-21: Seed quality parameters of 6 rape cultivars as affected by N supply (N0: soil mineral N, N1: 120 kg N ha^{-1}, N2: 240 kg N ha^{-1}) at maturity at Zuchtgarten in 2002. Statistics: Separate analysis of variance. Means with the same letter are not significantly different. ***, **, *, and + indicate significance at $p < 0.001$, 0.01, 0.05, and 0.1

Site: Zuchtgarten		**Seed quality**					
Year: 2002		**Oil**	**Protein**	**GSL**	**Fatty acid composition [%]**		
		content	**content**	**content**	**Oleic**	**Linolenic**	**Erucic**
Treatment	**Cultivar**	**[%]**	**[%]**	**[µmol g^{-1}]**	**C18:1**	**C18:3**	**C22:1**
	DH4	52.97 c	14.34 a	9.76 a	60.70 c	10.52 a	3.32 ab
	Apex	50.97 b	16.88 b	15.65 c	59.39 bc	10.91 ab	2.47 a
	DH42	48.25 a	19.12 c	15.55 c	60.05 bc	11.27 b	4.85 ab
N0	DH28	48.24 a	17.53 b	15.65 c	56.83 ab	12.04 c	5.19 ab
	DH15	49.77 b	19.31 c	12.47 b	54.53 a	13.02 d	5.41 b
	Capitol	50.01 b	17.58 b	9.37 a	57.79 bc	12.31 c	3.35 ab
	Mean	50.03	17.46	13.07	58.21	11.68	4.10
	DH4	51.05 c	16.36 a	10.86 a	59.43 c	11.18 ab	4.71 ab
	Apex	48.92 b	17.71 b	13.10 ab	59.55 c	11.64 bc	5.33 ab
	DH42	48.45 ab	19.18 cd	16.26 c	61.23 c	10.57 a	5.25 ab
N1	DH28	47.34 a	18.44 bc	15.04 bc	55.46 ab	12.17 cd	5.88 ab
	DH15	49.17 b	19.81 d	13.38 ab	54.35 a	12.43 d	6.50 b
	Capitol	48.98 b	18.42 bc	11.37 a	58.18 bc	11.84 cd	3.32 a
	Mean	48.99	18.32	13.34	58.03	11.64	5.17
	DH4	48.92 c	18.51 a	12.84 a	59.10 c	11.32 a	4.26 a
	Apex	48.09 c	19.72 b	14.43 ab	58.88 c	11.95 ab	5.43 ab
	DH42	46.71 b	20.97 c	18.25 c	58.10 bc	11.44 a	8.43 c
N2	DH28	44.48 a	21.11 c	18.20 c	53.09 a	13.06 d	9.50 c
	DH15	46.47 b	22.61 d	15.58 b	55.45 ab	12.78 cd	4.77 ab
	Capitol	46.37 b	20.85 bc	12.76 a	58.00 bc	12.30 bc	7.36 bc
	Mean	46.84	20.63	15.34	57.10	12.14	6.62
	DH4	50.98	16.40	11.15	59.74	11.01	4.10
	Apex	49.33	18.10	14.39	59.27	11.50	4.41
Mean	DH42	47.80	19.76	16.69	59.79	11.09	6.18
	DH28	46.69	19.03	16.30	55.13	12.42	6.86
	DH15	48.47	20.58	13.81	54.78	12.74	5.56
	Capitol	48.45	18.95	11.17	57.99	12.15	4.68
F test	N supply:	***	***	**	n.s.	**	**
	Cultivar:	***	***	***	***	***	**
	N x Cult:	n.s.	n.s.	n.s.	n.s.	**	n.s.
Oil-Protein correlation			**N0**: - 0.82 *		**N1**: - 0.61 n.s		**N2**: - 0.71 +

In the second field experiment (2001) the mean GSL content among genotypes varied in between 9 and 15 µmol g^{-1} at N0 and 10 and 16 µmol g^{-1} at N1 and 12 and 20 µmol g^{-1} at N2 supply (Tab. I-20). At three N rates the highest GLS and erucic acid contents were shown by Apex whereas the lowest GSL content was shown by Bristol. On the other hand, the lowest erucic acid contents were shown by Capitol and Mohican at all N rates. No significant differences were found among cultivars in oleic acid at N0. However, the highest oleic acid contents in the seed shown by Mohican at N1 and by Lirajet at N2. Constantly, Capitol had the highest linolenic acid contents at three N levels whereas Bristol showed the lowest linolenic acid contents at the same N rates.

The results of the last field experiment (2002) revealed that the GSL content among genotypes varied in between 9 and 16 µmol g^{-1} at N0 and 11 and 16 µmol g^{-1} at N1 and 13 and 18 µmol g^{-1} at N2 supply (Tab. I-21). Capitol showed significantly lowest GSL contents at all N rates. In terms of fatty acid composition results indicated that DH4 at N0, Apex, DH4 and DH42 at N1 and Apex and DH4 at N2 had the significantly highest oleic acid contents. The lowest oleic acid content and also the highest linolenic acid content were shown by DH15 at N0 and N1 supply. At N2, DH28 had the lowest oleic and the highest linolenic acid content in the seeds. At N0 and N1, DH15 had the highest erucic acid contents. However, at N2 supply, the significantly highest erucic acid contents were produced by DH42 and DH28. Apex at N0 and Capitol at N1 had the lowest erucic acid contents in the seeds. DH4 showed the lowest erucic acid contents at N2 supply.

4.9 Relationships between Seed Yield and N Efficiency Parameters

The correlation coefficients between seed yield and various N efficiency parameters of oilseed rape cultivars as affected by N supply were calculated for the field experiments in 2000 (A), 2001 (B) and 2002 (C) at Zuchtgarten (Tab. I-22). The grain yield correlated significantly positive with total N uptake at maturity under limiting N supply (N0) in the first (2000) and second (2001) field experiments indicating that high grain yield was achieved by high N-uptake efficiency that contributed to N efficiency (Tab. I-22 A, B). However, there was no relationship between N-uptake efficiency and grain yield in the last field experiment at N0 (Tab. I-22 C). In both field trails (2000 and 2001) the grain yield was negative correlated with total N uptake until beginning of flowering at N0.

Table I-22: Simple correlation coefficients between seed yield and various N efficiency parameters shoot characteristics of oilseed rape cultivars (8, 5 and 6 cultivars) as affected by N supply (N0: soil mineral N, N1: 120 kg N ha^{-1}, N2: 240 kg N ha^{-1}) at Zuchtgarten in 2000 (A), 2001(B) and 2002 (C). ***, **, *, and + indicate significance at $p < 0.001$, 0.01, 0.05, and 0.1

Site: Zuchtgarten		**Coefficient of correlation**		
		Treatment		
Year:	**N efficiency parameter**	**N0**	**N1**	**N2**
2000 (A)	• **N uptake**	**0.79 ****	**0.85 ****	**0.76 ***
	Beginning of flowering	- 0.26	0.34	- 0.46
	Beginning of flowering – End of Flowering	0.48	- 0.43	0.56
	Beginning of flowering – Maturity	0.60 +	0.52	0.39
	End of flowering – Maturity	0.16	0.74 *	0.39
	• **N-utilization**	**0.57 +**	**0.37**	**0.40**
	Biological Production Efficiency	0.61 +	0.17	- 0.42
	Harvest index	- 0.23	0.15	0.73 *
	N-Harvest index	- 0.38	- 0.19	0.14
	Seed N concentration	- 0.59 +	- 0.41	- 0.28
2001(B)	• **N uptake**	**0.95 ****	**0.34**	**0.45**
	Beginning of flowering	- 0.77 +	0.09	0.65
	Beginning of flowering – End of Flowering	- 0.48	- 0.05	0.82 +
	Beginning of flowering – Maturity	0.71	0.87 +	0.56
	End of flowering – Maturity	0.94 *	0.27	- 0.51
	• **N-utilization**	**- 0.22**	**0.52**	**0.57**
	Biological Production Efficiency	- 0.66	0.29	0.19
	Harvest index	0.56	0.53	0.57
	N-Harvest index	- 0.46	0.56	0.52
	Seed N concentration	- 0.20	- 0.42	- 0.45
2002 (C)	• **N uptake**	**0.25**	**0.92 ****	**0.80 ***
	Beginning of flowering	0.12	0.62	0.78 +
	Beginning of flowering – End of Flowering	0.16	0.51	0.36
	Beginning of flowering – Maturity	0.04	0.68 +	0.71 +
	End of flowering – Maturity	- 0.10	- 0.26	- 0.10
	• **N-utilization**	**0.80***	**0.87 ***	**0.49**
	Biological Production Efficiency	0.59	0.47	0.30
	Harvest index	0.36	0.69 +	0.29
	N-Harvest index	- 0.36	- 0.07	- 0.68 +
	Seed N concentration	- 0.85 *	- 0.79 +	- 0.86 *

However, significantly positive correlation between grain yield and the total N uptake was found from end of flowering until maturity at N0 (Tab. I-22 B). Furthermore, in terms of yield potential, high responsiveness in grain yield to supplied N also related with high N uptake at medium (N1) and high (N2) N supply in 2000 (Tab. I-22 A) and 2002 (Tab. I-22 C). The significant correlation at N1 was the result of the total N uptake during the reproductive growth (2000) whereas at N2 supply the N uptake up to flowering significantly correlated with grain yield (2002).

Besides of high N-uptake efficiency in the first field trail in 2000, N-utilization efficiency was also contributed to N efficiency under low N supply (N0). The parameters that contributed to N-utilization efficiency were the biological production efficiency (positive) and seed N concentration (negative) which was correlated with grain yields at N0. As well, although no contribution to N-utilization efficiency occurred, the harvest index (HI) positively correlated with grain yield at high N supply (N2) in 2000. However, no relationships between grain yield and N-utilization parameters were found in the second field trail (2001).

In the last field experiment (2002) correlation coefficient was significantly positive between grain yield and N-utilization efficiency under limiting N supply (N0) (Tab. I-22 C). The only N-utilization parameter that contributed to N efficiency was the seed N concentration which was negatively correlated with grain yield at low N supply (N0). As a result of positive correlation with HI and negative correlation with seed N concentration the grain yield was also significantly positive correlated with N-utilization at medium N supply (N1). Although significantly negative correlations between grain yield and N harvest index (NI) and seed N concentration at high N supply (N2), no significant contribution to N-utilization occurred.

5. Discussion

The aim in this chapter was to investigate the magnitude of genotypic variation for the nitrogen efficiency of winter oilseed rape cultivars and doubled haploid (DH) lines and determine the relationship between agronomic traits and both N efficiency components (N uptake and N utilization) which may be useful for indirect selection strategies.

5.1 Genotypic Differences in Nitrogen Efficiency

Genotypic difference in nutrient efficiency of crop plants is not a new issue, since it has been well known for at least 84 years (Hoffer, 1926; Smith, 1934). However, the discussion of genotypic differences in nutrient efficiency is complicated in the first place by the absence of a generally accepted definition of nitrogen efficiency, and the term is used in various ways in the literature. A genotype can be characterized as N-efficient either when realizing a yield above average under conditions of low or suboptimal N supply or when converting N fertilizer efficiently into yield under conditions of high N supply (Sattelmacher et al., 1994). In this work, N-efficient cultivars were defined as those realizing an above-average yield under suboptimal N supply (Graham, 1984), while cultivars having a high yield under optimum N supply were called “responsive”.

The result of the present study indicated that averaged over three experimental years and two sites (Zuchtgarten and Dragoneranger), highly significant ($P<0.001$) genotypic variation in grain yield among 12 rape genotypes (cultivars and DH lines) existed (Tab. I-4). Yield response to supplied N, i.e. the interaction between N and genotype, was highly significant ($P<0.001$). Based on seed yield at limiting N supply (N0), DH4 and Apex can be classified as N-efficient, while Prospa, Capitol and DH15 were N-inefficient genotypes. The other cultivars and double haploid (DH) lines attained medium seed yield at N0. The N-efficient genotype DH4 produced a high grain yield also at high N supply (N2) and was thus also responsive to N fertilization. This is in agreement with the results of Möllers et al. (1999) with oilseed rape and Anbessa et al. (2009) with barley who reported that the same cultivars were superior in grain yield at both low N and high N conditions.

Several studies also demonstrated that low yielding genotypes under suboptimal N supply can be responsive to applied N and hence convert the fertilizer N more efficiently into grain yield at high N supply (Yau and Thurling, 1987b; Lafitte and Edmeades, 1994b; Sattelmacher et al.,

1994). Similar result was shown in our study with the genotype Bristol, which had a rather low N efficiency (Tab. I-4), but showed high responsiveness in seed yield at high N supply. Consequently, all types of cultivars were present in this study: efficient or inefficient cultivars and responsive and non-responsive cultivars, whereby responsive cultivars could be efficient or inefficient. The genotypic variability to further determining the underlying mechanisms of N efficiency and responsiveness was, therefore, given in this study.

5.2 Factors Contributing to Genotypic Differences in Nitrogen Efficiency

The N efficiency of crops depends on two primary components: the uptake efficiency and the utilization efficiency (Moll et al., 1982). Moll et al. (1982) expressed uptake efficiency as the efficiency with which the soil N can be taken up by the plant (Nt/Ns) and utilization efficiency as the seed dry weight per unit of absorbed N fertilizer (Gw/Nt). Gw is the seed dry weight, Ns is N supply and Nt is total N in the plant at maturity. Genotypical differences in N efficiency are generally attributed to high N uptake and/or high N utilization (Sattelmacher et al., 1994).

In the present study the relationships between seed yield and N efficiency parameters have clearly shown that the high N efficiency in grain yield under limiting N supply (N0) was related more closely to N-uptake efficiency than utilization efficiency in both field experiments in 2000 and 2001 at Zuchtgarten (Tab. I-22). On the other hand, no relationship between grain yield and N uptake efficiency was found in the last field experiment (2002) at N0, where N efficiency was significantly correlated with N-utilization efficiency. In terms of yield potential, high responsiveness of the genotypes in seed yield production was positively correlated with high N uptake at N2 supply in the field experiments in 2000 and 2002 (Tab. I-22). Similar result was shown by Möllers et al. (1999) who reported a close correlation between total N uptake and seed yield among 18 winter oilseed rape genotypes at low and high N fertilizer supply.

5.2.1 Nitrogen Uptake Efficiency

Our results in two field experiments (Tab. I-22) have clearly demonstrated that N-uptake efficiency is an important agronomic trait for genotypic differences among oilseed rape cultivars in N efficiency under conditions of limiting N supply (N0). The N uptake until flowering was mainly negatively correlated with grain yield in both field experiments in 2000

and 2001 (Tab. I-22 A, B) under limiting N supply (N0). However, a positive significant correlation between N uptake and seed yield occurred during reproductive growth at N0. The differences in N uptake among two contrasting rape cultivars amounted to 20 kg N ha^{-1} in 2000 (Tab. I-12), 18 kg N ha^{-1} in 2001 (Tab. I-13) and 28 kg N ha^{-1} in 2002 (Tab. I-14) from beginning of flowering till maturity at low N supply. All these results clearly indicate that high N efficiency was achieved by the N-efficient cultivars (e.g. Apex) which maintained high N-uptake activity during the reproductive growth under low N supply. This is in agreement with the field studies of Wiesler et al. (2001b) who reported that grain yield under conditions of low N supply was significantly correlated with N uptake differences that varied among genotypes (25 kg N ha^{-1} for maize and 41 kg N ha^{-1} for oilseed rape) during reproductive growth (beginning of flowering until maturity). Another study by Worku et al. (2007) clearly demonstrated that high grain yield of maize hybrids under low N were consistently positively related with higher post-anthesis N uptake, whereas there was no correlation between N uptake before anthesis and grain yield.

To maintain high N-uptake activity during reproductive growth, the N-efficient cultivars might have a more resourceful and vigorous root growth that might be enabled by continuous assimilate allocation from vegetative tissues (Jackson et al., 1986). Wiesler and Horst (1992) demonstrated that the genotypic differences among ten maize hybrids in N uptake efficiency were achieved by vigorous root growth under low N conditions. Bänziger et al. (2002) revealed that preventing N remobilization from vegetative parts or delayed leaf senescence during grain filling is desirable for continued photosynthesis particularly under low N conditions.

5.2.2 Nitrogen Utilization Efficiency

In the present study the other primary N efficiency component, N-utilization efficiency, was calculated as grain dry weight per unit of absorbed N as described by Moll et al. (1982). A further investigation of N-utilization efficiency was performed by subdividing N-utilization efficiency into various utilization parameters which are considered to be interrelated with dry matter accumulation or partitioning (i.e. biological production efficiency and harvest index) and/or N partitioning and utilization for seed growth (i.e. N harvest index and seed N concentration).

Although generally a high positive correlation was found between N uptake and N efficiency in the first field experiment (2000), the correlation between grain yield and N utilization was also significant under limiting N supply (N0). This could be due to one of the high yielding cultivars (i.e. Bristol) which had the lowest N uptake from end of flowering till maturity at N0 (Tab. I-12). Due to the low uptake during reproductive growth Bristol had the significantly lowest shoot N concentration (Tab. I-9) whereas it produced a high shoot dry matter at maturity indicating that high biological production efficiency (Tab. I-16) contributed to N utilization efficiency. This was also clearly confirmed by the significant correlation between grain yield and biological production efficiency at N0 (Tab. I-22 A).

In the last field experiment (2002) no relationship was found between grain yield and N uptake at limiting N supply (N0), but a significantly positive correlation between grain yield and N utilization (Tab. I-22 C), indicating that N-utilization efficiency is an important agronomic trait for genotypic differences among newly introduced DH lines in N efficiency at N0. The ability to convert N into grain yield, i.e. utilization efficiency, was significantly higher for the genotype DH4 as compared to other genotypes under low N conditions (Tab. I-15). This genotype had the significantly highest grain yield (Tab. I-5); similar to Bristol it had a high shoot dry matter (Tab. I-3) together with the lowest shoot N concentration (Tab. I-11) at maturity indicating that high biological production efficiency (Tab. I-16) contributed to N utilization efficiency. A similar result was shown by Yau and Thurling (1987) who demonstrated that the significant genotypic variation among 40 genotypes in seed yield was highly correlated with total shoot dry weight at maturity which in turn was related to the growth rate that contributed to high N utilization efficiency at low N.

Sattelmacher et al. (1994) indicated that partitioning of N within the plant and efficient utilization of N at the cellular level are contributing factors for N-utilization efficiency when the supply of N is limited. In the present study Bristol in 2000 (Tab. I-18 A) and DH4 in 2002 (Tab. I-18 C) had the lowest seed N concentrations (Tab. I-18 C) compared to other genotypes, clearly indicating a high N utilization efficiency of Bristol and DH4. This was explicitly confirmed by the significant negative correlations between N utilization efficiency and seed N concentration that occurred at limiting N supply in 2000 and 2002 (Tab. I-22 A, C). Our result corroborated the results of Sinebo et al. (2004) who reported a negative correlation between grain yield and seed N concentration of barley genotypes. The

authors further revealed that the grain N concentration was correlated negatively with N utilization which is consistent with our results.

In a nutrient solution study Yau and Thurling (1987b) indicated that the more efficient spring rape genotypes had lower N concentrations in old leaves but higher concentrations in the young leaves than the less efficient genotypes at low N supply. Accordingly, they concluded that N remobilisation was a major determinant of N utilization efficiency. In agreement with this study our result clearly indicated that under limiting N supply the N retranslocation from the source organs to the seeds i.e. N harvest index (NHI) was comparatively higher (83%) than NHI found in several other studies (70% in Schjoerring et al. 1995; 73% in Sieling and Kage, 2007). Generally, a high NHI was found at low N supply (N0), indicating that this trait was probably not limiting for yield differences among genotypes. This was also confirmed by the fact that there was no correlation between NHI and grain yield (Tab. I-22 C).

5.2.3 Yield Components and Yield Quality Parameters

The result of the field experiment in 2000 clearly indicated that no significant differences were found in plant density between N rates but cultivars differed significantly at all N rates (Tab. I-7). There was no constant relationship between high yielding (e.g. Apex and Express) or low yielding (e.g. Mansholt and Prospa) genotypes and plant density. Significant differences between N supply and among cultivars also occurred in the number of pods per plant. Although slight relationship between high yielding genotypes and number of pod per plant occurred, which might have contributed to high N-uptake (Apex) or high N-utilization (Bristol) efficiency, the highest pod number per plant was produced by the N-inefficient genotype Prospa at three N rates. This could be the result of the lowest plant numbers since several studies demonstrated that the number of pods per plant was negatively correlated with the number of plants per unit area (Geisler and Stoy, 1987; Leach et al., 1999; Sieters et al., 1987).

In our study the number of seeds per pod decreased with increasing N supply which could be explained by reducing the assimilate availability by earlier formed pods for later formed seed set in the pods (Tayo and Morgan, 1979). High yielding genotypes tended to produce high seed numbers per pod under low N supply which was related both to high N utilization (Bristol) and N uptake (Apex and Express). Usually, oilseed rape contains from 18 to a maximum of 35 seeds per pod depending on variety (Peach and Morgan, 1983; Mendham et

al., 1984). Our results corroborated these seed number per pod in two field experiments. As a result of decline in seed number per pod a higher thousand grain weight was shown by the N-inefficient genotypes Capitol and Prospa at three N rates (Tab. I-7 and I-8). However, there was no relationship between grain yield among genotypes and thousand grain weight. This was also true for the genotypic differences in thousand grain weight in 2001 (Tab. I-18). In conclusion, no clear relationship between N efficiency and a single yield component was found. Number of seeds per pod was related best to yield under limiting N supply (N0) (Tab. I-17), however, significant genotypic differences in this trait could not be proven.

The seed quality was significantly affected by the different levels of N supply at three field experiments (Tab. I-19, I-20 and I-21). Increased N supply resulted in a decline in oil content while protein content increased, which was also demonstrated by Barlog and Grzebisz (2004) and Rathke et al. (2006). These results also corroborated those of Zhao et al. (1993) who indicated a negative correlation between oil and protein content in rapeseed between N rates. The N utilization-efficient and responsive cultivar Bristol showed high oil but low protein contents at all N rates (Tab. I-19), which is in line with its low seed N concentrations (Tab. I-18). This could be due to a high photosynthetic activity of pod hulls that might cause a better assimilate translocation to the grains thus producing higher oil contents. Similar results were shown by the N utilization-efficient and responsive genotype DH4 at three N levels (Tab. I-21). The N-efficient genotypes Apex and Express in the field experiment in 2000 had high protein contents, probably caused by their high total N uptake at maturity at all N rates (Tab. I-12, I-13 and I-14). Since oil contents not necessarily decreased with high protein concentrations, it can be concluded that N-efficient cultivars can attain a high seed quality, regardless, if they are N uptake- or N utilization-efficient.

CHAPTER II

SIGNIFICANCE OF ROOT GROWTH AND MORPHOLOGY FOR GENOTYPIC DIFFERENCES IN NITROGEN EFFICIENCY OF OILSEED RAPE (*BRASSICA NAPUS* L.)

1. Abstract

In field experiments performed over three years (2000, 2001 and 2002) and at two sites near Göttingen highly significant ($P<0.001$) genotypic variation in grain yield was found among 12 rape genotypes (cultivars and double haploid (DH) lines) at different nitrogen (N) rates. High grain yield and thus high N efficiency under limiting N (N0) supply significantly correlated with total N uptake and particularly N uptake during reproductive growth. It was hypothesized that N-efficient cultivars may be characterized by a more efficient and vigorous root growth, especially during reproductive growth at low N supply. The aim of this study was to determine the significance of root growth and morphology for genotypic differences in N efficiency of oilseed rape cultivars and DH lines. Two different root methods were examined at three N rates (N0: soil mineral N, N1: 120 kg N ha^{-1}, N2: 240 kg N ha^{-1}) at Zuchtgarten. Soil cores were taken at shooting, flowering and end of flowering in 2000, 2001 and 2002 to examine total root-length density and the distribution of roots in different soil layers. Rhizotrons were installed into the field to investigate non-destructively the formation of new fine roots from beginning of shooting until maturity in two-week intervals in 2000 and 2002. Total root length (core) was not significantly different between N rates whereas highly significant differences in total root counts (rhizotrons) were found. Total root counts were usually higher at N0 than at N2. Both methods revealed that roots were usually concentrated in the topsoil particularly at 0-15 and 15-30 cm soil depths. Roots were detected up to 90 cm soil depth (core) whereas new roots (rhizotron) could be detected up to 30, 45 and 60 cm soil depths at shooting, flowering, and end of flowering, respectively. Cultivars differed significantly in total root length, root-length densities, total root counts and root-count densities. The N-efficient cultivars were characterized by higher root-length densities and higher new fine root formation than the N-inefficient ones particularly in the top-soil layers. All these results indicate that high N-uptake efficiency under limiting N (N0) supply was associated not only with root growth during the reproductive growth. The high N-uptake efficiency was achieved by the cultivars which had a generally vigorous root growth during the whole vegetation period and irrespective of the level of N supply.

Key words: *Brassica napus* L., genotypic variation, cultivar, DH line, N efficiency, root length, root turnover, N_{min}, rhizotron.

2. Introduction

Nitrogen uptake is regulated by the demand of the growing crop if N supply is not limited (Clarkson 1985). In contrast, if the required N is limited in the soil, the N uptake depends on the extent and effectiveness of the root system (Jackson et al., 1986) so that the cultivars with a deeper root system and higher root-length densities deplete soil nitrate-N more (Wiesler and Horst, 1994; Oikeh et al., 1999). Therefore, morphological and physiological root characteristics such as inflow rate, maximum rooting depth, root radius, root length and root-length density at deeper soil layers might play a primary role for N-uptake efficiency (Claassen et al., 1986; Sattelmacher et al, 1994).

Due to its high ability to take up N amounting to almost 40-80 kg N ha^{-1} before winter (Cramer, 1993), winter oilseed rape (*Brassica napus* L.) can be characterized as a catch crop to reduce N leaching compared to cereals (Sieling and Kage, 2008). This might be due to its high capacity to take up nitrate from the soil (Malagoli et al., 2005), since the peak rate of nitrate uptake is usually higher in *Brassicas* than in many other catch crop families (Lainé et al., 1993). Despite a high capacity to take up nitrate from the soil, many authors have reported that oilseed rape has a very low N recovery among field-grown crops and, usually, only about 50% of the applied fertilizer N is recovered in the harvested seeds whatever the level of N fertilizer applied (Augustinussen, 1987; Schjoerring et al., 1995). Therefore, in European agriculture, winter oilseed rape is characterized by low recoveries of soil and fertilizer N in harvested organs, i.e. largest N-balance surplus as compared to other agricultural crops (Gäth, 1997).

The large N-balance surplus is mainly due to the characteristics of the traditional oilseed rape cultivars which always show a high N uptake until flowering, low N uptake during reproductive growth and incomplete N retranslocation from the source organs to the seeds (Aniol, 1993; Lickfett, 1993), leaving high soil mineral N contents and high N amounts in crop residues in the field (Aufhammer et al., 1994; Lickfett et al., 2001). An improvement in fertilization and soil and crop management practices may help to improve the N efficiency of this crop in both low- and high-input agricultural systems (Wiesler et al., 2001b). Among these, breeding and cultivation of N-efficient cultivars could contribute to a reduction of the large N balance surpluses of this crop (Schulte auf´m Erley et al., 2007) and thus optimize yields and minimize the environmental impact in high-input agriculture (Lynch, 1998). However, to facilitate the breeding process of N-efficient cultivars, the identification of

secondary plant traits correlating with N efficiency is necessary (Schulte auf´m Erley et al., 2007). An in-depth understanding of the physiological mechanisms leading to a high N efficiency is, thereby, a main pre-requisite to identify meaningful secondary plant traits.

Since it was found that maintaining a high N uptake activity during reproductive growth is an important characteristic of N-efficient cultivars (Behrens, 2002; Chapter I), the question remains how this trait is achieved in those genotypes. The "alternative rape ideotype", characterized by high N uptake efficiency during late growth phases, needs more efficient and vigorous root growth. Thus, root growth and morphology could play an essential role in N-uptake efficiency. Therefore, the aim in this study was to determine the significance of root growth and morphology for genotypic differences in N efficiency of oilseed rape. To check our "alternative rape ideotype" hypothesis, two different methods were examined to characterize the root growth and morphology of oilseed rape cultivars under different levels of N supply.

The root system is dynamic, and its net growth is a result of root production and mortality (Kamh et al., 2005). Root production depends on a number of factors, *e.g.* carbohydrate supply from the shoot (Thaler and Pages, 1998) and nutrient supply in the growth medium (Forde and Lorenzo, 2001). Due to the inaccessibility of the root system, different methods were studied to determine the root morphological and physiological characteristics of various plant species. Some of the studies used destructive root methods such as soil coring (Barraclough, 1989), in-growth core (Steingrobe et al., 2000; Kamh et al., 2005), whole root system excavation (Böhm, 1978), and trenching (Parker et al., 1991), while non-destructive root methods like rhizotrons and minirhizotrons (Bates, 1937; Taylor, 1987; Hendrick and Pregitzer, 1992; Box, 1996) can be used more widely as alternative quick methods. There are also a few root studies that used both methods together to compare and calibrate the relative data obtained by the minirhizotron method with the absolute data that can be obtained by the core method (Box and Ramseur, 1993; Wiesler and Horst, 1994).

In the present study, to determine the significance of root growth and root morphology for genotypic differences in nitrogen efficiency of winter oilseed rape cultivars and double habloid (DH) lines at different levels of N supply, both the root core and the rhizotron method were studied in three field experiments (2000, 2001 and 2002) at Zuchtgarten. The core method was applied each year of the study, whereas the rhizotron method was studied only in

the field experiments in 2000 and 2002, but for a higher number of genotypes. It was hypothesized that N-efficient cultivars are characterized by higher root growth rates especially during and after flowering.

3. Materials and Methods

3.1 Description of the Experimental Site

Root growth and distribution within the soil profile were studied in the field experiments conducted in the 1999/2000, 2000/2001 and 2001/2002 cropping periods at Zuchtgarten by the Institute of Plant Nutrition, Leibniz University of Hannover in cooperation with the Institute of Agronomy and Plant Breeding, University of Göttingen. The experimental station Zuchtgarten is located near to Göttingen (51.32° northern latitude and 09.56° eastern longitude). A detailed description of the experimental site and the growing conditions can be found in Chapter I.

Two different methods were used for root investigations in these experiments: Root length was determined in soil cores, and a non-destructive method was used by regularly counting roots in pre-installed rhizotrons.

3.2 Core Method

Soil cores were sampled at the beginning of shooting, beginning of flowering and end of flowering in the field experiments in 2000 and 2001. In the last field experiment (2002) the method was applied only at the beginning and end of flowering. Two contrasting oilseed rape cultivars; Apex (N-efficient) and Capitol (N-inefficient), were compared at low (N0: soil mineral N) and high (N2: 240 kg N ha^{-1}) N supply in 2000. The study was performed in the second year by comparing three rape cultivars (Apex, Capitol and Mohican) at three levels of N supply; low N (N0: soil mineral N), medium N (N1: 120 kg N ha^{-1}) and high N (N2: 240 kg N ha^{-1}). In the last field experiment, Apex and Capitol were compared again at N0, N1 and N2. In addition, four double haploid (DH) lines, DH4, DH15, DH28 and DH42, were included in the study only at N0 at the beginning of flowering.

3.2.1 Sampling of Soil Cores

Soil cores were taken immediately after intermediate harvests performed at the beginning of shooting, beginning of flowering, and end of flowering (see Chapter I) from the freshly harvested area. First, the long heavy steel tubes (9 cm diameter, 90 cm length) were driven into the soil with the aid of a portable electrical compressor hammer (Makitta HM1800) (Fig. MM II-1). This machine was externally energy-supplied on the field by a self-constructed generator. Due to the spatial variability of the root system, samples were taken at three positions in the plot between and within the plant rows (twice between the rows and once within the row).

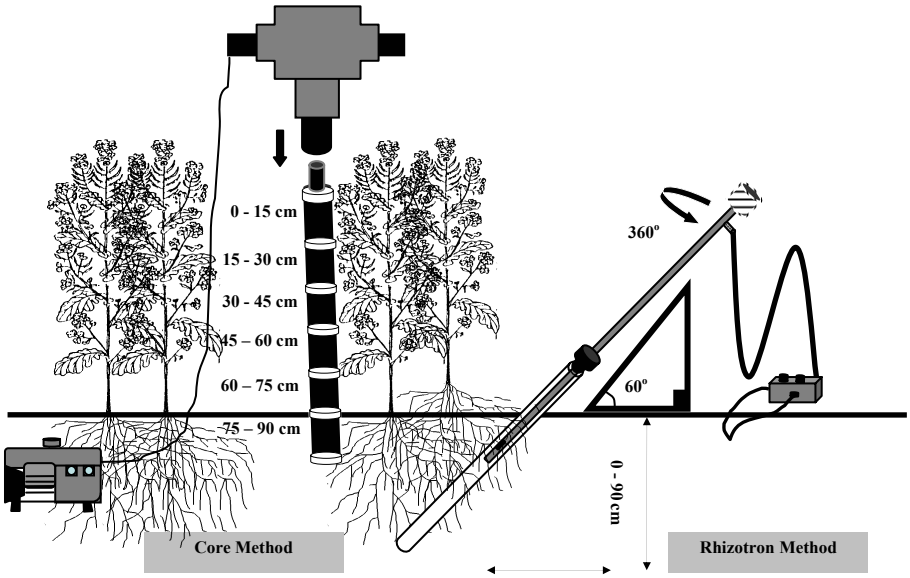


Figure MM II-1: Illustration of two root investigation methods applied on the field to assess the significance of root growth and root morphology for genotypic differences in nitrogen efficiency of oilseed rape cultivars. Left: Illustration of soil core sampling; right: Illustration of the installation of rhizotrons for non-destructive root counting.

The tubes were pulled from the soil manually with the aid of a mechanical puller. After removing the steel tubes from the soil, the 90-cm long soil cores were cut into 15-cm intervals and removed from the tubes separately. Each soil-core interval was placed separately in a sealed polyethylene bag and kept in a cool-box for the transport from Göttingen to Hannover. The core samples were stored under refrigeration at +5 °C until root washing.

3.2.2 Determination of Mineral Nitrogen Content (N_{min}) in the Soil Cores

From the soil cores extracted from 0-90 cm soil depth and separated into the different soil depths (0-15, 15-30, 30-45, 45-60, 60-75, and 75-90 cm soil depth), a sub-sample was taken from each core for the N_{min} determination. Each sub-sample was placed separately in a sealed polyethylene bag and kept in a cool-box for the transport from Göttingen to Hannover. The samples were stored under refrigeration at +5 °C until N_{min} extraction. In the laboratory the core sub-samples were sieved and from each sieved soil sample a sub-sample of 50 g fresh weight was taken. After that, the sub-samples were shaken for one hour in 200 ml extraction solution (0.1 M KCl). All samples were filtered through blue ribbon filter paper. In all extracts mineral N was determined as ammonium-N and nitrate-N (mg l^{-1}) by colorimetric methods using an autoanalyzer (Technicon Autoanalyzer II, Brahn and Lübbe, Norderstedt).

3.2.3 Root Washing

Because of the high silt and clay content of the soil the roots were separated from the bulk soil by hand washing with the aid of hydrogen peroxide (H_2O_2 30%) as chemical dispersing agent. In detail, each core sample was transferred in a 5 L vessel filled with water and 150 ml hydrogen peroxide and soaked overnight. The soaked samples were agitated gently under flowing water. To minimize root loss, two types of sieves were used. A small hand sieve (0.4 mm diameter) was used to collect the roots from the water poured out of the vessel. Another big sieve (15 x 15 cm length and 0.4 mm diameter) was placed below a second vessel to catch the overflowing roots from the first sieve. Roots were freed from the bulk soil by repeated washings, including filling the vessel with water and sieving until no roots remained in the vessel. After this repeated process the roots collected on both sieves were transferred to 250 ml plastic boxes filled with water. Afterwards, all the samples were stored in a freezer until root measurements.

3.2.4 Root-Length Determination

The plant roots extracted from the soil were removed from the freezer and thawed. Roots were cut into small pieces and homogenized in a 6 L water-filled vessel. After agitating shortly, heavy soil, sand fractions and heavy seeds precipitated quickly (mechanical rotation technique, Schuurman and Goedewaagen, 1971). From this homogenized medium, either a 300 ml sub-sample was taken for root-length determination using the line-intersection method

(Tennant, 1975) or around 150 ml for the root image analysis. The precise weight of the sub-sample was recorded in order to be able to calculate the fraction of the sub-sample in relation to the whole sample. **T**he roots obtained from the field experiment in 2000 were measured by the Tennant Line Intersect Method and the roots from the other two field experiments (2001 and 2002) were measured by the Root Image Analysis System (see below).

For the Tennant method the 300 ml sub-sample was spread on a glass tray with a 2 cm grid square. To improve the contrast of roots, a black nylon sheet was placed under the glass tray and artificial light was used during counting. Roots were placed with minimum overlapping on the glass tray. Roots were counted as the total number of intersections between the roots and the horizontal (H) and vertical (V) grid lines using a manual counter. A count of 1 was assigned when a root crossed a line or touched a line. Curved root portions which lie on or along a grid line were assigned as two countings. After each measurement, the sub-sample was poured back into the vessel and a new sub-sample was taken. After 4 replications a mean value for root length was calculated. The relationship between root length and the number of root intersections with the grid lines is given by:

Root length (cm) = π/4 x no. of intersects x grid unit (2 cm).

To optimize working efficiency at an acceptable random error, the grid size should be chosen to obtain about 400 intercepts per sample (Van Noordwijk, 1993). For our measurement the grid size was chosen to obtain about 300 intercepts per sample.

For root image analysis, the software WinRHIZO (WinRHIZO Pro V. 2002c Regent Instruments Inc. Quebec, Canada) was used. For the calculation of root length and morphology parameters with WinRHIZO, a digital image is required. For this, roots of the 150 ml sub-sample were spread on the on a shallow transparent plastic tray (20 x 30 cm) and scanned from below by a flatbed optical scanner (Epson Expression STD 1600+ Regent Instruments Inc.). The obtained picture was a grey level image with a resolution of 300 dpi (dots per inch). When the scanning process was completed, the image was saved for further calculations. Afterwards, the sub-sample in the transparent tray was refilled into the 6 L water filled vessel and another sub-sample for scanning was taken. For each root sample four replications were scanned. With the WinRHIZO software, both root length according to Tennant (1975) method and root morphological parameters (root diameter, root tips, root surface area) were obtained. Unwanted objects like soil particles, etc. were removed from the

calculation by image smoothing and by discarding objects with a length/width ratio smaller than 4. The threshold value to distinguish between roots and the background was set manually to a grey level value of 222 that turned out in calibration tests to give the most reliable results.

3.3 Rhizotron Method

Root monitoring in rhizotrons was performed from beginning of shooting till maturity in two-week intervals in the field experiments in 2000 and 2002. Four rape cultivars (Apex, Bristol, Capitol and Lirajet) were examined at N0 and N2 supply in 2000, whereas only two contrasting cultivars, Apex and Capitol, were compared at N0, N1 and N2 supply in the last field experiment (2002).

3.3.1 Installation of Rhizotrons into the Soil

The technique for installing the transparent plexiglas tubes (rhizotrons) in an undisturbed soil profile in the field is critical for rhizotron observations. The main concern is to establish good contact between the tube and the surrounding soil. In both field studies in 2000 and 2002 three rhizotrons (outside diameter: 3.0 cm, inner diameter: 2.4 cm, length: 124 cm) per research plot were installed into the soil up to 90 cm soil depth at an angle of 60°. This was done after emergence of the rape plants to prevent root damaging. The tubes were installed between the plant rows and around 1 m from the adjacent end of the plot. To prevent light and temperature effects the upper 10 cm of the tubes which remained above the soil surface were coated with aluminium foil.

3.3.2 Root Counting in the Rhizontrons

From the beginning of shooting up to maturity, root counts were carried out in 7-14 days intervals with the aid of an endoscope called rhizoscope (Richard Wolf GmbH, Knittlingen, Germany) with 159 cm length and 1.5 cm diameter. Light was provided by an external light projector and conducted to the top of the endoscope over fiber-glass cables. To quantify the root counts, cutting of roots at 7.5 (0-15), 22.5 (15-30), 37.5 (30-45), 52.5 (45-60), 67.5 (60-75) and 82.5 (75-90) cm soil depth with a crosshair engraved in the optic of the rhizoscope were counted for the whole perimeter of the rhizotrons.

4. Results

4.1 Root Growth and Morphology

4.1.1 Total Root Length, Root Length Densities and Soil Mineral Nitrogen Content in the Soil Profile Determined in Soil Cores

Total root length of oilseed rape cultivars from 0 to 90 cm soil depth as affected by N supply (low (N0), medium (N1) and high (N2)) in the field experiments in 2000, 2001 and 2002 at Zuchtgarten is shown in Figure II-1. The results indicated that no significant differences in total root length between N rates occurred, neither at the beginning of flowering nor at the end of flowering in three field experiments. In the first field experiment (2000), averaged over cultivars, total root length amounted to about 27 km m^{-2} at N0 and 30 km m^{-2} at N2 at the beginning of flowering. At the end of flowering plants slightly increased their total root length (1.0 km m^{-2}) at N0 while a reduction in total root length occured (4.0 km m^{-2}) at N2. Neither at the beginning of flowering nor at the end of flowering significant differences among two contrasting rape cultivars (Apex: N-efficient Capitol: N-inefficient) in total root length were found at two N rates.

Compared to the previous field experiment, total root length was increased by almost 44% at N0 and 43% at N2 in the second field experiment (2001) at the beginning of flowering. At this stage total root length amounted to 39 km m^{-2} at N0, 40 km m^{-2} at N1 and 43 km m^{-2} at N2 supply. Similar to the previous year a decline in total root length was found at the end of flowering in 2001. However, under limiting N supply (N0) the total root length remained constant while slight root reductions were found at N1 (3.0 km m^{-2}) and N2 (1.0 km m^{-2}). Although similar and higher total root lengths tended to be shown by Apex and Mohican compared to Capitol at both growth stages and at all N rates, significant differences were found only at the end of the flowering under moderate (N1) N supply.

In contrast to the other two field trials, an increase in total root length (3% at N0, 19% at N1 and 17% at N2) from the beginning of flowering up to the end of flowering was found in the last field experiment (2002) at all N rates. Averaged over cultivars the total root length increased from 39 to 40 km m^{-2} at N0, 37 to 44 km m^{-2} at N1 and 36 to 42 km m^{-2} at N2 from the beginning until the end of flowering.

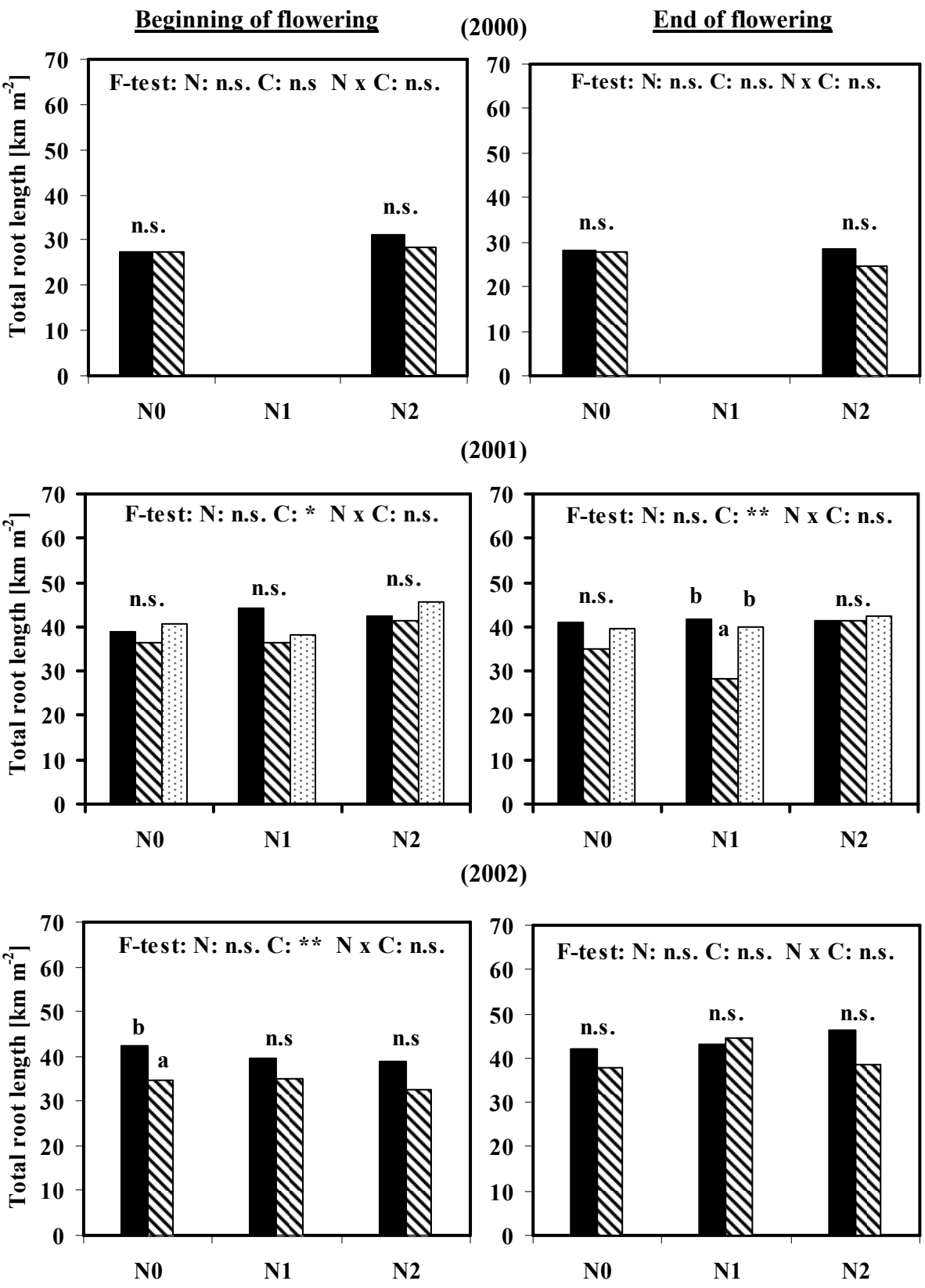


Figure II-1: Total root length of oilseed rape cultivars (Apex: ■, Capitol: ▨, Mohican: ⬚) as affected by N supply (N0: soil mineral N supply, N2: 240 kg N ha^{-1}) at different growth stages at Zuchtgarten in 2000, 2001 and 2002. Statistics: Separate analysis of variance for different growth stages. Means with the same letter are not significantly different at $\alpha = 0.05$

Significant differences among two cultivars in total root length occurred at the beginning of flowering, especially at low N (N0) supply. Under this N condition Apex produced almost 7 km m^{-2} more roots than Capitol, however, Apex tended to have a higher total root length than Capitol at all N rates. Similar results were found among these cultivars at the end of flowering particularly at N0 and N2. Clear cultivar differences in total root length were found when six different genotypes (Apex, Capitol, DH4, DH15, DH28 and DH42) were compared at the beginning of flowering only under conditions of low N (N0) supply in the last field experiment (2002) (Fig. II-2). Genotypes differed significantly in total root length and varied between 35 and 47 km m^{-2} at N0. The highest total root lengths were produced by Apex, DH15 and DH42 whereas the lowest root lengths were produced by Capitol, DH4 and DH28.

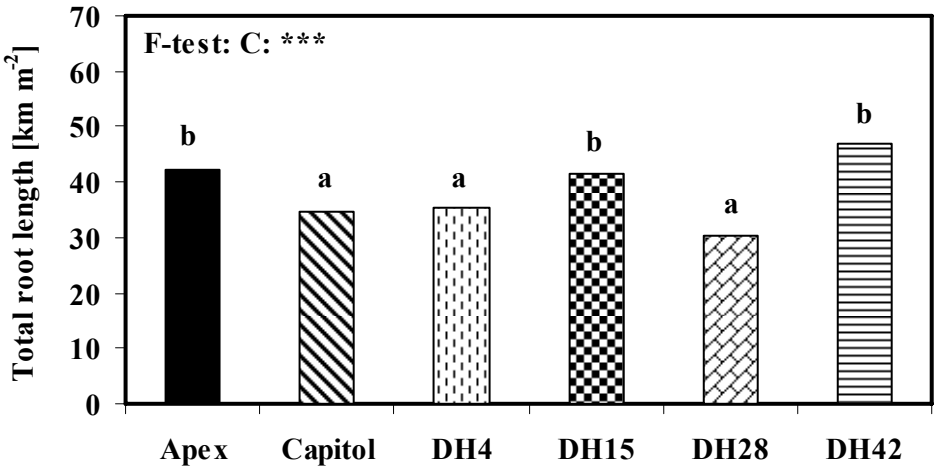


Figure II-2: Total root length densities of six oilseed rape cultivars at low N supply (N0: soil mineral N) at the beginning of flowering at Zuchtgarten in 2002. Statistics: Separate analysis of variance for different growth stages. Means with the same letter are not significantly different at $\alpha = 0.05$

Distribution of the total root length at different soil depths, i.e. root length density, of two contrasting rape cultivars (Apex and Capitol) as affected by low N (N0) and high N (N2) supply in 2000 is shown in Figure II-3. At the beginning and the end of flowering, roots of both cultivars were able to penetrate the soil down to a depth of 90 cm. At both N treatments, highest root length densities were produced at 0-15 cm and 15-30 cm soil depth. Furthermore, at the beginning of flowering and end of flowering, the root length densities were higher at 15-30 cm than 0-15 cm soil layers at N0 and N2. At the beginning of flowering Apex produced a significantly higher root length density than Capitol at 60-75 cm soil depth at N0 and at 45-60 cm at N2 supply. At the end of flowering Apex usually tended to have a higher root length density than Capitol, although a significant difference was found only at 0-15 cm soil depth at N2.

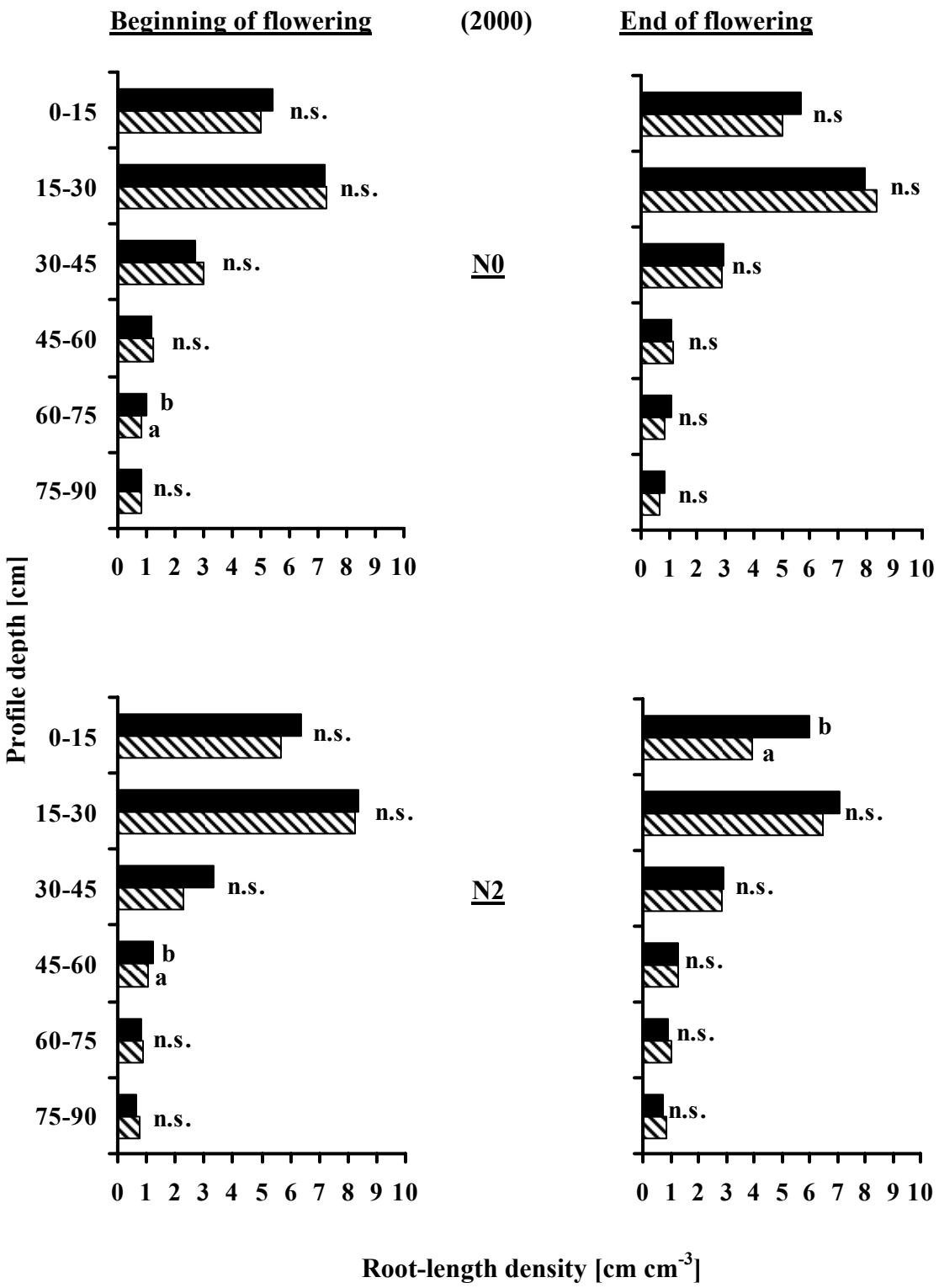


Figure II-3: Root length densities of two oilseed rape cultivars (Apex: ■, Capitol: ▨) as affected by N supply (N0: soil mineral N supply, N2: 240 kg N ha^{-1}) at different growth stages at Zuchtgarten in 2000. Statistics: Separate analysis of variance for different growth stages and soil layers. Means with the same letter are not significantly different at $\alpha = 0.05$.

Figure II-4 shows the total mineral N (N_{min}) in 0-90 cm soil depth and the distribution of the total N_{min} at different soil layers of two contrasting rape cultivars (Apex and Capitol) as affected by low N (N0) and high N (N2) supply in the first field experiment (2000). Averaged over cultivars the remaining nitrogen in the soil (N_{min}) amounted to about 16 kg N ha^{-1} at low N (N0) and 83 kg N ha^{-1} at high N (N2) conditions at the beginning of flowering. Total N_{min} increased by almost 2 kg N ha^{-1} at N0, indicating that only newly mineralized N was taken up during this period, whereas a substantial reduction (54%) from 83 to 38 kg N ha^{-1} occurred at N2 during flowering. At both growth stages, under limiting N (N0) supply most of the soil N_{min} was found at 0-45 cm soil depth whereas at high N (N2) supply most soil N_{min} was found at 0-15 cm soil depth. High soil N_{min} particularly at 0-15 cm at N2 could be the result of soil dryness that caused a reduction in root-length density particularly at 0-15 cm soil depth at both growth stages (Fig. II-3).

Although the "N-efficient" cultivar Apex tended to leave lower N_{min} amounts at 0-90 cm soil depth than the "N-inefficient" cultivar Capitol, no significant differences were found neither at the beginning of flowering nor at the end of flowering at low N (N0) supply in 2000 (Fig. II-4). However, cultivars differed significantly in soil N_{min} at both growth stages at high N (N2) rate. Apex left lower soil N_{min} contents at 45-60 and 60-75 cm soil depths than Capitol at the beginning of flowering. Similar results were shown again for Apex at 0-15, 30-45, 45-60 and 60-75 cm soil depths at the end of the flowering. All these results clearly indicate that the N uptake of the "N-efficient" cultivar was higher than of the "N-inefficient" one which was confirmed also by the root-length densities at different soil depths (Fig. II-2).

Figure II-5 shows the root length densities of three rape cultivars as affected by N supply in the second field trial (2001). Plant roots penetrated down to a depth of 90 cm at the beginning of flowering and at the end of flowering indicating no differences in maximum rooting depth among cultivars within this soil depth. Different from the previous field trial, the root-lengths were similarly high in the 0-15 and 15-30 cm soil layers in 2001. At the beginning of flowering cultivars differed significantly in root length density at 0-15 cm soil depth at N0 and N1 supply and at 60-75 and 75-90 cm soil depth at N2 supply. Particularly in the top soil Apex and Mohican produced similar and significantly higher root-length densities than Capitol at N0 and N2. Opposite results were found at the deepest soil layer (75-90 cm) at N2 supply and thus Capitol had significantly higher root length density than Apex and Mohican.

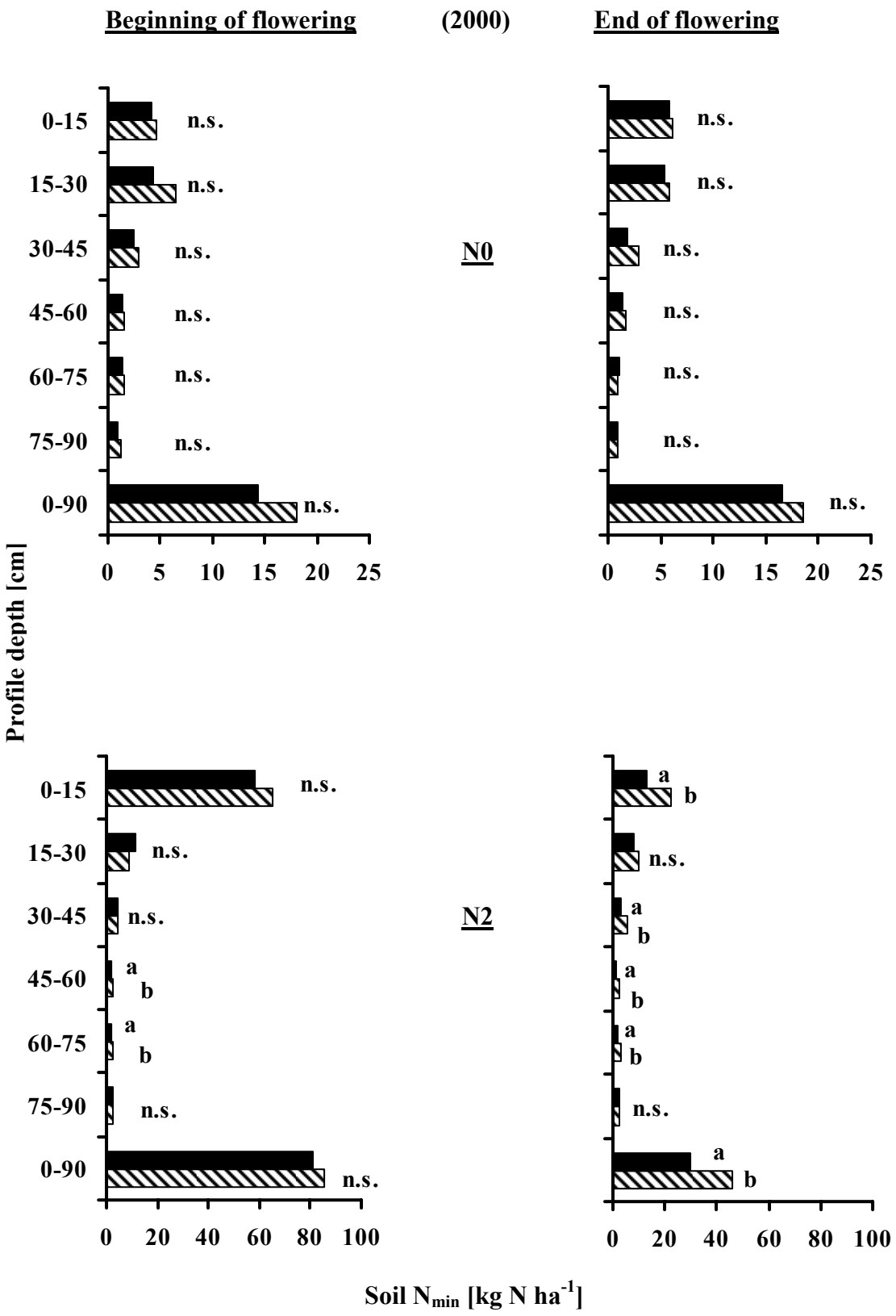


Figure II-4: Soil N_{min} contents underneath two oilseed rape cultivars (Apex: ■; Capitol: ▨) as affected by N supply (N0: soil mineral N supply, N2: 240 kg N ha^{-1}) at different growth stages at Zuchtgarten in 2000. Statistics: Separate analysis of variance for different growth stages and soil layers. Means with the same letter are not significantly different at $\alpha = 0.05$.

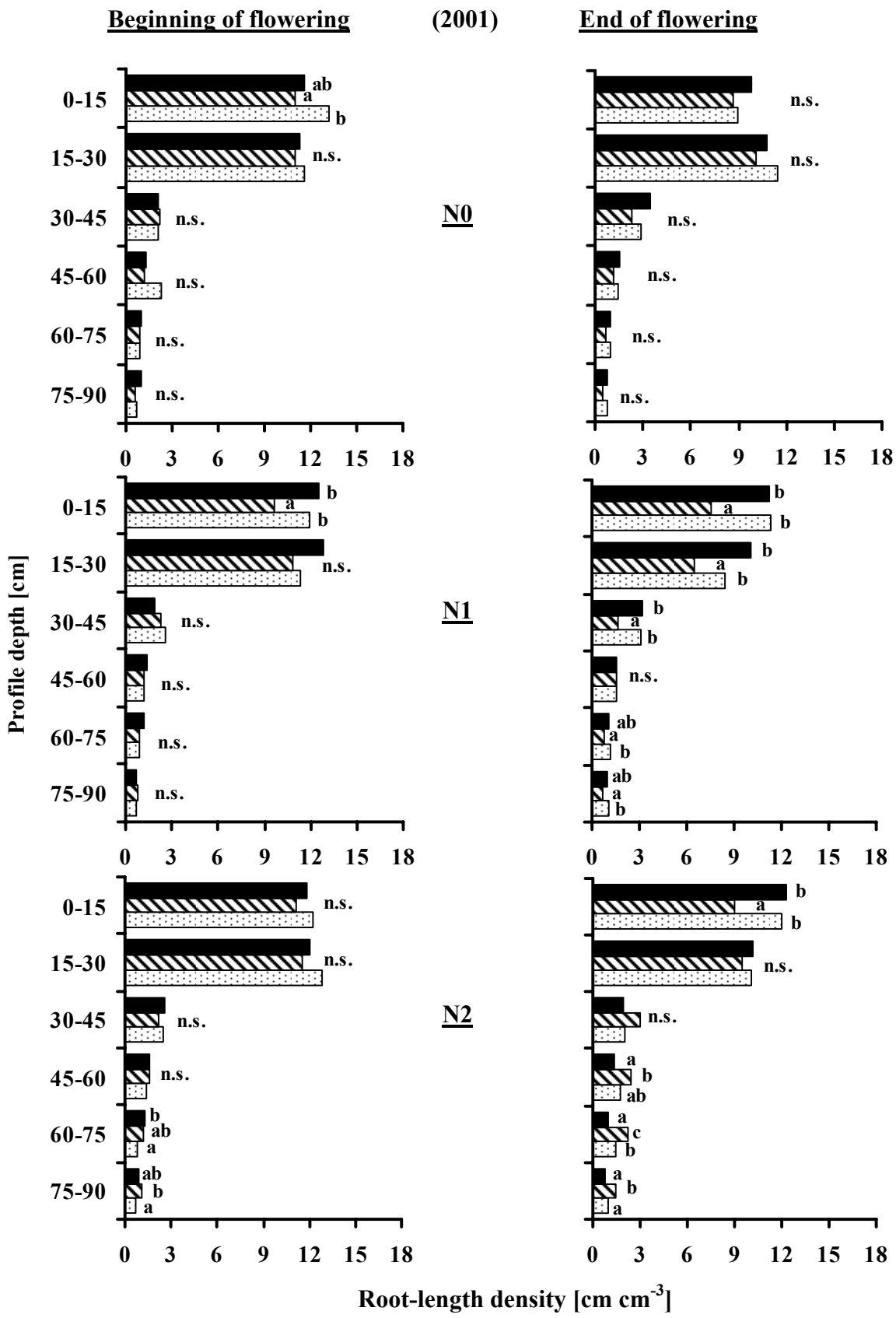


Figure II-5: Root length densities of three oilseed rape cultivars (Apex: ■, Capitol: ▨, Mohican: ⬚) as affected by N supply (N0: soil mineral N, N1: 120 kg N ha^{-1}, N2: 240 kg N ha^{-1}) at different growth stages at Zuchtgarten in 2001. Statistics: Separate analysis of variance for different growth stages and soil layers. Means with the same letter are not significantly different at $\alpha = 0.05$.

At the end of flowering in 2001, although the root length densities of the cultivars Apex and Mohican tended to be similarly high and higher than for Capitol at all soil layers, the differences were not significant at limiting N (N0) supply. On the other hand, except at 45-60 cm soil depth, Apex and Mohican had similar and significantly higher root length densities than Capitol at all soil layers at medium N (N1) supply. Similarly high root length densities at 0-15 cm soil depth at high N (N2) supply were shown by Apex and Mohican, and they were higher than for Capitol, however, the opposite was shown from 45 cm up to 90 cm soil depth, where Capitol had the significantly highest root length density.

The total N_{min} content in 0-90 cm soil depth and the distribution of total N_{min} at different soil layers of three rape cultivars (Apex, Capitol and Mohican) as affected by N supply in the second field experiment (2001) is shown in Figure II-6. Averaged over cultivars the remaining N in the soil was about 26 kg N ha^{-1} at N0, 29 kg N ha^{-1} at N1 and 46 kg N ha^{-1} at N2 at the beginning of flowering. Later on, total N_{min} increased almost by 14 kg N ha^{-1} at N0 and 8 kg N ha^{-1} at N1 at the end of flowering. At this stage, a decline in total N_{min} from 46 to 42 kg N ha^{-1} occurred only at N2. Similar to the previous field experiment at the beginning of flowering, under limiting N (N0) supply most of the soil N_{min} was present in 0-45 cm soil depth whereas at medium N (N1) and high N (N2) rates soil N_{min} was concentrated mainly in 0-15 cm soil layer. High soil N_{min} particularly at 0-15 cm depth at N1 and N2 probably originated from the N fertilizer applied on the soil surface.

At both growth stages, no significant differences were found in total N_{min} in 0-90 cm soil depth or N_{min} in different soil layers between the three cultivars under low N (N0) supply. However, cultivars differed significantly in soil N_{min} at both growth stages at moderate N (N1) supply. Generally, Apex tended to have lower remaining total N_{min} and N_{min} contents at different soil layers than Capitol and Mohican at both growth stages at N1. Particularly in the 75-90 cm subsoil layer Capitol had the highest soil N_{min} contents. However, at the end of the flowering especially at 45-60 and 60-75 cm soil depths, the highest soil N_{min} was shown by Mohican and the lowest was shown by Apex. All these results corroborate the results found for root-length densities at the same soil layers (Fig. II-4). Although Capitol tended to leave higher total N_{min} and N_{min} in different soil layers at the beginning and end of flowering at high N (N2) supply than the other cultivars, cultivars did not differ significantly at both growth stages.

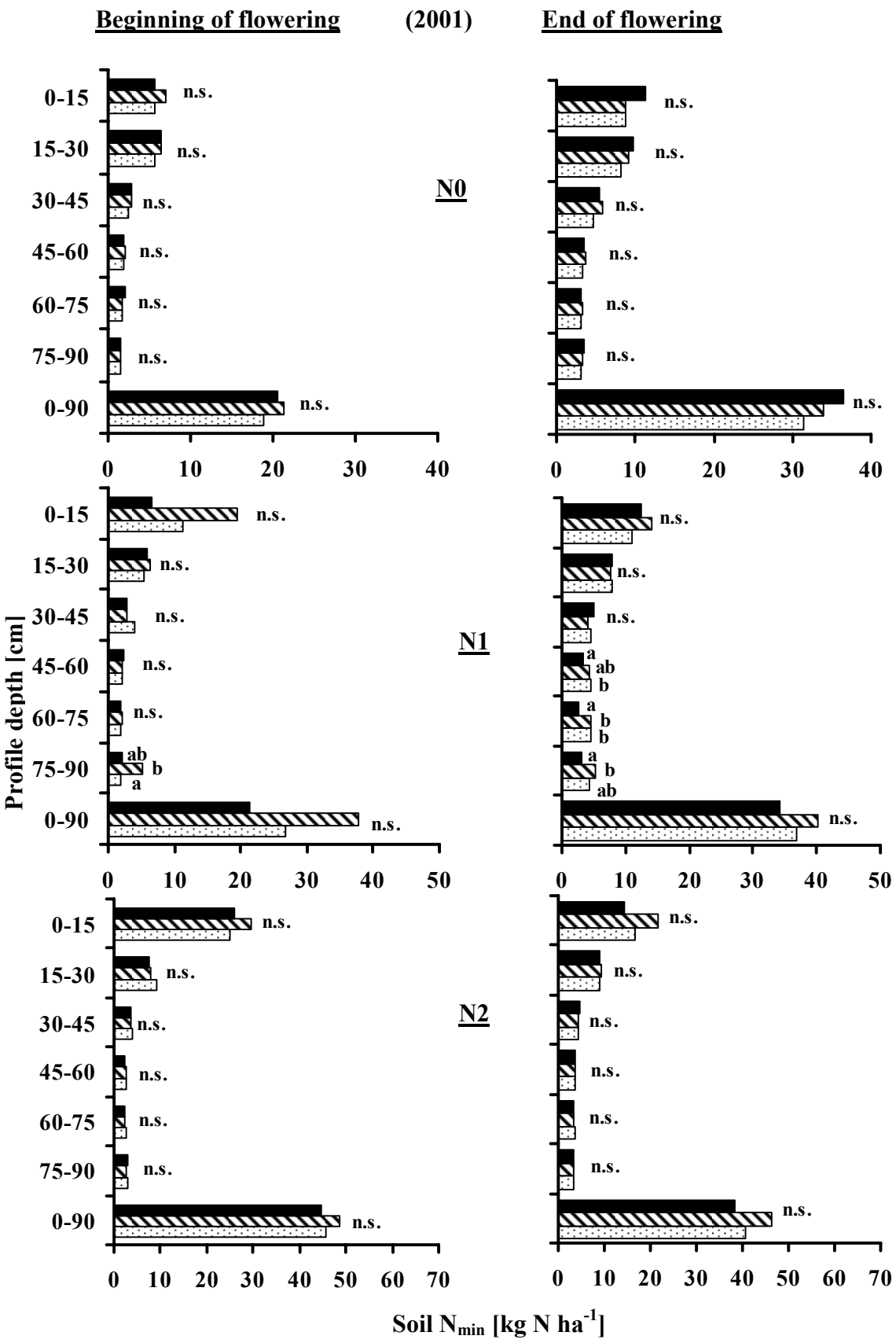


Figure II-6: Soil N_{min} contents underneath three oilseed rape cultivars (Apex: ■, Capitol: ▨, Mohican: ▩) as affected by N supply (N0: soil mineral N, N1: 120 kg N ha^{-1}, N2: 240 kg N ha^{-1}) at different growth stages at Zuchtgarten in 2001.Statistics: Separate analysis of variance for different growth stages and soil layers. Means with the same letter are not significantly different at $\alpha = 0.05$.

In the last field experiment (2002), the root length densities of two contrasting cultivars (Apex and Capitol) differed significantly in the 0-15 cm soil layer at low N (N0) and 30-45 cm at high N (N2) supply at the beginning of flowering (Fig. II-7). Apex produced higher root length densities than Capitol in these soil layers, and the same trend could also be seen at the other soil layers under all N levels (except 60-75 cm at N0). At the end of flowering significant differences in root length densities among cultivars were found only in the subsoil. In contrast to previous growth stage Capitol had a higher root length density than Apex at 45-60 cm (N0) and 75-90 cm (N1) soil depths. Especially in the top soil layers (N0 and N2) and partly also in the sub-soil (N2) Apex tended to have higher root length densities than Capitol.

The comparison of six genotypes in root length densities under limiting N (N0) supply in the last field experiment (2002) demonstrated highly significant differences particularly at 0-15 cm and 15-30 cm soil depths (Fig. II-8). The highest root length densities at 0-15 cm soil depth were shown by two "N-inefficient" DH lines, DH15 and DH42. In the same soil layer the lowest root length densities were produced by the "N-inefficient" cultivar Capitol and by DH28. At 15-30 cm soil depth the highest root length densities were produced again by DH15 and DH42 and by the "N-efficient" cultivar Apex. The lowest root length densities were recorded for Capitol and DH28 and the "N-efficient" DH line DH4. Furthermore, at the other soil depths no significant differences in root length density were found among the six oilseed rape genotypes.

Total N_{min} in 0-90 cm soil depth and the distribution of N_{min} at different soil depths of two cultivars and four DH lines at low N (N0) supply at the beginning of flowering is shown in Figure II-9. Averaged over cultivars the remaining N in the soil amounted to almost 13 kg N ha^{-1} at N0. This is about half of the total nitrogen amount remaining as N_{min} in the soil in the previous field experiment at the same growth stage and N rate. This could be the result of considerably lower N_{min} content of the soil in early spring (Chapter I, Tab. MI-2). On the other hand, the remaining nitrogen in the soil was about 18 kg N ha^{-1} at medium N (N1) and 49 kg N ha^{-1} at high N (N2) supply at the beginning of flowering. After that, N_{min} in the soil continued to be low and amounted to almost 14 kg N ha^{-1} at N0, 17 kg N ha^{-1} at N1 and 22 kg N ha^{-1} at N2 at the end of flowering. This might due to high root growth during this period (Fig. II-1) that might have contributed to a high N uptake activity between the two growth stages (Chapter I, Tab. I-14).

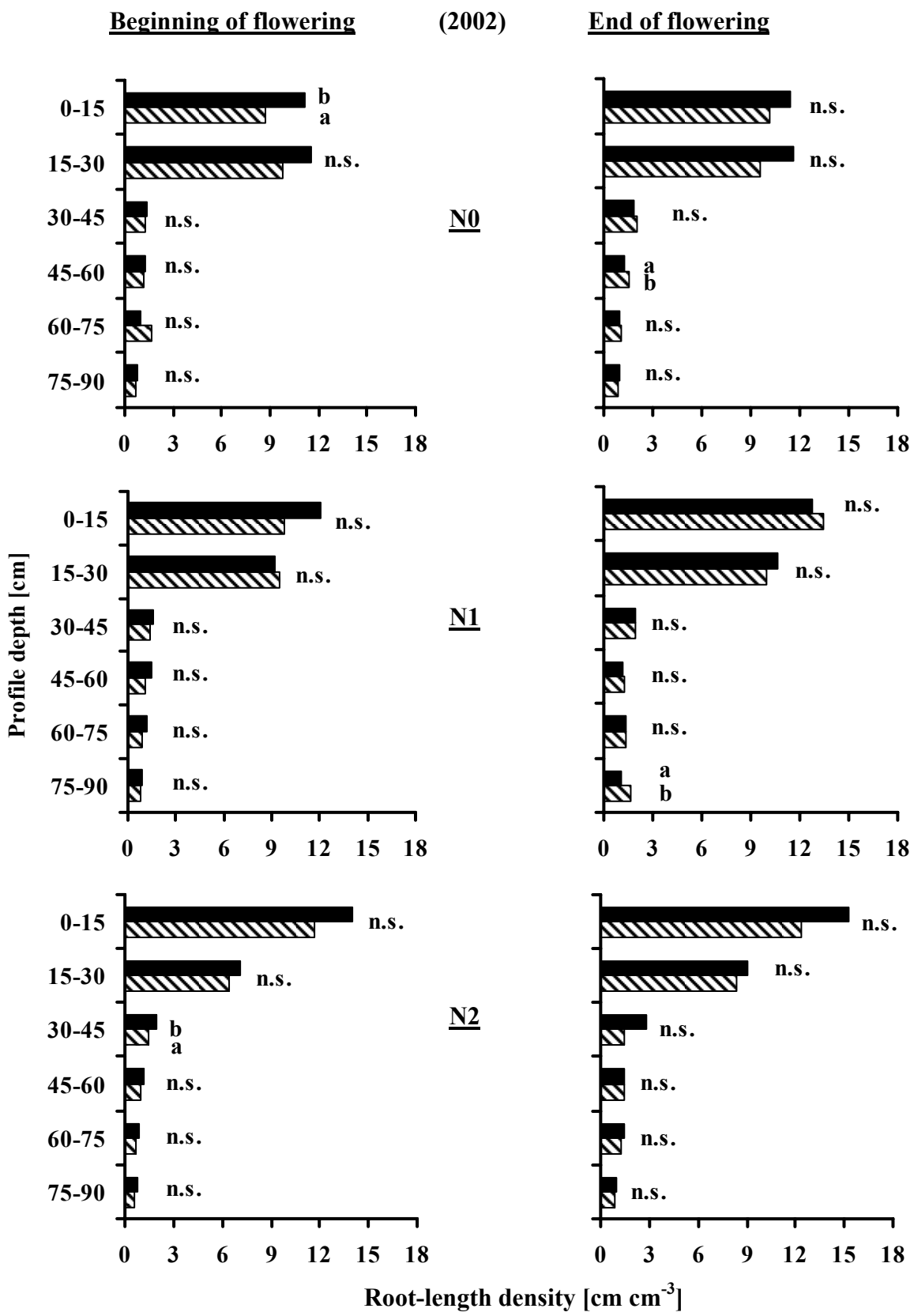


Figure II-7: Root length densities of two oilseed rape cultivars (Apex: ■, Capitol: ▨) as affected by N supply (N0: soil mineral N supply, N2: 240 kg N ha^{-1}) at different growth stages at Zuchtgarten in 2002.Statistics: Separate analysis of variance for different growth stages and soil layers. Means with the same letter are not significantly different at $\alpha = 0.05$.

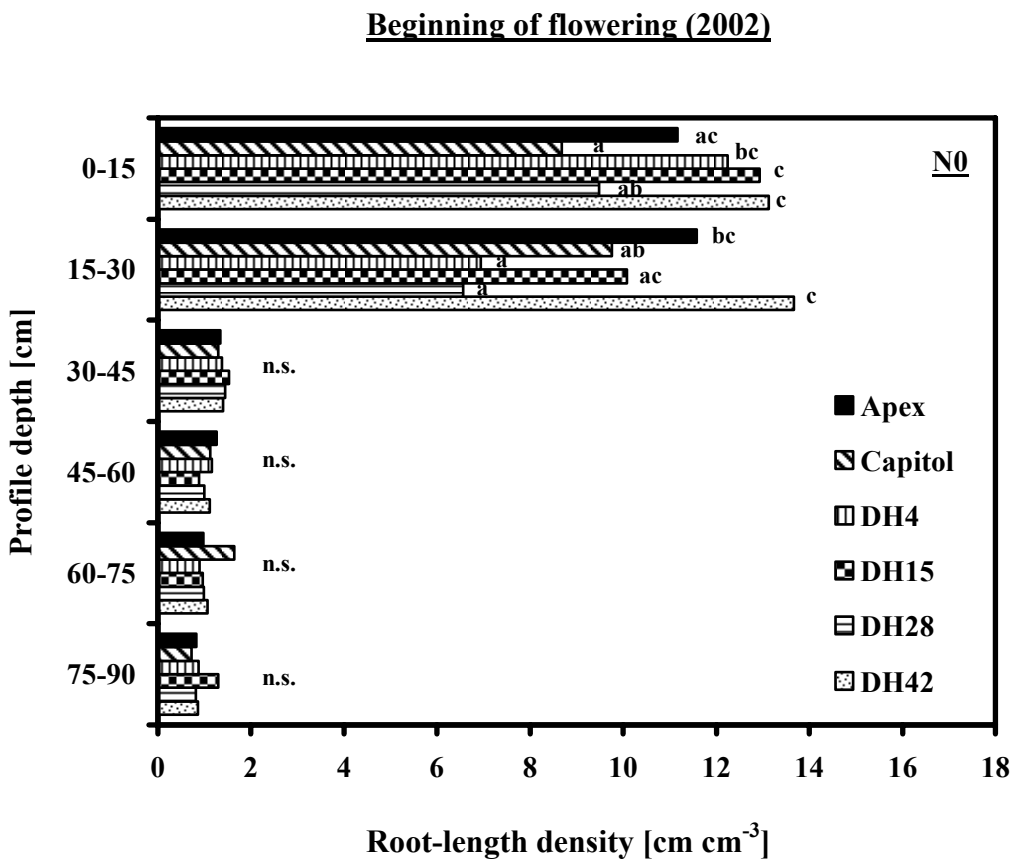


Figure II-8: Root length densities of six oilseed rape cultivars at low N supply (N0: soil mineral N supply) at the beginning of flowering at Zuchtgarten in 2002. Statistics: Separate analysis of variance for different growth stages and soil layers. Means with the same letter are not significantly different at $\alpha = 0.05$.

At the beginning of flowering, significant differences in N_{min} among six genotypes were found only at 0-15 cm soil depth at N0. At this soil depth the high N_{min} values remained in the soil underneath DH4, DH15, and DH42 whereas the lowest remained underneath Apex. Apex also tended to leave lower total N_{min} and N_{min} values in different soil layers than Capitol at N1. However, significant differences occurred among these two cultivars at 0-15 cm and 45-60 cm soil depths at N2. In the top soil layer Apex had the lowest N_{min} whereas in the subsoil layer at 45-60 cm Capitol left a lower residual N.

At the end of flowering the two cultivars did not differ either in total N_{min} or N_{min} at different soil depths at all N rates. However, Apex tended to leave lower N_{min} values at 0-15 cm and 15-30 cm soil depths under limiting N (N0) supply than Capitol. A similar trend in genotypic differences could also be seen for the 0-15 cm soil layer at medium N (N1) and high N (N2) supply.

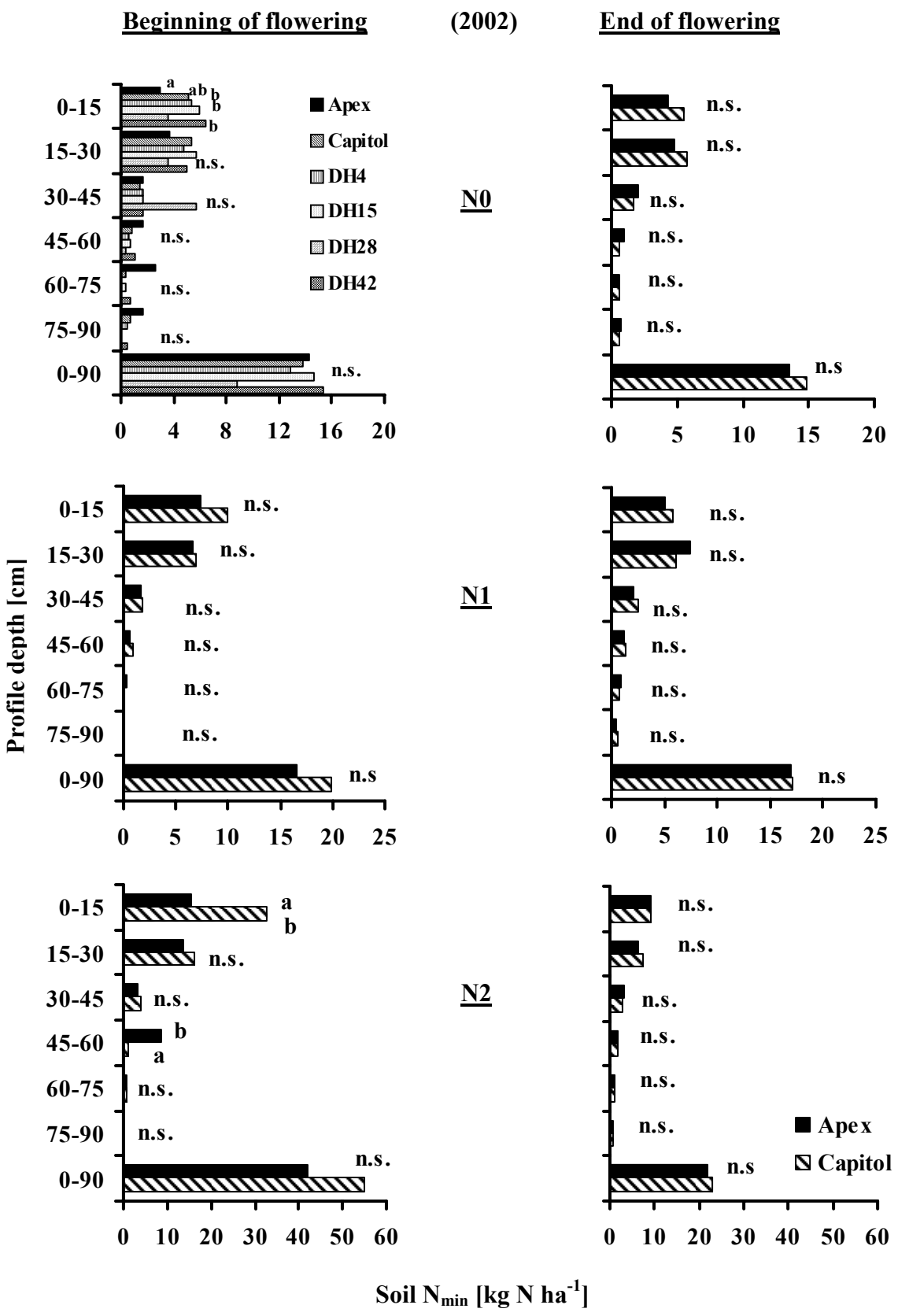


Figure II-9: Soil N_{min} contents underneath two oilseed rape cultivars and four DH lines as affected by N supply (N0: soil mineral N, N1: 120 kg N ha^{-1}, N2: 240 kg N ha^{-1}) at different growth stages at Zuchtgarten in 2002. Statistics: Separate analysis of variance for different growth stages and soil layers. Means with the same letter are not significantly different at $\alpha = 0.05$.

4.1.2 Root Counts and Root Count Distribution in the Soil Profile Determined in Rhizotrons

Figure II-10 shows the total number of root counts of four rape cultivars (Apex, Bristol, Capitol and Lirajet) in 0-90 cm soil depth as affected by low N (N0) and high N (N2) supply in the first field experiment (2000) at Zuchtgarten. The results indicated that from beginning of shooting, the total number of root counts increased up to the end of flowering in both N treatments, followed by a slight decline during seed filling phase. Usually the total number of root counts was significantly higher at N0 than at N2 supply. The difference was evident already at the beginning of shooting but became more significant at later growth stages. Averaged over cultivars the total number of the root counts along the tubes in 0-90 cm soil depth was in the range of 5 and 8 at the beginning of shooting, 16 and 24 at the beginning of flowering, 22 and 37 at the end of flowering, and 23 and 37 at seed filling phase at N0 and N2 supply, respectively.

The oilseed rape cultivars differed significantly in total number of root counts from beginning of shooting until maturity under limiting N (N0) supply in 2000. From beginning of shooting until shortly before the end of flowering the "N-efficient" cultivar Apex produced consistently the highest total root number along the tubes. At the end of flowering Apex and the "N-inefficient" cultivar Capitol produced similarly high total root counts whereas after that period a sharp decline in total root counts until maturity was found for Capitol. On the other hand, Apex and Bristol produced most total root counts during the last weeks before maturity. Furthermore, from beginning of shooting until maturity the significantly lowest total root counts were recorded for Lirajet.

Similar to the low N (N0) conditions, highly significant differences in total root counts among the four genotypes were found from beginning of shooting until maturity at high N (N2) supply in 2000. From beginning of shooting up to maturity Apex had the highest total root counts in the 0-90 cm soil depth. Bristol showed a similar root count number as Apex from shortly before end of flowering up to maturity. However, in contrast to low N supply, Capitol produced a significantly lower root count number than Apex and Bristol from the end of flowering till maturity at high N supply. Moreover from beginning of shooting till maturity the lowest total root count number at N2 was produced again by Lirajet.

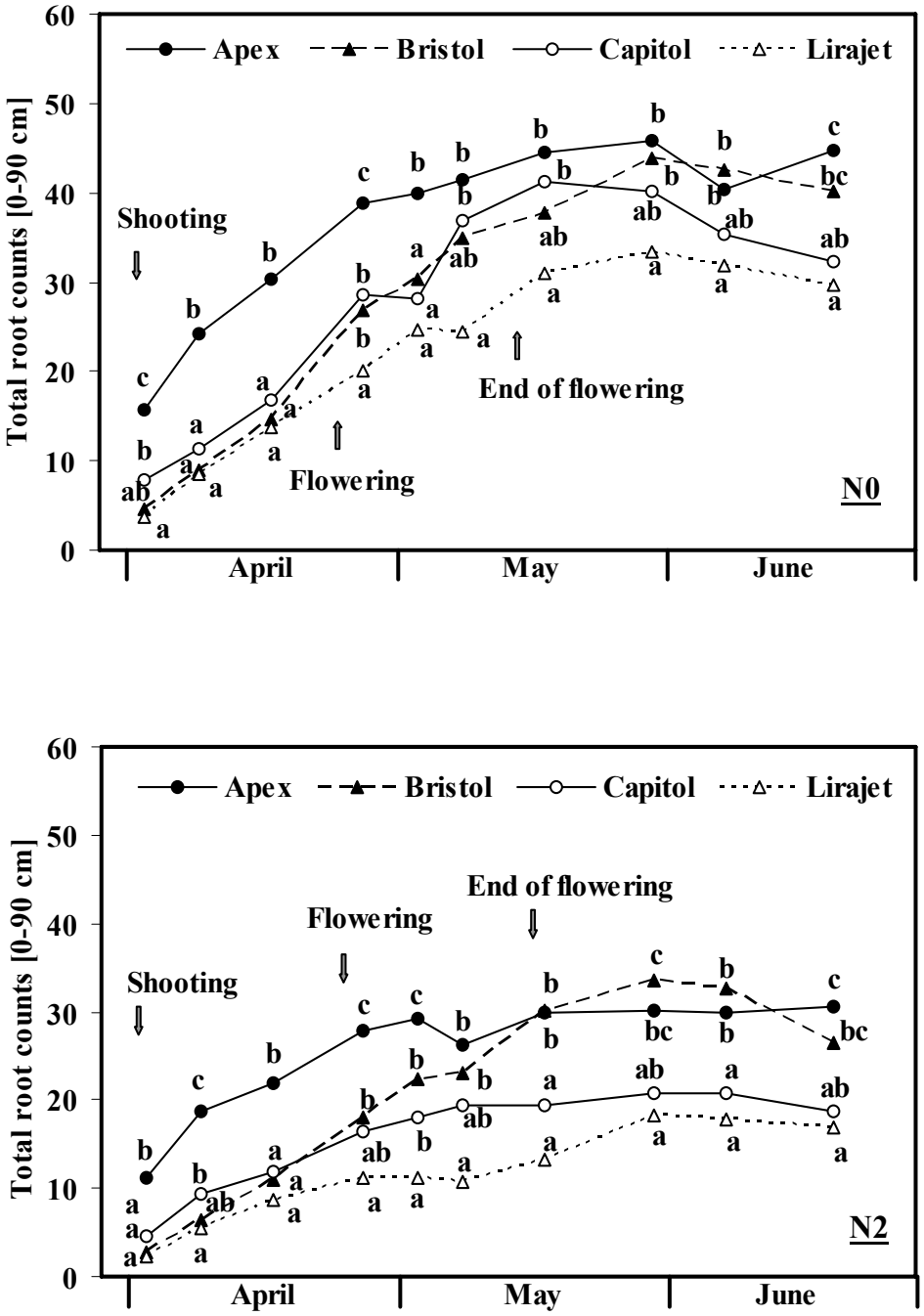


Figure II-10: Total root counts of four oilseed rape cultivars as affected by N supply (N0: soil mineral N, N2: 240 kg N ha^{-1}) at different growth stages at Zuchtgarten in 2000. Statistics: Separate analysis of variance for different growth stages. Means with the same letter are not significantly different at $\alpha = 0.05$.

The distribution of root counts among different soil depths, i.e. root-count density, of the four rape cultivars (Apex, Bristol, Capitol and Lirajet) as affected by low N (N0) and high N (N2) supply in 2000 is shown in Figure II-11. At the beginning of shooting cultivars penetrated the soil down to a depth of 30 cm at N0 and 45 cm at N2. Significant differences in root-count density were found among cultivars. Either at 0-15 or 15-30 cm soil depth the highest root-count density was shown by Apex whereas the lowest was shown by Lirajet. At both soil layers, a moderate root-count density was shown by Capitol.

At the beginning of flowering the root-count density increased considerably and the cultivars penetrated the soil down to a depth of 45 cm both at N0 and N2. Cultivars differed significantly in root-count density at 0-15 and 15-30 cm soil depth under limiting N (N0) supply. Apex had the highest, whereas Lirajet had the lowest root-count density. However, no significant differences among cultivars occurred at 30-45 cm soil depth. At high N (N2) supply, variation among cultivars in root-count density was significant at 0-15, 15-30 and 30-45 cm soil depth. Like at N0, Apex had the highest and Lirajet the lowest root number in all these soil layers.

Compared to the previous growth stage, cultivars increased the soil penetration down to a depth of 60 cm at N0 and 75 cm at N2 supply at the end of the flowering. Significant differences in root-count density were found among cultivars at 0-15 cm soil depth under low N (N0) conditions. At this soil depth the highest root-count density was produced by Apex while the lowest was produced by Lirajet. However, no significant differences among cultivars occurred at 15-30, 30-45 and 45-60 cm soil depth. On the other hand, cultivars differed significantly at 0-15, 15-30, and 30-45 cm soil depth under high N (N2) supply. At the top soil layer Apex had the highest root-count density compared to the other cultivars. However, in the second (15-30 cm) and third (30-45 cm) soil layer Bristol had the highest root-count density. Usually the lowest root-count densities at all soil depths were shown by Lirajet at N2.

Summarizing, from beginning of shooting up to maturity the total root counts at 0-90 cm soil depth and in different soil layers were usually highest for the “N-efficient” cultivar Apex compared to the other three cultivars at both low N (N0) and high N (N2) conditions in the first field experiment (2000). The “N-inefficient” cultivar Capitol as well as Lirajet usually showed a low root count number. A moderate performance in root formation was shown by Bristol at both N rates.

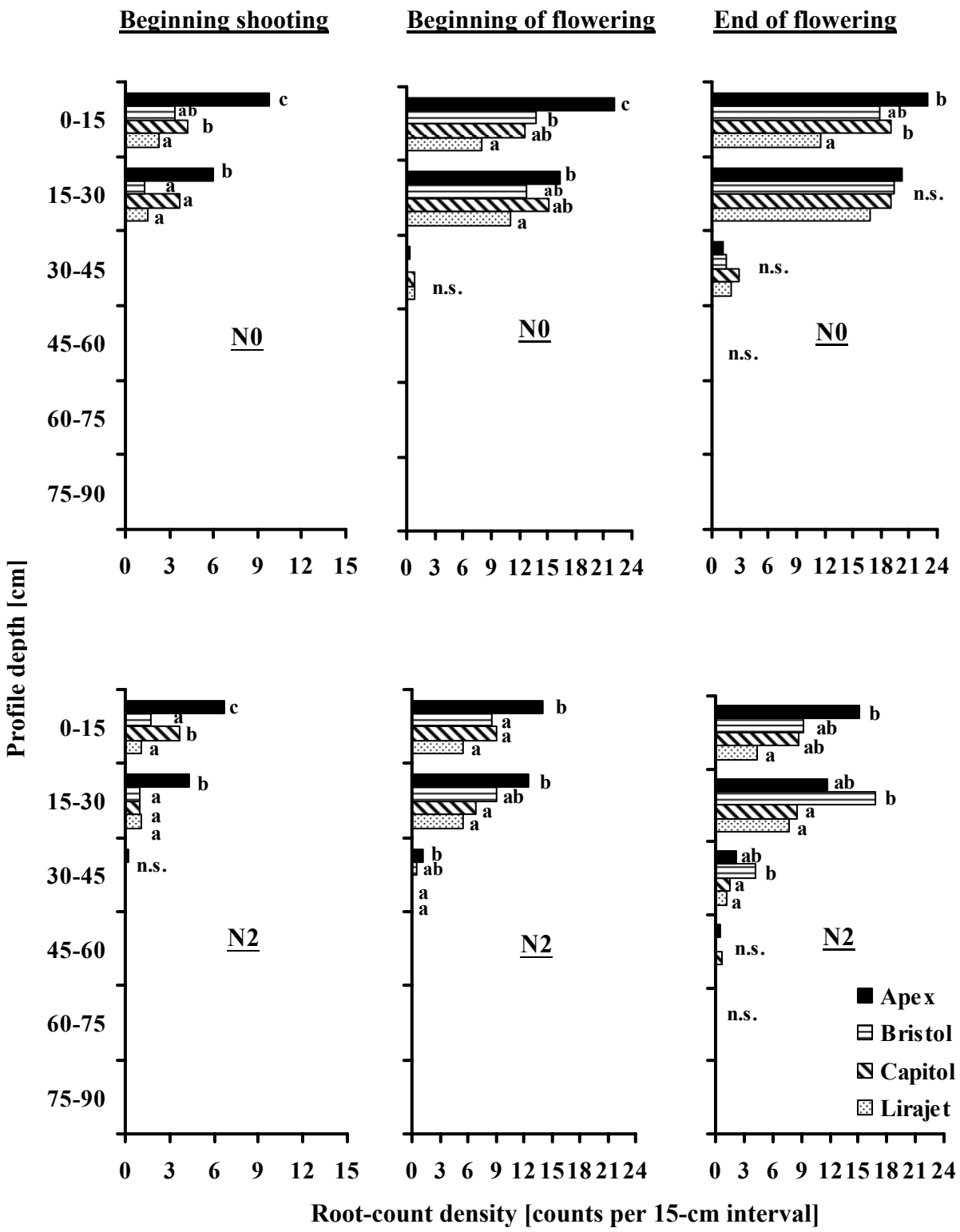


Figure II-11: Root count density in different soil layers of four oilseed rape cultivars as affected by N supply (N0: soil mineral N, N2: 240 kg N ha^{-1}) at different growth stages at Zuchtgarten in 2000. Statistics: Separate analysis of variance for different growth stages. Means with the same letter are not significantly different at $\alpha = 0.05$

The total number of root counts of two contrasting cultivars (Apex and Capitol) in 0-90 cm soil depth as affected by low N (N0), medium N (N1) and high N (N2) supply in the last field experiment (2002) at Zuchtgarten is shown in Figure II-12. The results indicated that from beginning of shooting the total root counts increased up to the end of flowering at all N rates, followed by a slight decline during seed filling. In contrast to the field experiment in 2000 (Fig. II-10), no differences were found between N rates in total root counts from beginning of shooting until maturity in this field experiment (2002) (Fig. II-12). Nevertheless the total number of root counts tended to be higher at N0 than at N1 and N2. On the other hand substantially more root counts were found in this field experiment compared to the previous one, at all N rates. Averaged over cultivars the mean total number of the root counts along the tubes in 0-90 cm soil depth was in the range of 22, 23 and 25 at the beginning of shooting, 32, 30 and 30 at the beginning of flowering and end of the flowering, and 24, 21, and 20 during seed filling at N0, N1 and N2 supply, respectively.

Under limiting N (N0) supply, from beginning of shooting until the end of flowering the total root counts of Apex tended to be higher than for Capitol. A significant difference among these cultivars, however, occurred only at the beginning of shooting. Similar results among the two cultivars were found at medium N (N1) supply. At this N rate, Apex produced significantly higher total root counts than Capitol only at the beginning of shooting. Compared to N0, the differences in total root counts between the two cultivars tended to be higher at N1 particularly between flowering and seed filling. Significant cultivar differences during this period, however, could not be found. Highly significant differences in total root count between the two cultivars occurred from beginning of shooting until beginning of seed filling at high N (N2). Usually Apex had higher total root counts than Capitol up to the beginning of seed filling. After that, no significant differences between cultivars were found until maturity due to a sharper decline in root count number for Apex than for Capitol.

Figure II-13 demonstrates the distribution of the total number of root counts of two rape cultivars differing in N efficiency at different soil depths from 0 to 90 cm as affected by low N (N0), medium N (N1) and high N (N2) supply in 2002. At the beginning of shooting roots of the cultivars penetrated into the soil down to a depth of 30 cm at N0 and 45 cm at N1 and N2. Significant differences in root-count density were found among cultivars at 0-15 cm soil depth at all N rates, and Apex produced a higher root-count density than Capitol. Apex also tended to have a higher total root-count density at 30-45 soil depth at all N rates.

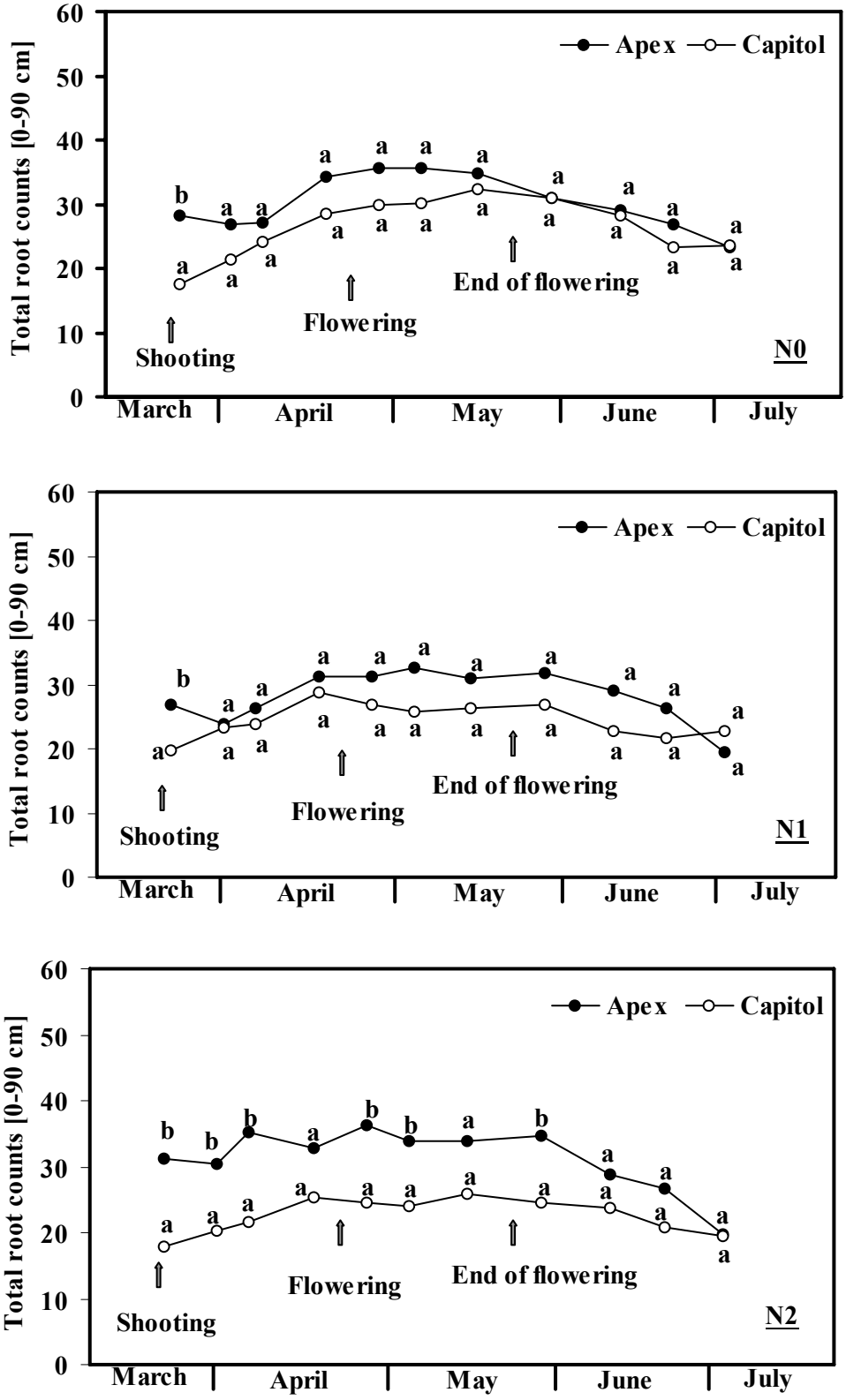


Figure II-12: Total root counts of two oilseed rape cultivars as affected by N supply (N0: soil mineral N, N1: 120 kg N ha^{-1}, N2: 240 kg N ha^{-1}) at different growth stages at Zuchtgarten in 2002. Statistics: Separate analysis of variance for different growth stages. Means with the same letter are not significantly different at $\alpha = 0.05$.

The soil penetration increased from 30 to 60 cm soil depth at low N supply by both cultivars at the beginning of flowering. At the other two N levels soil penetration remained constant at 45 cm soil depth. Cultivars differed significantly in root-count density only at 0-15 cm soil depth at N0 and at 30-45 cm at N2. Apex had higher root-count densities than Capitol. Actually, Apex showed a tendency to a higher root-count density than Capitol particularly in the 0-30 cm soil layers (except 15-30 cm at N1) at all N rates.

At the end of flowering roots of the cultivars penetrated the soil down to a depth of 60 cm at N0. However, an extremely deeper soil penetration down to a depth of 90 cm occurred at N1. A slight increase (from 45 to 60 cm) in soil penetration from the beginning until the end of flowering was also found at N2. At limiting N (N0) supply no significant differences occurred between two cultivars in root-count density at all soil layers. Although cultivars did not differ in root counts in the top soil, significant differences in root-count density were found among two cultivars in the subsoil (45-60 and 60-75 cm) under moderate N (N1) supply. At deeper soil layers Apex had higher root-count densities than Capitol. Another significant difference in root-count density among both cultivars occurred at 0-15 cm soil depth at high N (N2) supply. At this soil depth, Apex had a higher root-count density than Capitol.

In conclusion, the results of the total root counts in 0-90 cm soil depth as well as the root-count density in different soil layers in the last field experiment (2002) clearly indicated that from beginning of shooting until beginning of seed filling the “N-efficient” cultivar Apex usually had a more vigorous new root production compared to the “N-inefficient” cultivar Capitol. However, constantly significant differences among these two cultivars could be found only at high N (N2) supply, while at low N (N0) and medium N (N1) supply significant differences could be found only at the beginning of shooting. On the other hand, highest root-count densities of Apex particularly in the top soil (0-15 and 15-30 cm) and sometimes in the subsoil (30-45 cm at N2, 45-60 cm and 60-75 cm at N1) clearly confirmed that this cultivar had a more vigorous root growth than Capitol.

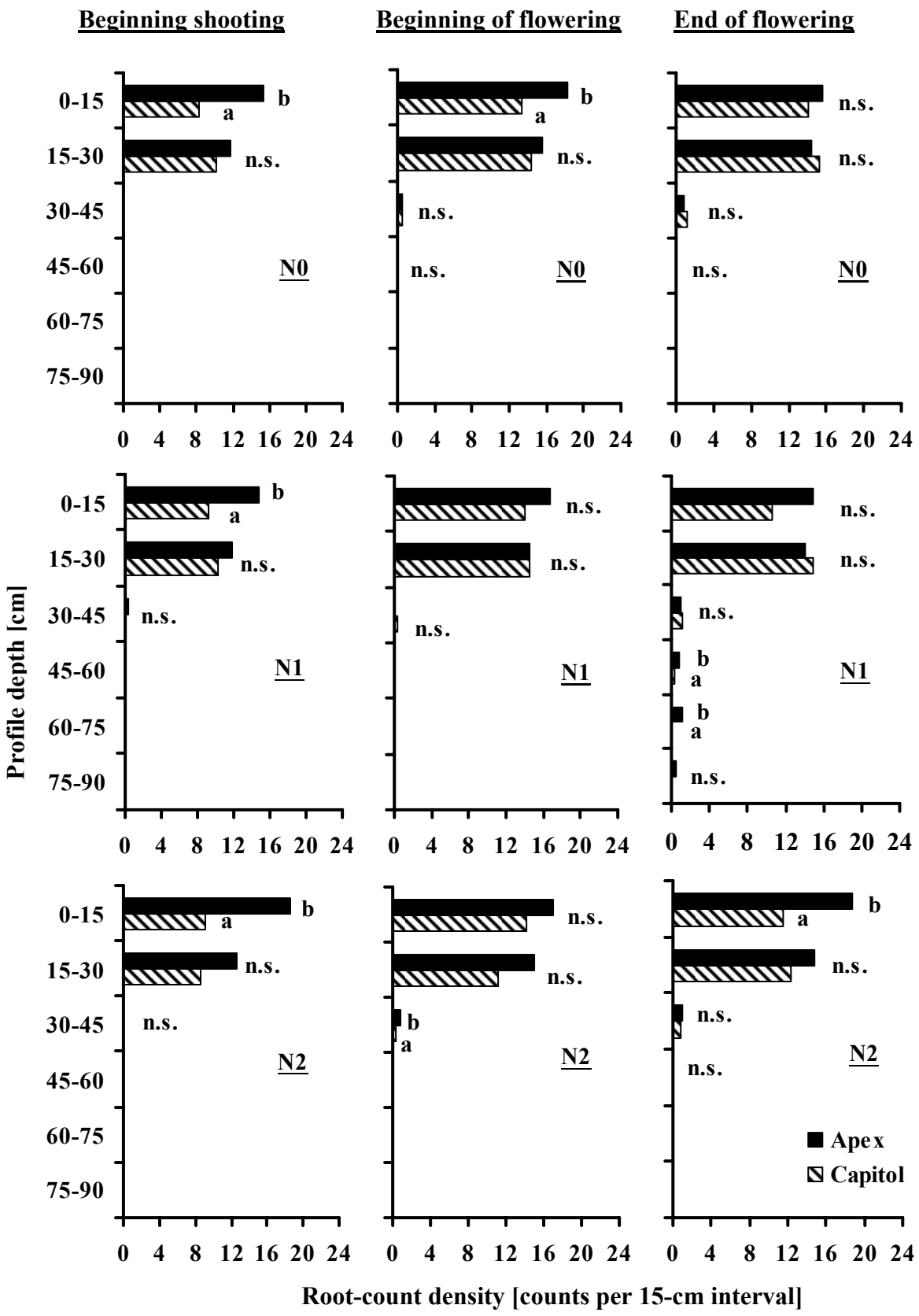


Figure II-13: Root counts density in different soil layers of two oilseed rape cultivars as affected by N supply (N0: soil mineral N, N2: 240 kg N ha^{-1}) at different growth stages at Zuchtgarten in 2002. Statistics: Separate analysis of variance for different growth stages. Means with the same letter are not significantly different at $\alpha = 0.05$

5 Discussion

The aim in this chapter was to investigate the significance of root growth and morphology for genotypic differences in N efficiency of winter oilseed rape cultivars and double haploid (DH) lines and to determine the morphological root characteristics contributing to genotypic differences in N-uptake efficiency.

Our previous results in Chapter I clearly demonstrated that averaged over three experimental years and two sites, highly significant ($P<0.001$) genotypic variation in grain yield among twelve genotypes existed (Tab. I-4). High grain yield and thus high N efficiency under limiting N (N0) supply significantly correlated with total N uptake and N uptake during reproductive growth in the field experiments in 2000 and 2001 at Zuchtgarten (Tab. I-22). From beginning of flowering till maturity N uptake differences among two contrasting rape cultivars amounted to about 20 kg N ha^{-1} in 2000 (Tab. I-12), 18 kg N ha^{-1} in 2001 (Tab. I-13) and 28 kg N ha^{-1} in 2002 (Tab. I-14).

Based on grain yield at N0 that was associated with high N-uptake activity during reproductive growth, the cultivar Apex could be characterized as “N-efficient”, whereas the cultivar (Capitol) with low grain yield that also had a low N-uptake activity was characterized as “N-inefficient”. For a high soil-N acquisition and to maintain high N-uptake activity during reproductive growth, the N-efficient genotypes might have a more vigorous root growth that might be enabled by continuous assimilate allocation from vegetative tissues (Jackson et al., 1986). Thus morphological root characteristics might have an essential role in contributing to genotypic differences in N-uptake efficiency.

5.1 Significance of Root Growth and Morphology for Nitrogen Uptake

Nitrogen uptake is regulated by the demand of the growing crop if N supply is not limited (Clarkson 1985). In contrast, if the required N is limited in the soil, N uptake depends on the extent and effectiveness of the root system (Jackson et al., 1986) and also morphological root characteristics such as maximum rooting depth, and root length density at deeper soil layers (Claassen et al., 1986; Sattelmacher et al., 1994).

In the present study, the results of the core method used in three field experiments (2000, 2001 and 2002) at Zuchtgarten indicated that averaged over N rates the total root length

increased up to beginning of flowering and then slightly declined (2000 and 2001) or increased (2002) up to the end of flowering (Fig. II-1). At the beginning of flowering maximum total root length varied in between 29, 42 and 37 km m^2 in 2000, 2001 and 2002, respectively. Production of maximum total root length until flowering and a substantial reduction in root length after flowering for oilseed rape was also found in several other studies (Barraclough, 1989; Kjellström and Kirchmann; 1994; Kappen et al., 2000). The divergent result of the last field experiment (2002) can be explained by the variable weather conditions that occurred in the three field experiments. Therefore, the prolonged root growth up to end of the flowering in 2002 might be the result of higher rainfall (annual rainfall 863 mm) particularly in April and May compared to the long-term average monthly rainfall (Fig. MM I-1). In contrast, due to a warm and dry period (annual rainfall 591 mm) particularly in April and May in 2000 the total root length was substantially reduced. A similar reduction in root growth due to drought was demonstrated in the studies of Barraclough (1989) and Kjellström and Kirchmann (1994).

Root monitoring in the rhizotrones allowed following root growth over the whole growing period from shooting to maturity in two field experiments (2000 and 2002) at Zuchtgarten. The rhizotrone results indicated that averaged over N rates the total root counts of rape plants in 0-90 cm soil depth continuously increased from beginning of shooting up to end of flowering (2002) or even were maintained up to seed filling (2000) followed by a slight decline until maturity (Fig. II-10, II-12). In contrast to the results obtained by the core method (Fig. II-1), highly significant differences in total root counts (rhizotron) were found in 2000 between two N rates (Fig. II-10). During all growth stages usually more root counts were found at limiting N (N0) than at high N (N2) supply in 2000. The contrasting results obtained by the two methods demonstrate that different root fractions are assessed. During the root washing process from the soil core, fine roots may be are lost and only the steady coarse roots (>2 mm) can be determined during root length measurements. In contrast, in the rhizotrones especially the dynamic fine roots (<2 mm) are identified (Johnson et al., 2001). Therefore, the core results represent more the total root length achieved by the plants, while the rhizotron results represent the new formation of short-lived fine roots.

A higher fine root formation under limiting N supply than under non-limiting N supply was also found by Vogt et al. (1986) and Pregitzer et al. (1995). High root counts at N0 might be the result of increased carbohydrate sink strength of the roots under N deficiency that usually

leads to greater allocation of assimilates to the roots for new root formation (Zagal, 1994; Merrill et al., 2002). Newly developed roots are of particular importance for nutrient uptake (Gao et al., 1998).

Maintaining high new root formation up to seed filling in 2000 at N0 resulted in a high N uptake activity during reproductive growth. This can be seen from total shoot N uptake, which increased by almost 5% from end of flowering till maturity (Fig. I-3 A). This is also confirmed by the results of the core method showing that the total root length slightly increased from beginning of flowering until end of flowering at N0 while substantial root decay was found at N2 in 2000 (Fig. II-1). The total shoot N uptake was therefore reduced by almost 10% from end of flowering till maturity at N2 (Fig. I-3 A). Our results are thus in agreement with the study of Worku et al. (2007), who demonstrated that high N efficiency (high grain yield) of maize under limiting N supply was the result of higher N-uptake efficiency associated with maintaining root growth during flowering and early grain fill. Furthermore, Eghball and Maranville (1993) demonstrated that root growth of maize during reproductive growth was substantially higher at low N than at high N supply.

The results of the core method in three field experiments indicated that the roots of oilseed rape plants were usually concentrated in the topsoil, particularly in 0-15 and 15-30 cm soil depth, and with a small proportion in deeper horizons at the beginning and end of flowering (Fig. II-3, II-5, II-7, II-8). Similar patterns in root count distribution were also found by the rhizotone method in two field experiments (Fig. II-11, II-13). Our results corroborated other studies performed for various crop species such as wheat (Barraclough et al., 1991), maize (Wiesler and Horst, 1994) and oilseed rape (Barraclough, 1989; Kjellström and Kirchmann, 1994) which demonstrated a similar root distribution pattern. The root distribution among various soil layers did not markedly change with the level of N supply (Fig. II-3, II-5, II-7, II-8). High root-length densities in the subsoil might be advantageous to extract nitrate-N that was leached from upper soil layers earlier in the growth cycle (Oikeh et al., 1999; Wiesler and Horst, 1994). In the current field experiments, however, soil mineral N contents in the subsoil were similarly low for limiting and high N conditions (Fig. II-4, II-6, II-9).

5.2 Genotypic Differences in Root Growth and Root Morphology in Relation to Nitrogen-uptake Efficiency

Genotypic differences in root growth and morphology associated with N-uptake efficiency were studied intensively among crop cultivars such as maize (Eghball and Maranville, 1993; Wiesler and Horst, 1994; Bänziger et al., 2002), wheat (Box and Johnson, 1987) and winter oilseed rape (Kappen et al., 2000; Horst et al., 2003; Kamh et al., 2005). Most of the authors reported that genotypic differences among cultivars were highly associated with maintaining higher root length density and thus N uptake particularly during reproductive growth.

In the present study, the results of the core method showed no significant differences among two contrasting rape cultivars (Apex and Capitol) in total root production either at limiting N (N0) or at non-limiting (N2) N rate at the beginning of flowering and end of the flowering in 2000 (Fig. II-1). On the other hand, cultivars differed significantly in root length density in both topsoil and subsoil layers at the beginning of flowering and end of flowering at N2 (Fig. II-3). Our results corroborated the studies of Wiesler and Horst (1994) and Schenk and Barber (1980) who demonstrated highly significant genotypic differences among maize cultivars in root length density in various soil layers. On the other hand, the study of Mackay and Barber (1986) demonstrated that maize cultivars differed significantly in root length density particularly in the topsoil layer. Either in subsoil or topsoil layers our results clearly indicated that usually the "N-efficient" cultivar Apex had significantly higher root length density than "N-inefficient" cultivar Capitol. This was confirmed also by the depletion of N in the soil which was determined as mineral N in the soil (Fig. II-4). Highly corroborative results were shown by Liao et al. (2004) who examined wheat lines in terms of N efficiency and demonstrated that N-efficient wheat lines had vigorous root growth and higher root length densities than N-inefficient lines.

In terms of fine root dynamics (rhizotron) highly significant differences among four rape cultivars (Apex, Bristol, Capitol and Lirajet) in fine root production from beginning of shooting until maturity were found at both N0 and N2 supply in 2000 (Fig. II-9). Generally, Apex produced more fine roots than Capitol at both N rates. Particularly maintaining high new root formation up to seed filling in 2000 at N0 clearly show that Apex could achieve a high N efficiency (high grain yield) by maintaining high N-uptake activity during reproductive growth at N0. Our results are in agreement with Horst et al. (2003) who

demonstrated that the new fine root formation of Apex was usually higher than Capitol under low N conditions.

The "N-efficient" cultivars Apex and Mohican tended to have higher total root lengths than the "N-inefficient" cultivar Capitol in the second (2001) field experiment at all N rates, and significant differences among cultivars were found at the end of the flowering at N1 (Fig. II-1). However, cultivars differed significantly in root length density in the topsoil at the beginning of flowering at N0 and N1 whereas differences occurred at deeper soil layer at N2 (Fig. II-5). Interestingly, at the end of the flowering significant differences in root length density occurred among cultivars in root length density at both topsoil and subsoil layers. Generally Apex and Mohican had both a higher root length density than Capitol.

In the last field experiment (2002), Apex and Capitol differed only at the beginning of flowering under limiting N (N0) supply and Apex produced a higher root length than Capitol (Fig. II-1). In addition to the two cultivars, significant differences were also found in total root length among the double haploid (DH) lines at the beginning of flowering in 2002 at N0 (Fig. II-2). Apex, DH15 and DH42 had higher total root length than Capitol, DH4 and DH28. These results clearly indicated that the "N-efficient" genotype DH4 achieved highest grain yield without a high root production while the other "N-efficient" cultivar Apex achieved highest grain yield with high N uptake during reproductive growth at N0. On the other hand, a similarly high root growth as for Apex was shown also by DH15 and DH42 although grain yields were low.

In agreement with the core method, the rhizotrone results clearly showed that from beginning of shooting till maturity Apex tended to produced continuously more new roots than Capitol at N0, N1 and N2 in 2002 (Fig. II-12). Highly significant differences between both cultivars were found at N2. The root count density results clearly indicated that Apex had more root counts than Capitol at 0-15 cm soil depth at the beginning of shooting at all N rates. This is in agreement with the study of Mackay and Barber (1986) who reported cultivar differences in root density in the topsoil (Fig. II-13). However, at the beginning and end of flowering new fine root formation increased in subsoil layers especially for Apex which highly corroborates the study of Wiesler and Horst (1994). Furthermore, Kamh et al. (2005) reported that higher N-uptake efficiency of Apex was due to its higher root growth as compared to Capitol in a field study.

In conclusion, the results of the core method in three field experiments (2000, 2001 and 2002) and results of the rhizotron method in two field experiment (2000 and 2002) clearly indicated that from the beginning of the vegetative stage until maturity the "N-efficient" cultivar Apex had a vigorous root growth which was associated usually with a higherer root length density and a higher root turn over (fine root formation) than the "N-inefficient" cultivar Capitol. Although Apex showed a higher N uptake only during reproductive growth, this cultivar built up a bigger root system already before flowering. A high new root formation only during reproductive growth, as could be seen for Bristol (Fig. II-6) thus seems to be less effective to achieve a high N efficiency.

Although genotypic differences in N uptake during reproductive growth were often found to be associated with a high root length density in the subsoil layers (Wiesler and Horst, 1994), Apex produced more roots especially in the topsoil. Generally, most N is supplied to the roots by mass flow (79%) due to the highly mobility of nitrate (NO_3^-) in the soil (Barber, 1995). Therefore, rather low root length densities have been considered to be sufficient for nitrate-N uptake. In our study, particularly at limiting N (N0) conditions, most N might have been available as ammonium (NH_4^+) which is 10-100 times less mobile in the soil than NO_3^- (Barber, 1995). Therefore, a high root length density in the topsoil might have been important to take up ammonium that was mineralized from soil organic matter. Indeed, most of the soil mineral N in our study was ammonium (data not shown). Bruce et al (2002) reported that there is considerable variation in root length density in crops which could be utilized to breed for this trait.

In conclusion, the results of the present study indicate that, both destructive (core) and non-destructive (rhizotron) root methods can be easily used to identify genotypic differences in root growth and morphology of oilseed rape. The N-efficient cultivars could be characterized by a high investment in root growth during vegetative stage with a comparatively slow growth and thus a low N-uptake rate until flowering, which, however, continued with a high N uptake activity during reproductive growth. A high vigorous root system building only during reproductive growth seems to be less effective to achieve a high N efficiency.

CHAPTER III

ROLE OF LEAVES FOR GENOTYPIC DIFFERENCES IN NITROGEN EFFICIENCY OF OILSEED RAPE (*BRASSICA NAPUS* L.)

1. Abstract

Identification of leaf characteristics correlating with N efficiency could facilitate the selection process of N-efficient cultivars during plant breeding. It was found that maintaining a high N uptake activity during reproductive growth is an important characteristic of N-efficient rape cultivars (Chapter I). This was associated with an efficient and vigorous root growth (Chapter II). However, without continuous assimilate allocation from the leaves, root growth and activity cannot be maintained during reproductive growth. The aim in this study was to investigate the role of leaves for genotypic differences in N efficiency of rape cultivars and double haploid (DH) lines. In three field experiments five oilseed rape cultivars and four DH lines were evaluated in terms of leaf area development (2000, 2001, 2002), leaf dropping (2000, 2001) and leaf defoliation (2000, 2001) at three N rates (N0: soil mineral N, N1: 120 kg N ha^{-1}, N2: 240 kg N ha^{-1}) at Zuchtgarten, near Göttingen. Significant differences were found among cultivars in leaf characteristics. The leaf area index (LAI) increased with increasing N supply. The N-efficient cultivars generally had lower LAI reduction, prolonged leaf area duration, and thus a delayed N retranslocation from leaves to the seeds during reproductive growth at N0. Leaf dropping increased with increasing N supply but terminated earlier under limiting N (N0) supply. The N-efficient cultivars showed generally a low dropped leaf dry matter and leaf N content than N-inefficient ones. The N losses varied between 1.6 and 14.0 kg N ha^{-1}. Thus they play a negligible role in genotypic differences in N harvest index (NHI) compared to genotypic differences in remaining N in the straw which varied between 7.0 and 45 kg N ha^{-1}. 50% leaf defoliation reduced slightly the shoot dry matter, shoot N uptake and seed yield at all N rates. Reduction in shoot dry matter, shoot N uptake and seed yield was not significant for N-efficient cultivars, while significant reduction was shown for the N-inefficient cultivars. Altogether, the results indicate that higher N efficiency was achieved by those cultivars which generally had a low LAI reduction, prolonged leaf area duration and thus a delayed N retranslocation from leaves to the seeds during reproductive growth under low N (N0) conditions. The N-efficient cultivars had a better light interception and higher photosynthetic rate of the defoliated canopy than the N-inefficient cultivars.

Key words: Leaf dropping, defoliation, retranslocation, genotypic variation, cultivar, DH line, N efficiency, *Brassica napus* L.

2. Introduction

Photosynthesis is the most important biological process for plant growth and development. For this process morphological and physiological leaf characteristics during vegetative and generative development stages play a significant role in yield determination of field grown crops (Pavlik, 1983; Bhagsari and Brown; 1986). The leaf area and leaf area duration play an important role for the light interception and carbon assimilation by crops (Grosse et al., 1989; Muchow and Sinclair, 1994). Biomass production and yield of a crop is strongly dependent on its leaf area as well as the rate of leaf photosynthesis (Hirasawa and Hsiao, 1999). Leaf area is assessed as the one sided green leaf area per unit ground area in broadleaf canopies, *i.e.* leaf area index (LAI) (Mae, 1997). As a rule, enhancement in crop yield occurs when an optimal LAI value is reached which depends on plant species, light intensity, leaf shape or leaf angle (Marschner, 1995).

Nitrogen (N) availability during growth and development plays a major role in establishing and maintaining a photosynthetic active canopy (Rathke et al., 2006). In general, an optimal external N supply has a substantial effect on the LAI and the amount of N per unit leaf area (Mae, 1997; Jensen et al., 1996). Several studies demonstrated that an increase in external N supply substantially increased the LAI and crop growth rate (Porter and Remkes, 1990). Porter and Evans (1998) demonstrated that the activity of Rubisco (ribulose-1,5-bisphosphate carboxylase) in the leaves increased with increasing N supply. On the other hand, increased N supply resulted only in a slight effect on the rate of photosynthetic capacity but a strong positive effect on the productivity due to higher LAI and extended period of photosynthetic activity (Gammelvind et al., 1996; Kappen et al., 1998). Despite a low leaf N content a high photosynthetic rate under low N conditions may be maintained occur because of high incoming photosynthetic active ration (PAR) at low plant density (Chapman et al., 1984; Zhaou and Lin 1997).

Although the maximum surface area of the pods is nearly the same as that of the leaves (Allen and Morgen, 1972), from regrowth in early spring until end of flowering the leaf area is the major source of light interception and carbon assimilation of oilseed rape (*Brassica napus* L.) and plays a key role in yield determination of this crop (Ogunlela et al., 1989; Grosse et al., 1992a; Diepenbrock, 2000). However, as all other winter crops (Gabrielle et al., 1998b), the LAI of oilseed rape is substantially affected by leaf losses occurring during vegetative growth. During the winter period due to low temperature and low light intensity (Diepenbrock, 1981;

Grosse et al., 1992a) and in spring shortly after beginning of flowering due to shading initially by the flowers and later by the pods (Gabrielle et al., 1998b) substantial leaf dropping and thus losses in dry matter, stored N and a decline in LAI occurred. The N released to the soil in leaf litter during winter is partially recovered as mineral N during stem extension (Dejoux et al., 2000). The N returned to the soil during spring by the dropped leaves is not taken up again by this crop (Malagoli, 2005). The N content of lost leaves of winter oilseed rape can reach 1.2 - 4.5% of dry weight in winter (Dejoux et al., 2000) and 2 - 2.5% of dry weight in spring (Wright et al., 1988). Moreover, Rossato et al. (2001) reported that the oilseed rape plant can loose up to 15% of its entire N content.

A problem in the cultivation of winter oilseed rape is the large N-balance surplus which is mainly due to the characteristics of the traditional oilseed rape cultivars which always show a high N uptake until flowering, low N uptake during reproductive growth and incomplete N retranslocation from the source organs to the seeds (Aniol, 1993; Lickfett, 1993), leaving high soil mineral N contents and high N amounts in crop residues in the field (Aufhammer et al., 1994; Lickfett et al., 2001). Dropping leaves constitute a substantial proportion of crop residues which return a significant amount of N to the soil (Malagoli, 2005) and may thus contribute to the low N recoveries in harvested organs of oilseed rape (Lickfett and Przemeck, 1997; Lickfett et al., 2001).

It was found that maintaining a high N uptake activity during reproductive growth is an important characteristic of N-efficient cultivars (Behrens, 2002; Chapter I). A high N uptake activity during reproductive growth was associated with an efficient and vigorous root growth of the "N-efficient" cultivar (total root and new root formation) (Chapter II). However, the question remains how these important morphological root traits are achieved. Without continuous assimilate allocation from the leaves, root growth and activity cannot be maintained (Jackson et al., 1986) during reproductive growth. For this, a high leaf area duration or an ongoing photosynthetic activity of the canopy would be essential. On the other hand, a high N retranslocation from the vegetative organs, especially the leaves, to the seeds is desirable. However, if N translocation to the seeds starts too early, the photosynthetic capacity of the canopy will decrease. Therefore, the aim in this study was to investigate the role of leaves for genotypic differences in N efficiency of winter oilseed rape cultivars. Both aspects, the carbon assimilation of the leaves and the importance of the leaves as N source for the seeds were considered.

3. Materials and Methods

3.1 Description of the Experimental Site

To determine the role of leaves for genotypical differences in N efficiency of oilseed rape cultivars, various leaf parameters were investigated in the field experiments conducted in the 1999/2000, 2000/2001 and 2001/2002 cropping periods at Zuchtgarten by the Institute of Plant Nutrition, Leibniz University of Hannover in cooperation with the Institute of Agronomy and Plant Breeding, University of Göttingen. The experimental station Zuchtgarten is located near to Göttingen (51.32° northern latitude and 09.56° eastern longitude). A detailed description of the field experimental site, soil characteristics, and weather conditions can be found in Chapter I.

3.2 Timing and Layout of Measurements

Leaf area development, leaf dropping and leaf defoliation were studied in the field experiments conducted in the 1999/2000, 2000/2001 and 2001/2002 cropping periods at Zuchtgarten. A detailed description of the respective experimental designs can be found in Chapter I. The leaf area index (LAI) was determined at beginning and end of flowering at three levels of N supply (N0: soil mineral N, N1: 120 kg N ha^{-1}, N2: 240 kg N ha^{-1}) in the 2000, 2001 and 2002 field experiments. In 2000 four rape cultivars (Apex, Bristol, Capitol, Lirajet), in 2001 the same cultivars plus one additional (Mohican) and in 2002 two contrasting rape cultivars (Apex and Capitol) and four DH lines (DH4, DH15, DH28, DH42) were compared.

Leaf dropping was assessed from beginning of the flowering until maturity by sampling of dropped leaves in both field experiments in 2000 and 2001 at N0, N1 and N2 supply.

Leaf defoliation was performed at the beginning of flowering and harvests were conducted at the beginning of flowering and at early maturity in the 2000 and 2001 field experiments at N0, N1 and N2 supply. Four rape cultivars (Apex, Bristol, Capitol and Lirajet) were defoliated in 2000 while only two rape cultivars (Apex and Capitol) were used for the leaf defoliation in 2001.

3.3 Measurements and Analysis

3.3.1 Leaf Area Development

Leaf Area Index (LAI) is defined as the one sided green leaf area per unit ground area (m^2) in broadleaf canopies. In three field experiments (2000, 2001 and 2002), LAI was determined at the beginning and end of the flowering. After cutting the plants they were separated into stem, leaf and pod fractions by destructive sampling. A more detailed description of the pre-harvests can be found in Chapter I. After determination of the fresh weight, the leaf area was measured using a leaf area meter (LI-3100, LI-COR Inc., Lincoln, Nebraska, USA).

3.3.2 Sampling of Dropped Leaves

The dropped leaves were collected in the field experiments in 2000 and 2001. In both field experiments, leaf sampling was done either in one or two week intervals from beginning of flowering until no leaves remained on the plants. The leaves were collected from 1 m^2 ground area with the aid of mesh nets covered lath frame (0.20 m wide, 0.15 m high and 2.5 m long). For each research plot two frames (2 x 0.5 m^2 sampling area) were placed in the middle of the second and in the fifth plant row. Each research plot consisted of six plant rows of 7.5 m length and 1.5 m width. The distance between two rows was 25 cm. After each sampling, the collected leaves were dried at 65 °C unto constant weight in a drying oven and, thereafter, the samples were weighed and ground for further analysis.

3.3.3 Leaf Defoliation

Leaf defoliation was carried out at the beginning of flowering and assessed at early maturity in the first (2000) and second (2001) field experiment. Before starting defoliation, from each research plot 1 m^2 area was marked with a blue string. Thereafter, about half of the total leaves (every second leaf from the base) were cut with scissors from the plants in the marked area. All cut leaves were collected in paper bags to determine leaf area, leaf dry weight and leaf N concentration. After defoliation, the marked plots were kept until early maturity. At this stage the plots surrounded by blue strings were harvested manually and plants were separated into leaves, stems and pods. Also, in the same plot 1 m^2 of untreated plants were harvested as control. The plant fractions were dried at 65 °C in a dry chamber, then the samples were weight and ground for further analysis.

3.3.4 Nitrogen Analysis in Leaf Dry Matter

The N concentration (mg N g^{-1}d.w.) in excised and dropped leaves was determined using a CNS analyzer (Vario EL Macro element-analyzer, Elementar Analysensysteme, Hanau, Germany). Dried and ground leaf samples of 15-30 mg weight were placed in tin capsules (6 x 6 x 12 mm), which were carefully closed and pressed using a hand presser to the size fitting exactly into the CNS analyzer sample holder. As a standard, around 3-4 mg sulfanilic acid (MERCK, Germany) (C: 41.6%, N: 8.1% and S: 18.5%) was weighed and placed in tin capsules (0.05 ml). The samples were burnt in 1150 °C and 850 °C in the reducing cup.

4. Results

4.1 Leaf Area Index at Different Growth Stages

At the beginning of flowering, rape plants developed the highest leaf area index (LAI) in three field experiments (Tab. III-1). At this growth stage the differences in LAI between N rates were highly significant in the field experiment in 2000 (A), 2001 (B) and 2002 (C). Plants usually increased their LAI with increasing N supply. Averaged over cultivars the LAI in three field experiments varied between 1.05 and 1.27 m^2 m^{-2} at low N (N0), 2.04 and 2.26 m^2 m^{-2} at medium N (N1) and 2.71 and 3.49 m^2 m^{-2} at high N (N2) at the beginning of flowering. However, due to leaf senescence a substantial decline in LAI occurred from beginning until end of flowering in all field experiments at all N rates. In spite of the reduction the differences in LAI between N rates were highly significant and the LAI was higher with increasing N supply at the end of flowering in all three field experiments. At this growth stage, averaged over cultivars the LAI ranged between 0.24 and 0.62 m^2 m^{-2} at low N (N0), 0.85 and 1.46 m^2 m^{-2} at medium N (N1) and 1.59 and 2.31 m^2 m^{-2} at high N (N2) supply in the three field experiments.

In general, the reduction in LAI was higher at N0 than at N1 and N2 supply. Compared to the previous growth stage plants decreased their LAI by almost 81, 59 and 41% at N0, N1 and N2 supply, respectively, at the end of flowering in 2000 (Tab. III-1 A). Compared to previous field experiment (2000), the decline in LAI was lower at the end of flowering in 2001 (Tab. III-1 B). From beginning until the end of the flowering the decline in LAI was about 41, 28 and 23% at N0, N1 and N2 supply, respectively. In 2002, the reduction in LAI was substantially higher again similar to the 2000 experiment at the end of flowering (Tab. III-1 C). From beginning of flowering till end of the flowering plants reduced their LAI by about 74, 38 and 37% at N0, N1 and N2 supply, respectively, in 2002. Substantial reduction in LAI at all N rates at the end of flowering particularly in 2000 and 2002 might be the result of extremely dry (annual rainfall 591 mm in 2000) and wet seasons (annual rainfall 863 mm in 2002) compared to the favourable season in 2001 (annual rainfall 647 mm) (Chapter I, Fig. MM I-1).

Table III-1: Leaf area indices of oilseed rape cultivars (4, 5 and 6 cultivars) as affected by N supply (N0: soil mineral N, N1: 120 kg N ha^{-1}, N2: 240 kg N ha^{-1}) at Zuchtgarten in 2000 (A), 2001(B) and 2002 (C). Statistics: Separate analysis of variance for different growth stages and experimental years. Means with the same letter are not significantly different at $\alpha = 0.05$ within each N rate.

		Leaf area index [m^2 m^{-2}]				
		Treatment				
Growth stage	**Cultivar**	**N0**	**N1**	**N2**	**Mean**	**F test**
2000 (A)						
Beginning of flowering	Apex	1.33 n.s.	2.41 b	3.07 c	2.27	N supply: ***
	Bristol	1.22 n.s.	1.55 a	2.02 a	1.60	Cultivar: ***
	Capitol	1.33 n.s.	2.18 b	2.63 b	2.05	N x Cult: *
	Lirajet	1.19 n.s.	2.19 b	3.11 c	2.17	
	Mean	1.27 A	2.08 B	2.71 C		
End of flowering	Apex	0.29 n.s.	0.82 n.s.	2.08 b	1.06	N supply: ***
	Bristol	0.21 n.s.	0.77 n.s.	1.40 a	0.80	Cultivar: n.s.
	Capitol	0.23 n.s.	0.95 n.s.	1.41 a	0.86	N x Cult: n.s.
	Lirajet	0.22 n.s.	0.84 n.s.	1.48 a	0.85	
	Mean	0.24 A	0.85 B	1.59 C		
2001 (B)						
Beginning of flowering	Apex	0.98	2.12	2.82	1.97	N supply: ***
	Bristol	0.86	1.92	2.82	1.86	Cultivar: n.s.
	Capitol	1.24	1.96	2.92	2.04	N x Cult: n.s.
	Lirajet	1.04	2.06	3.19	2.10	
	Mohican	1.15	2.15	3.14	2.15	
	Mean	1.05 A	2.04 B	2.98 C		
End of flowering	Apex	0.60 ab	1.85 b	2.49 ab	1.65	N supply: ***
	Bristol	0.57 ab	1.58 ab	2.70 b	1.62	Cultivar: n.s.
	Capitol	0.82 b	1.18 a	2.16 a	1.39	N x Cult: *
	Lirajet	0.29 a	1.42 ab	2.44 ab	1.38	
	Mohican	0.98 b	1.72 b	2.10 a	1.60	
	Mean	0.65 A	1.55 B	2.38 C		
2002 (C)						
Beginning of flowering	Apex	1.11	2.28	3.51	2.30	N supply: ***
	Capitol	1.42	2.29	3.56	2.42	Cultivar: n.s.
	DH4	1.46	2.57	3.63	2.55	N x Cult: n.s.
	DH15	1.12	2.13	3.25	2.17	
	DH28	1.04	2.12	3.44	2.20	
	DH42	1.38	2.16	3.52	2.35	
	Mean	1.25 A	2.26 B	3.49 C		
End of flowering	Apex	0.28 n.s.	1.31 a	2.02 ab	1.20	N supply: ***
	Capitol	0.25 n.s.	1.28 a	2.06 ab	1.20	Cultivar: **
	DH4	0.46 n.s.	2.10 b	2.59 c	1.72	N x Cult: n.s.
	DH15	0.28 n.s.	1.07 a	1.91 a	1.09	
	DH28	0.36 n.s.	1.35 a	1.80 a	1.17	
	DH42	0.32 n.s.	1.36 a	2.28 bc	1.32	
	Mean	0.32 A	1.41 B	2.11 C		

Averaged over N rates, highly significant differences in LAI were found among four rape cultivars at the beginning of flowering, whereas no significant differences existed at the end of flowering in 2000 (Tab. III-1 A). The interaction between N rate and cultivar for LAI was significant at the beginning of flowering, but no interaction between N rate and cultivar occurred at the end of flowering. Cultivars differed significantly in LAI at N1 and N2 at the beginning of flowering and significant differences in LAI among cultivars were also found at the end of flowering at N2. Among cultivars the LAI varied in between 1.55 - 2.41 m^2 m^{-2} at N1 and 2.02 – 3.11 m^2 m^{-2} at N2 at the beginning of flowering. At this stage either at N1 and N2 the highest LAI were shown by Apex and Lirajet whereas the lowest LAI was shown by Bristol at both N rates. At the end of the flowering the LAI among cultivars varied in between 1.40 - 2.08 m^2 m^{-2} at N2. Compared to other cultivars Apex usually tended to be higher in LAI at N0 although a significantly higher LAI than for other cultivars was shown only at N2.

In the second field experiment (2001) averaged over N rates five rape cultivars did not differ in LAI at the beginning of flowering while significant differences in LAI occurred at end of flowering among cultivars at all N rates and the interaction between N rate and cultivar was also significant (Tab. III-1 B). The LAI varied among cultivars in between 0.29 - 0.98 m^2 m^{-2} at N0, 1.18 – 1.85 m^2 m^{-2} at N1 and 2.10 – 2.70 m^2 m^{-2} at N2. Mohican and Capitol showed highest LAI at N0 while the lowest was shown by Lirajet. However, Apex had the highest LAI at N1 while the lowest LAI was shown by Capitol. At high N (N) supply Bristol showed the highest LAI whereas Mohican had the lowest LAI at this N rate. Together this clearly showed that the genotypes (Mohican and Capitol) which had the highest LAI at limiting N (N0) condition showed lowest performance in LAI development at non-limiting N (N2) conditions.

In 2002 no significant differences in LAI occurred among six rape genotypes at the beginning of flowering but highly significant differences were found at the end of flowering (Tab. III-1 C). At the end of the flowering LAI varied among six genotypes in between 1.07 - 2.10 m^2 m^{-2} at N1 and 1.80 – 2.59 m^2 m^{-2} at N2. Consistently either at medium N (N1) or at high N (N2) the highest LAI was shown by the double haploid (DH) genotype DH4. The lowest LAI's at N1 and N2 were shown by DH15 and DH28.

4.2 Leaf Dropping

4.2.1 Cumulative Dry Matter of Dropped Leaves

Figure III-1 shows the cumulative dry matter of dropped leaves of oilseed rape cultivars (means of 4 and 5 cultivars, respectively) as affected by N supply at Zuchtgarten in the field experiments in 2000 (A) and 2001 (B). The results indicate that cumulative dry matter of dropped leaves continuously increased from beginning up to end of flowering at all N rates in both field experiments. In general no more leaf dropping occurred during seed filling at low N (N0) while leaf dropping continued until maturity at medium N (N1) and high N (N2) supply in both experimental years. However, averaged over N rates the cumulative dry matter of dropped leaves was considerably higher in the second field experiment (0.70 t ha^{-1} in 2001) compared to first field experiment (0.34 t ha^{-1} in 2000).

The differences in dry matter of dropped leaves between N levels were small at the beginning of flowering whereas significant differences were found at later growth stages in the first (2000) field experiment. On the other hand, although a similar pattern in leaf dropping could be observed in the second field experiment (2001), the differences were not significant neither at the beginning of flowering or at later developmental stages. From beginning of flowering until no leaves remained on the plants the cumulative dry matter of dropped leaves was in the range of 0.19 t ha^{-1} at low (N0), 0.38 t ha^{-1} at medium (N1) and 0.44 t ha^{-1} at high N (N2) supply in 2000. Thus the dry matter losses via leaf dropping amounted to about 9, 11 and 11% of the total amount of shoot dry matter produced at maturity at N0, N1 and N2, respectively, in 2000 (Fig. I-1 A, Chapter I). In the second field experiment (2001) the cumulative dry matter of dropped leaves at three N rates amounted to 0.55 (N0), 0.73 (N1) and 0.82 (N2) t ha^{-1} which was about 12, 13 and 12% of the total amount of shoot dry matter produced at maturity at N0, N1 and N2, respectively, in 2001 (Chapter I, Fig. I-1 B).

In terms of genotypic differences four oilseed rape cultivars differed significantly in cumulative dry matter of dropped leaves in the first field experiment (2000) at all N rates (Fig. III-2 A). However, in the second field trial (2001) five rape cultivars differed significantly in cumulative dry matter of dropped leaves only at N1 and N2 but not at N0 (Fig. III-2 B).

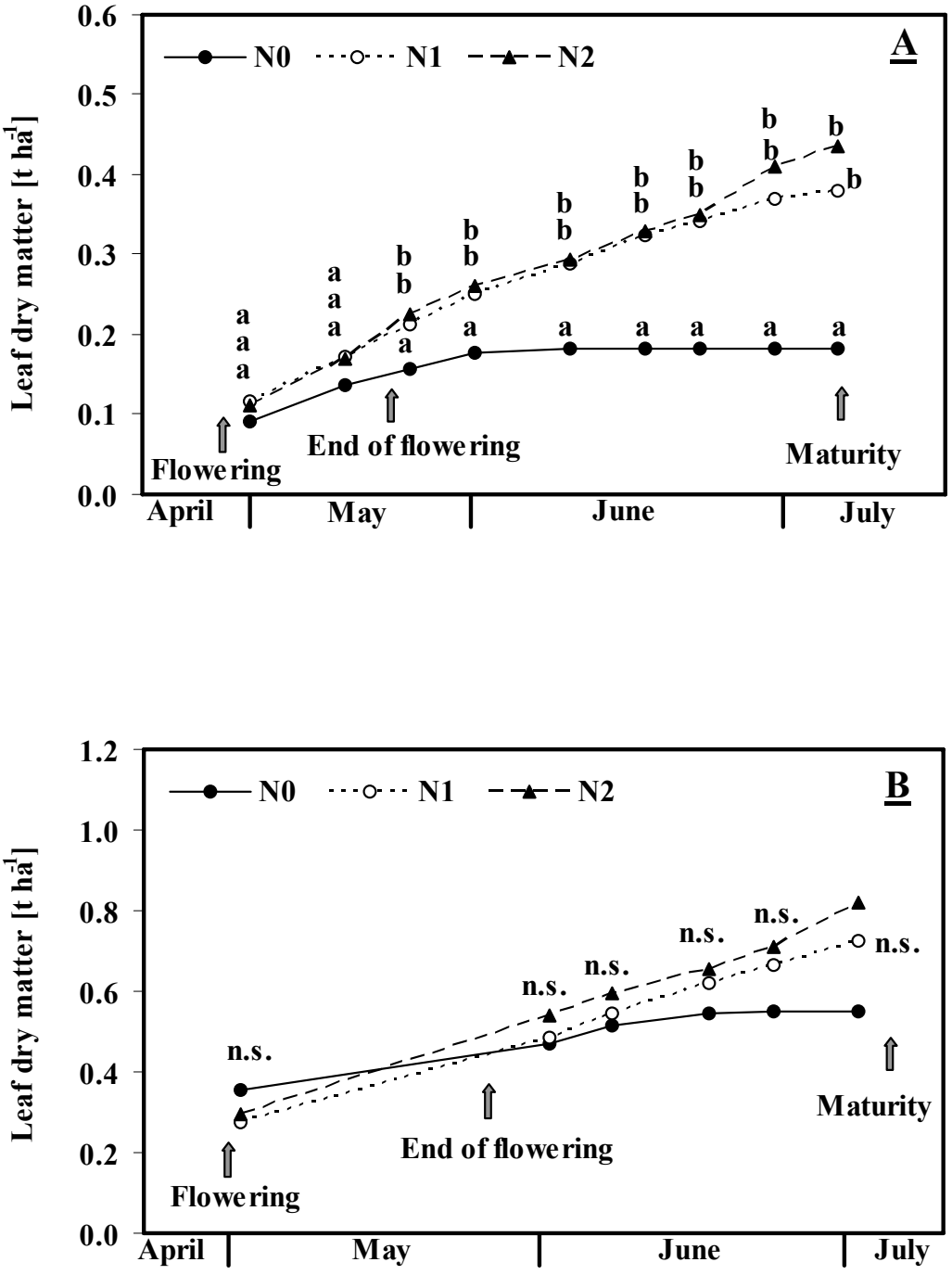


Figure III-1: Cumulative dry matter of dropped leaves of oilseed rape (means of 4 and 5 cultivars in 2000 and 2001, respectively) as affected by N supply (N0: soil mineral N, N1: 120 kg N ha^{-1}, N2: 240 kg N ha^{-1}) at Zuchtgarten in 2000 (A) and 2001 (B) from beginning of flowering until no leaves remained on the plants. Statistics: Separate analysis of variance for different measurement intervals. Means with the same letter are not significantly different at $\alpha = 0.05$.

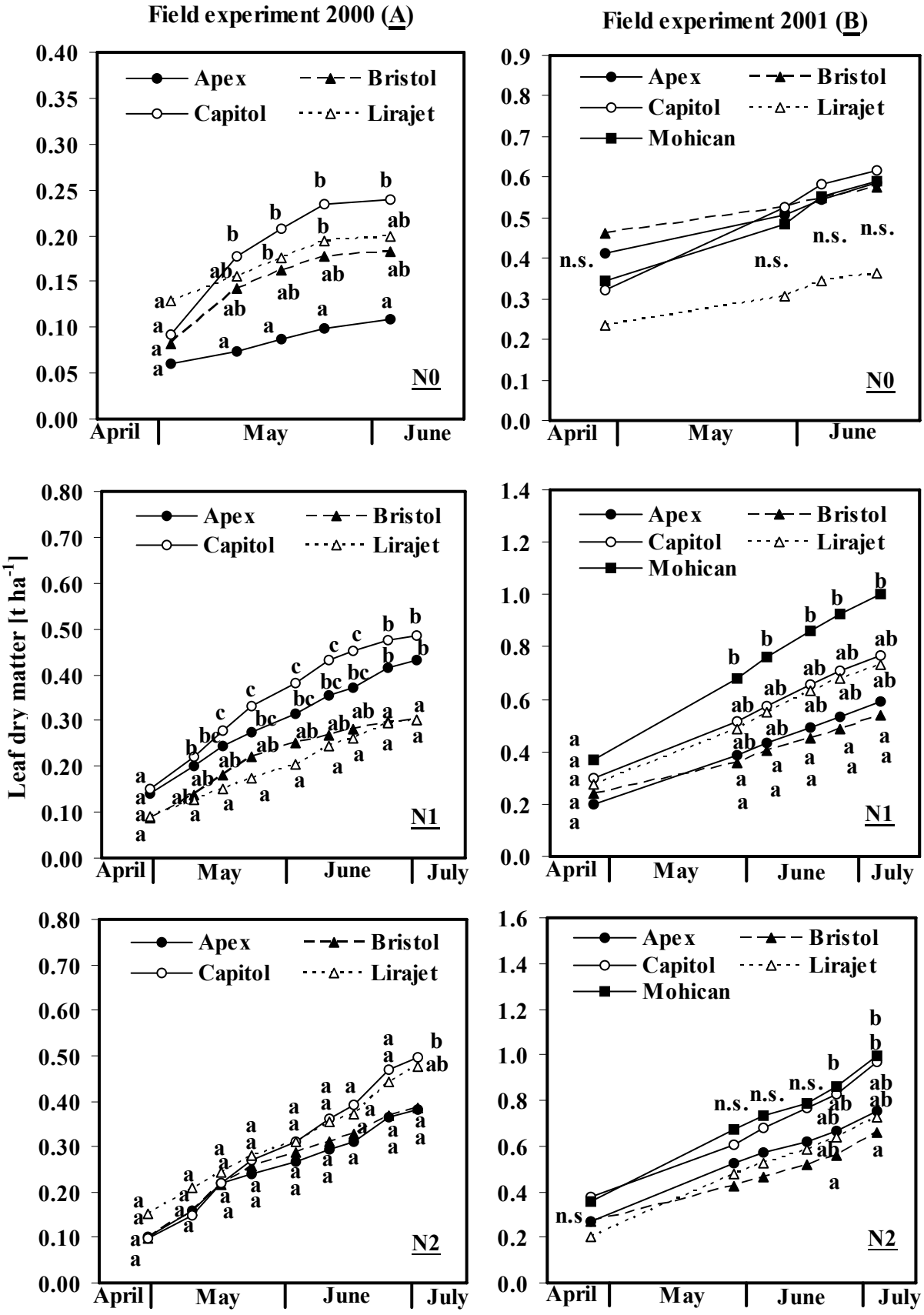


Figure III-2: Cumulative dry matter of dropped leaves of oilseed rape cultivars as affected by N supply (N0: soil mineral N, N1: 120 kg N ha^{-1}, N2: 240 kg N ha^{-1}) at Zuchtgarten in 2000 (A) and 2001 (B). Statistics: Separate analysis of variance for different measurement intervals. Means with the same letter are not significantly different at $\alpha = 0.05$.

The accumulated dry matter of dropped leaves from beginning of flowering until no leaves remained on the plants varied among cultivars between 0.11 and 0.24 t ha^{-1} at N0, 0.30 and 0.49 t ha^{-1} at N1, and 0.38 and 0.50 t ha^{-1} at N2 in 2000 (Fig. III-2 A). Under limiting N (N0) supply the highest cumulative dry matter loss via leaf dropping was shown by the "N-inefficient" cultivar Capitol (0.24 t ha^{-1}) whereas the lowest leaf dry matter loss was shown by the "N-efficient" cultivar Apex (0.11 t ha^{-1}). In terms of leaf dropping pattern, Apex showed a significantly lower leaf dry matter loss than all other cultivars from middle of flowering until no leaves remained on the plants at N0.

Under medium N (N1) supply, Capitol still had the significantly highest dropped leaf dry matter from mid of flowering until maturity compared to the other cultivars. However, opposite to limiting N (N0), leaf dry matter loss of Apex was nearly as high as for Capitol at N1. The lowest dropped leaf dry matter was shown by Lirajet at N1. Although no significant differences occurred among the four rape cultivars in cumulative dry matter of dropped leaves until maturity, cultivars differed in dropped leaf dry matter at maturity at high N (N2) supply. Capitol and Lirajet showed a significantly higher dropped leaf dry matter than Bristol and Apex at this N rate.

In the second field experiment (2001) the cumulative dropped leaf dry matter from beginning of flowering until no leaves remained on the plants varied among cultivars between 0.36 and 0.62 t ha^{-1} at N0, 0.54 and 1.00 t ha^{-1} at N1, and 0.66 and 1.00 t ha^{-1} at N2 supply (Fig. III-2 B). Although the absolute amounts of leaf dry matter losses were substantially lower for Lirajet, no significant differences were found among five rape cultivars in cumulative dropped leaves dry matter from beginning of flowering until no leaves remained on the plants at low N (N0) supply. On the other hand, under medium N (N1) supply the highest cumulative dry matter loss via leaf dropping was shown by Mohican (1.00 t ha^{-1}) whereas the lowest leaf dry matter losses were shown by Apex (0.59 t ha^{-1}) and Bristol (0.54 t ha^{-1}). In terms of leaf dropping pattern, Mohican had the highest leaf dry matter losses compared to the other cultivars from mid of flowering until maturity at N1. Although a similar leaf dropping pattern was evident for Mohican under high N (N2) supply, significant differences among cultivars could be found only at early maturity at his N rate. Capitol showed similar amounts of dropped leaf dry matter as Mohican at N2, while Bristol had the lowest dropped leaf dry matter.

Differences in leaf dry matter losses among N rates or cultivars may either reflect variation in the retranslocation of assimilates prior to leaf shedding or differences in total leaf dry matter produced until the beginning of flowering. Results indicated that plants produced around 1.0, 1.4 and 1.6 t ha^{-1} leaf dry matter at N0, N1 and N2, respectively, at the beginning of flowering in 2000 (Tab. III-2, at page 133). From these amounts about 18, 28 and 27% dry matter was lost via leaf dropping until maturity at N0, N1 and N2 supply, respectively.

Among four rape cultivars highly significant differences were found in leaf dry matter production at the beginning of flowering and the dry matter losses (%) in dropped leaves until maturity. The highest leaf dry matter losses were shown by Capitol (23%) and Lirajet (24%) while the lowest leaf dry matter was lost by Apex (11%) at N0. Interestingly, in spite of similarly high leaf dry matter productions, Bristol lost much less leaf dry matter than Capitol at N0, indicating that leaf loss was not only dependent on the initial leaf dry matter production. Also, in spite of a low leaf dry matter production, leaf loss was significantly highest for Capitol (49%) at N1. On the other hand, Apex and Bristol had significantly highest leaf dry matter productions although the leaf dry matter losses (%) were comparatively low at N1. Furthermore, Apex had the highest leaf dry matter but the lowest cumulative dropped leaf dry matter and thus showed the lowest dry matter loss (22%) at N2. In contrast, Capitol had the lowest leaf dry matter but had highest cumulative dropped leaf dry matter and thus showed highest dry matter loss (50%) at N2.

In the second field experiment (2001) the results indicated that the rape plants produced around 0.9, 1.4 and 1.8 t ha^{-1} leaf dry matter at N0, N1 and N2, respectively, at the beginning of flowering (Tab. III-3, at page 134). From these amounts of leaf dry matter about 65, 51 and 50% dry matter was lost via leaf dropping up to maturity at N0, N1 and N2 supply, respectively, in 2001. Among five rape cultivars no significant differences were found in leaf dry matter production at the beginning of flowering and the dry matter losses (%) in dropped leaves up to maturity at all N rates. However, cultivars differed significantly in cumulative dry matter (t ha^{-1}) of dropped leaves at N1 and N2. The highest cumulative dry matter of dropped leaves was shown by Mohican at N1. At N2, Mohican and Capitol had the highest cumulative dry matter of dropped leaves.

4.2.2 Nitrogen Concentration of Dropped Leaves

Figure III-3 shows the leaf N concentration of dropped leaves of oilseed rape cultivars (means of 4 and 5 cultivars, respectively) as affected by N supply in 2000 (A) and 2001 (B) at Zuchtgarten from beginning of flowering until no leaves remained on the plants. Averaged over N rates the nitrogen concentration was highest for leaves collected at the beginning of flowering in both field experiments. However, a decline in leaf nitrogen concentration occurred at later developmental stages at all N rates in 2000 and 2001. After continuous decline in leaf N concentration, a slight increase occurred after the end of flowering at all N rates and at seed filling under medium N (N1) and high N (N2) rates in the field experiment in 2000. This could be due to dropping of some younger leaves which contained more N, and thus the leaf N concentration slightly increased. In both field experiments leaf N concentration at low N (N0) could be determined only until seed filling since no more leaf dropping occurred after that. On the other hand, leaf N concentration could be determined until maturity due to continuous leaf dropping at medium N (N1) and high N (N2) supply.

In spite of the substantial difference in cumulative dropped leaf dry matter between the two experimental years (Fig. III-1 A, B), leaf N concentrations were similar averaged over N rates (Fig. III-3 A, B). However, during the whole period of leaf dropping significant differences were found between the three N rates in both field experiments. Generally, in both field experiments the dropped leaves under non-limiting N (N2) supply had the highest N concentrations, medium leaf N concentrations occurred at moderate N supply and the lowest leaf N concentrations were found under limiting N (N0) supply.

In the first field experiment (2000) leaf N concentrations were in the range of 8.84, 15.18 and 20.94 mg g^{-1} d.w. at N0, N1 and N2, respectively, at the beginning of flowering. Leaf N concentrations were reduced to 5.69, 11.44 and 16.12 mg g^{-1} d.w. at N0, N1 and N2, respectively, at the end of flowering. However, slight increases occurred at later growth stages and thus leaf N concentrations were 6.86 mg g^{-1} d.w. at N0 at seed filling. Similar enhancements in leaf N concentrations were found also at maturity and hence the leaf N concentrations were 16.27 mg g^{-1} d.w. at N1 and 19.09 mg g^{-1} d.w. at N2.

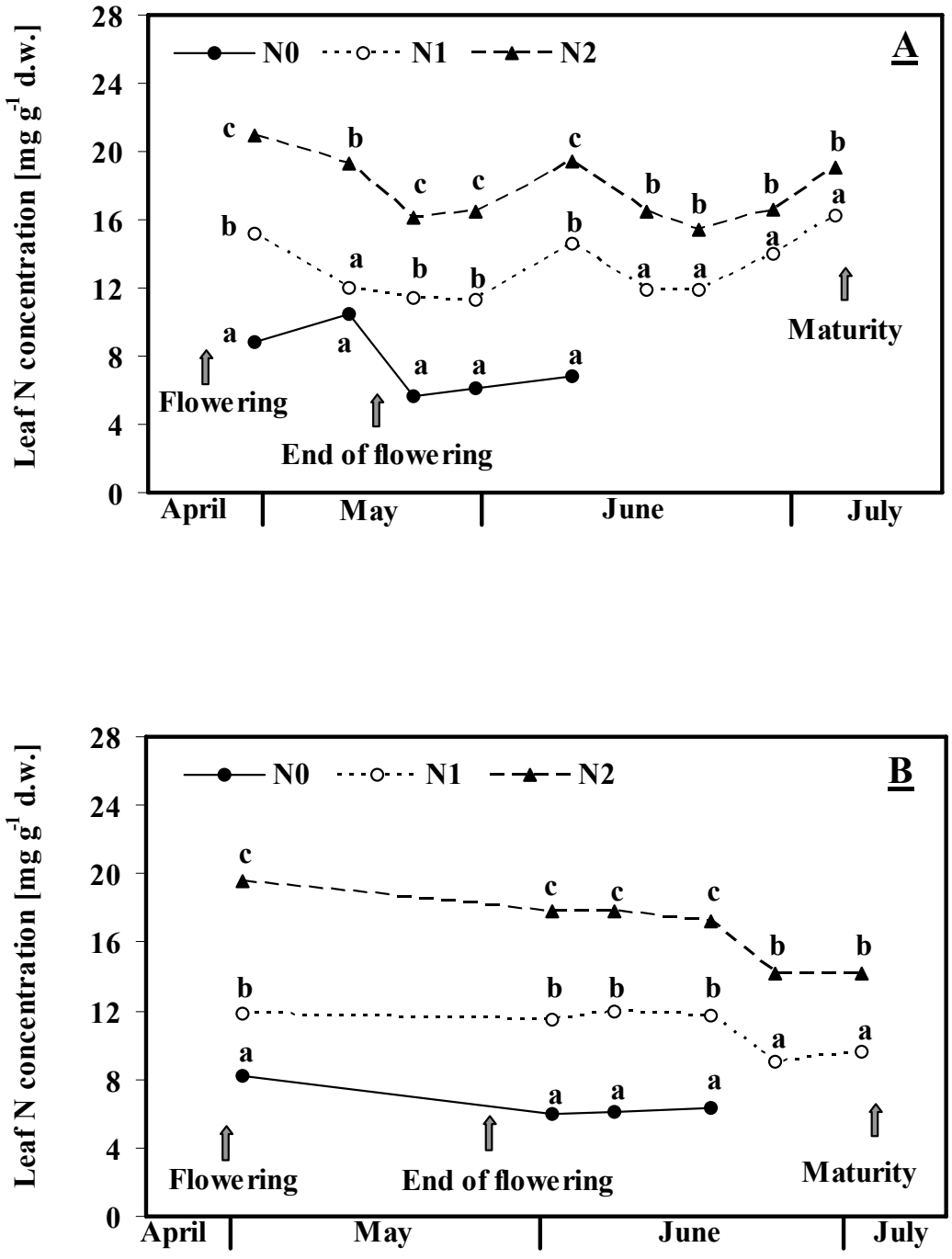


Figure III-3: Nitrogen concentration of dropped leaves of oilseed rape (means of 4 and 5 cultivars, respectively) as affected by N supply (N0: soil mineral N, N1: 120 kg N ha^{-1}, N2: 240 kg N ha^{-1}) at Zuchtgarten in 2000 (A) and 2001 (B) from beginning of flowering until no leaves remained on the plants. Statistics: Separate analysis of variance for different measurement intervals. Means with the same letter are not significantly different at $\alpha = 0.05$.

In the second field experiment (2001) leaf nitrogen concentrations were in the range of 8.23, 11.88 and 19.56 mg g^{-1} d.w. at N0, N1 and N2, respectively, at the beginning of flowering. Thereafter leaf N concentrations declined to 6.02, 11.48 and 17.77 mg g^{-1} d.w. at N0, N1 and N2, respectively, at the end of flowering. However, opposite to the 2000 field experiment no increase occurred at later growth stages in 2001 and thus leaf N concentrations were 6.31 mg g^{-1} d.w. at N0 at seed filling and 9.63 mg g^{-1} d.w. at N1 and 14.23 mg g^{-1} d.w. at N2 at maturity.

Cultivars differed significantly in leaf N concentrations of dropped leaves at all N rates in both 2000 and 2001 field experiments (Fig. III-4 A, B). In 2000 cultivars differed significantly at almost all measurement dates from beginning of flowering until seed filling (N0) and maturity (N1 and N2). Under limiting N supply Lirajet had the significantly highest leaf N concentration in dropped leaves at the beginning of flowering, during flowering and at seed filling whereas Capitol had the lowest N concentration at most measurement dates. At medium N (N1) supply Apex showed the highest N concentration in dropped leaves at the beginning of flowering while the lowest was shown by Capitol. Thereafter, similar to limiting N supply (N0), Lirajet had the highest leaf N concentration and Capitol the lowest. Similar and highest leaf N concentrations were shown by Lirajet and Apex at N2 supply until the end of flowering, During seed filling until maturity Lirajet had significantly higher leaf N concentrations than Capitol with leaf N concentrations of Apex and Bristol ranging in between.

Among five rape cultivars the N concentrations in dropped leaves varied in between 7.25 and 9.77 mg g^{-1} d.w. at N0, 10.79 and 13.32 mg g^{-1} d.w. at N1 and 15.52 and 25.05 mg g^{-1} d.w. at N2 supply at the beginning of flowering in 2001 (Fig. III-4 B). Similar to the previous field experiment (2000), Lirajet showed the highest leaf N concentrations at this growth stage whereas the lowest were shown by Bristol and Capitol at N0. Also at the higher N rates (N1 and N2) Lirajet still had the highest N concentrations in dropped leaves while the lowest were shown by Bristol and Capitol. During later growth stages these cultivar differences basically remained the same. Although no significant differences in dropped leaf N concentrations among cultivars occurred at seed filling at N0, the cultivars differed significantly at maturity at N1 and N2. Usually the highest leaf N concentrations were shown by Lirajet and Apex at N1 and N2 whereas the lowest were shown by Bristol and Capitol.

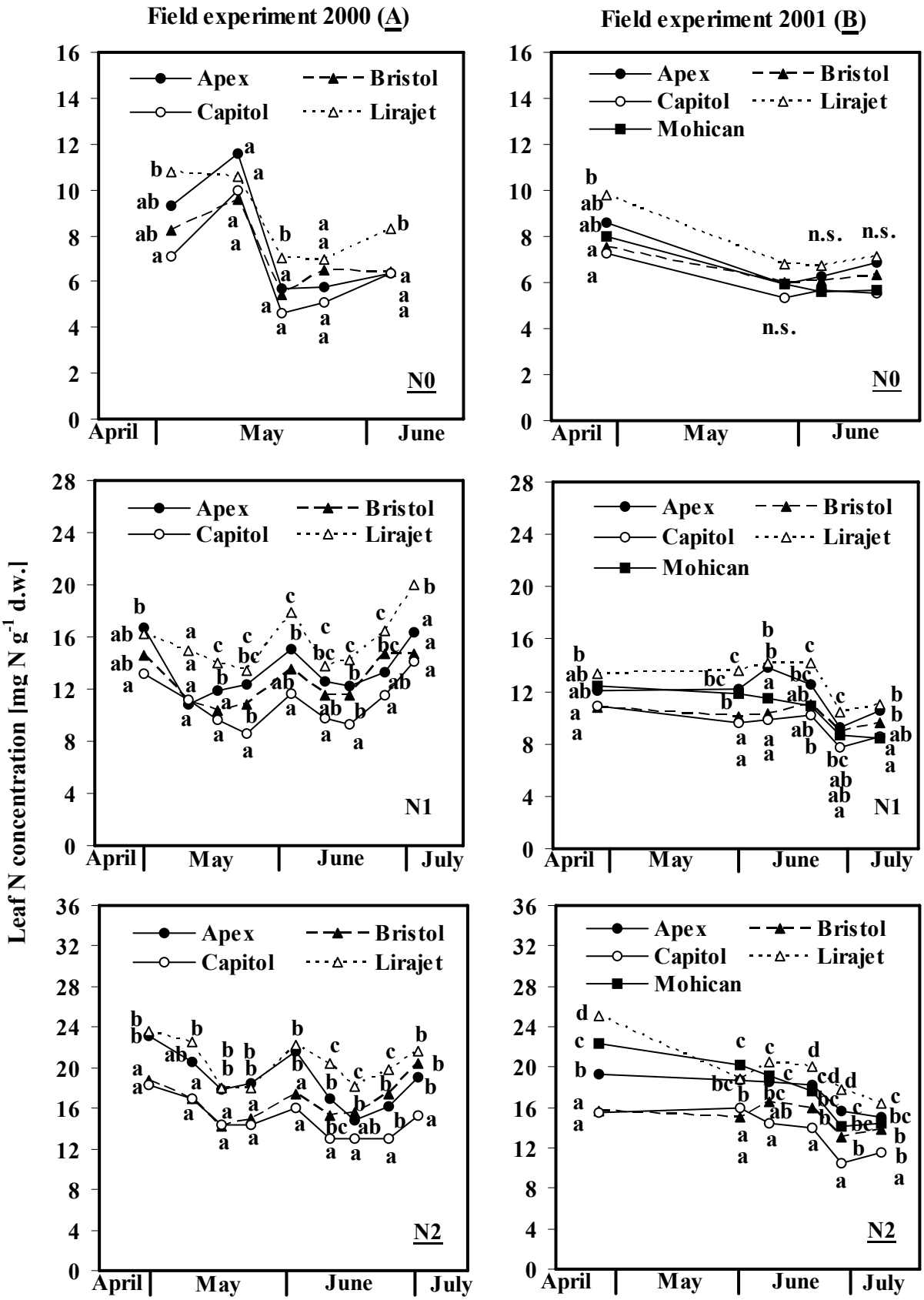


Figure III-4: Nitrogen concentration of dropped leaves of oilseed rape cultivars as affected by N supply (N0: soil mineral N, N1: 120 kg N ha^{-1}, N2: 240 kg N ha^{-1}) at Zuchtgarten in 2000 (A) and 2001 (B). Statistics: Separate analysis of variance for different measurement intervals. Means with the same letter are not significantly different at $\alpha = 0.05$.

4.2.3 Cumulative Nitrogen Content of Dropped Leaves

The results indicate that the cumulative N content of dropped leaves continuously increased from beginning of flowering until the end of flowering at all N rates in the first (2000) and second (2001) field experiment (Fig. III-5 A, B). Due to cessation of leaf dropping during seed filling at low N (N0), the leaf N content remained constant while N accumulation in dropped leaves continued to increase at medium N (N1) and high N (N2) supply due to continued leaf dropping up to early maturity in both field experiments. Averaged over N rates the cumulative N content of dropped leaves was considerably higher in the second field experiment (8.9 kg N ha^{-1} in 2001) compared to first field experiment (4.8 kg N ha^{-1} in 2000). As well, averaged over two field trials the cumulative N content of dropped leaves was substantially lower at limiting N (N0) supply than at medium N (N1) and high N (N2) supply.

The differences in accumulated leaf dry matter between N levels were small at the beginning of flowering whereas significant differences were found at later growth stages in both field experiments. Although no significant differences between N rates in cumulative dry matter of dropped leaves were found either at the beginning of flowering or at later development stages in the second field experiment (2001) (Fig. III-1 B), the differences between N rates in cumulative N content of dropped leaves were highly significant from end of flowering until maturity (Fig. III-5 B).

In both field experiments the highest cumulative N content of dropped leaves from beginning of flowering until maturity was found under non-limiting N (N2) supply whereas the lowest leaf N content was found under limiting N (N0) supply (Fig. III-5 A, B). As well, a moderate leaf N content of dropped leaves was found under medium N (N) supply. From beginning of flowering until no leaves remained on the plants the cumulative N content of dropped leaves was in the range of 1.6 kg N ha^{-1} at N0, 5.0 kg N ha^{-1} at N1 and 7.9 kg N ha^{-1} at N2 in 2000. This indicates that the N losses via leaf dropping were 2.4, 4.0 and 4.4% of the total amount of shoot N content accumulated at maturity at N0, N1 and N2, respectively, in 2000 (Chap. I, Fig. III-1 A). In the second field experiment (2001) the cumulative N content of dropped leaves at three N rates was 4.0 (N0), 8.3 (N1) and 14.4 (N2) kg N ha^{-1} which was 4.4, 5.4 and 6.5% of the total amount of shoot N content accumulated at maturity at N0, N1 and N2, respectively, in 2001 (Chap. I, Fig. III-1 B).

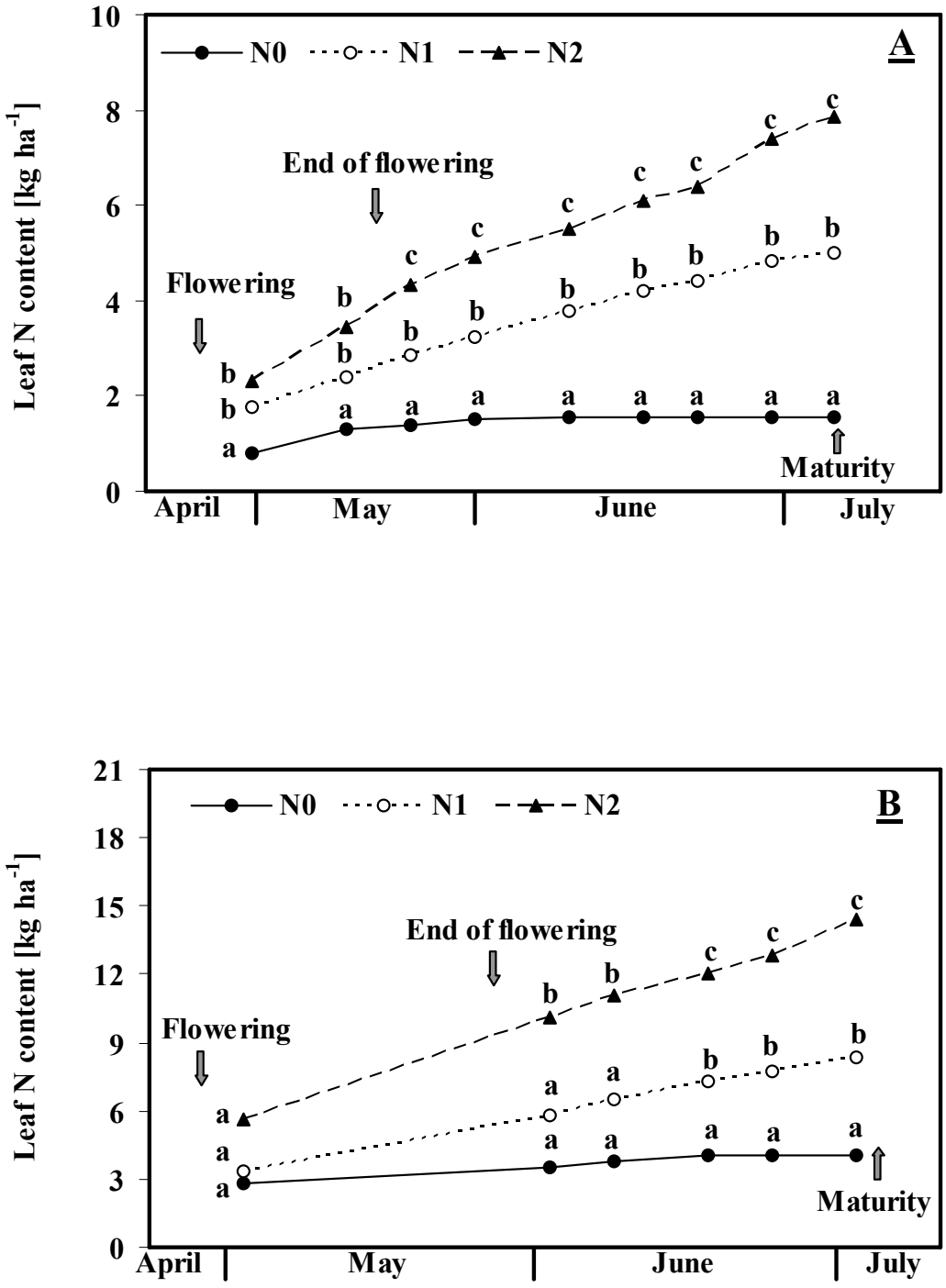


Figure III-5: Cumulative N content of dropped leaves of oilseed rape (means of 4 and 5 cultivars, respectively) as affected by N supply (N0: soil mineral N, N1: 120 kg N ha^{-1}, N2: 240 kg N ha^{-1}) at Zuchtgarten in 2000 (A) and 2001 (B) from beginning of flowering until no leaves remained on the plants. Statistics: Separate analysis of variance for different measurement intervals. Means with the same letter are not significantly different at $\alpha = 0.05$.

In the first field experiment (2000) the four rape cultivars differed significantly in cumulative N content of dropped leaves (Fig. III-6 A). Similar results were found also in the second field experiment (2001) among five rape cultivars (Fig. III-6 B). However, in both field experiments no significant differences among cultivars in leaf N content occurred at low (N0) N supply while highly significant differences were found at medium (N1) and high (N2) N supply. Among four rape cultivars the cumulative N content in dropped leaves was between 0.9 and 1.9 kg N ha^{-1} at N0, 3.8 and 6.0 kg N ha^{-1} at N1 and 6.4 and 10.1 kg N ha^{-1} at N2 at maturity in 2000 (Fig. III-6 A). Although no significant differences were found, Capitol and Lirajet tended to be higher than the other cultivars in cumulative N contents of dropped leaves at N0 in 2000. On the other hand, in the same field trial Apex and Capitol showed significantly highest cumulative N contents from end of flowering till maturity whereas the lowest leaf N contents were shown by Bristol and Lirajet at N1. Furthermore, from beginning of flowering until maturity the highest leaf N content in dropped leaves was shown by Lirajet compared to the other three cultivars at N2 in 2000.

In the second field experiment (2001) among five rape cultivars the cumulative N content in dropped leaves was between 3.4 and 4.4 kg N ha^{-1} at N0, 5.7 and 11.5 kg N ha^{-1} at N1 and 9.8 and 19.3 kg N ha^{-1} at N2 at maturity (Fig. III-6 B). Although no significant differences were found among cultivars at any development stage, Lirajet tended to be lower than the other four rape cultivars in cumulative N contents of dropped leaves at N0 in 2001 which is the opposite result of the previous field trail (2000). On the other hand from end of flowering until maturity Mohican had the highest cumulative N content at N1 and N2, followed by Lirajet, whereas the lowest leaf N content was shown by Bristol.

In order to be able to evaluate the efficiency of N retranslocation from the leaves, N losses via leaf dropping were related to total leaf N content at the beginning of flowering. Results indicated that the plants accumulated about 22, 48 and 67 kg N ha^{-1} in the leaves at N0, N1 and N2, respectively, at the beginning of flowering in 2000 (Tab. III-2 at page 133). From these amounts of leaf N almost 7, 11 and 12% was lost via leaf dropping up to maturity at N0, N1 and N2 supply, respectively

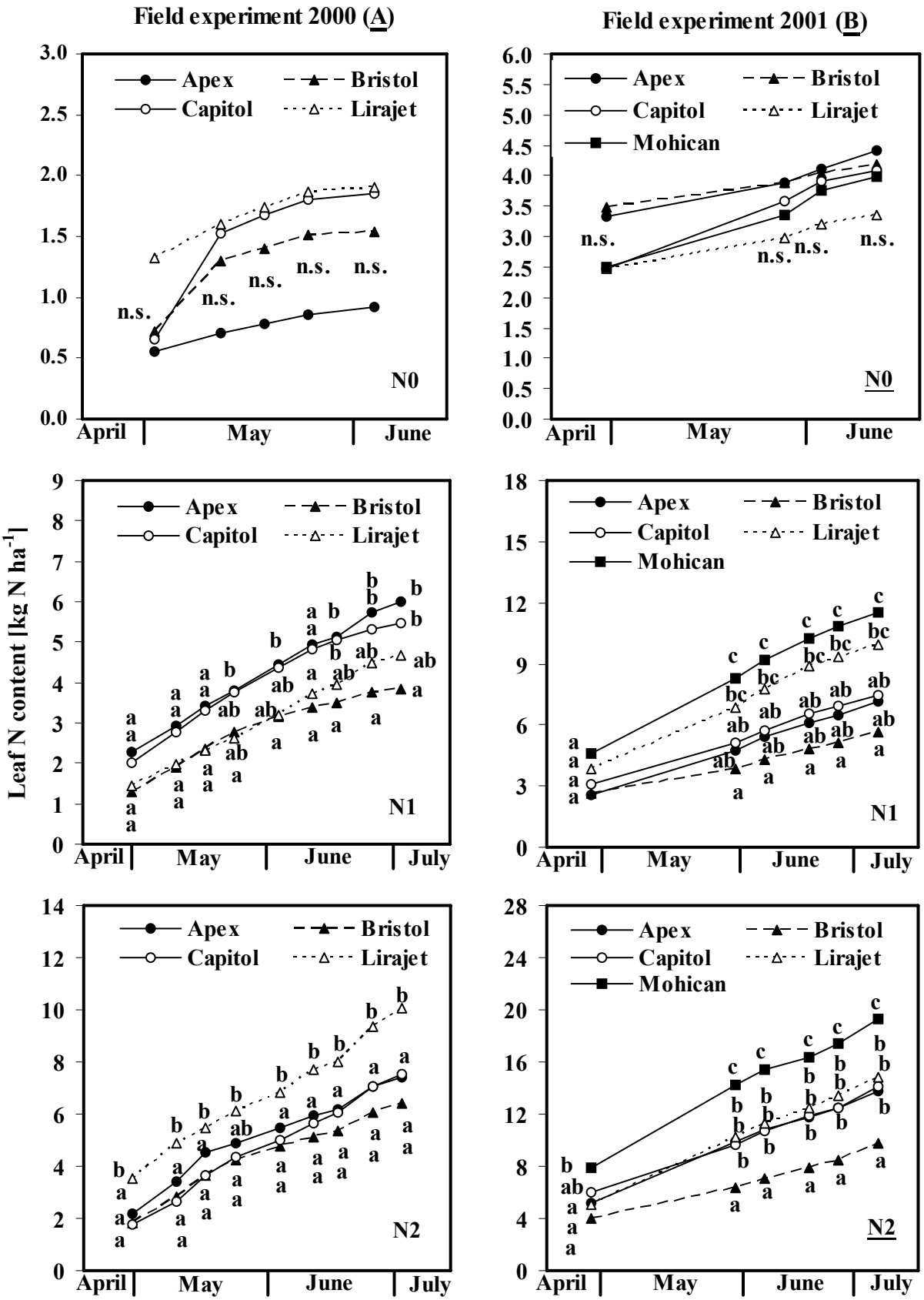


Figure III-6: Cumulative N content of dropped leaves of oilseed rape cultivars as affected by N supply (N0: soil mineral N, N1: 120 kg N ha^{-1}, N2: 240 kg N ha^{-1}) at Zuchtgarten in 2000 (A) and 2001 (B). Statistics: Separate analysis of variance for different measurement intervals. Means with the same letter are not significantly different at $\alpha = 0.05$.

The four rape cultivars differed significantly in total leaf N content at the beginning of flowering and also in absolute and relative N losses (%) of dropped leaves until maturity. Under limiting N (N0) supply no significant differences among cultivars occurred neither in leaf N contents at the beginning of flowering nor in cumulative leaf N content in dropped leaves at maturity. However, cultivars differed significantly in relative leaf N losses (%) at N0. Significantly most leaf N was lost by Lirajet (10%) while least leaf N was lost by Apex (4%) at this N rate. Apex showed the highest leaf N contents at the beginning of flowering at medium N (N1) supply. Although the significantly highest cumulative N content of dropped leaves was shown by Apex and Capitol, no differences in relative leaf N losses (%) were found among cultivars at N1. Under non-limiting N supply (N2), Apex had the highest leaf N content whereas the lowest was shown by Bristol at the beginning of flowering. At this N rate the highest cumulative N content of dropped leaves (10 kg N ha^{-1}) and thus the highest leaf N loss (15%) was shown by Lirajet. By contrast, the lowest leaf N loss was shown by Apex at N2.

Results of the second field experiment (2001) indicated that plants accumulated around 24, 52 and 82 kg N ha^{-1} in the leaves at N0, N1 and N2, respectively, at the beginning of flowering (Tab. III-3). From these amounts of leaf N about 18, 16 and 19% was lost via leaf dropping until maturity at N0, N1 and N2 supply, respectively, in 2001. Among five rape cultivars no significant differences were found in total leaf N content, cumulative N content of dropped leaves and relative N losses under limiting N (N0) supply. However, cultivars differed significantly in cumulative N content of dropped leaves and leaf N losses (%) at medium N (N1) supply. At this N rate the highest cumulative N content of dropped leaves and also the highest relative leaf N loss (23%) was shown by Mohican. In contrast, the lowest N content in dropped leaves and the lowest relative leaf N loss (11%) was shown by Bristol at N1. Bristol had the lowest leaf N loss (13%) also at N2, where Apex showed the highest leaf N loss (26%). Like at N1, Mohican had a comparatively high relative leaf N loss (24%) also at N2.

Table III-2: Total leaf dry matter and leaf N content at the beginning of flowering and dry matter and N content of dropped leaves of 4 oilseed rape cultivars at different N rates (N0: soil mineral N, N1: 120 kg N ha^{-1}, N2: 240 kg N ha^{-1}) at Zuchtgarten in 2000. Statistics: Analysis of variance. Means with the same letter are not significantly different at $\alpha = 0.05$ within each N rate.

Year:2000	**Leaf dry matter [t ha^{-1}]**								
Cultivar	**Total N0**	**Drop N0**	**Loss %**	**Total N1**	**Drop N1**	**Loss %**	**Total N2**	**Drop N2**	**Loss %**
Apex	0.96 ab	0.11 a	11.3 a	1.48 b	0.44 b	29.0 ab	1.81 b	0.38 a	21.5 a
Bristol	1.14 c	0.19 ab	15.8 ab	1.49 b	0.30 a	20.8 a	1.61 a	0.39 a	23.8 ab
Capitol	1.07 bc	0.24 b	22.5 b	1.36 ab	0.49 b	36.3 b	1.51 a	0.50 b	33.3 b
Lirajet	0.87 a	0.20 ab	24.0 b	1.23 a	0.30a	24.8 a	1.61 a	0.48 ab	29.8 ab
Mean	1.01	0.19	18.4	1.39	0.38	27.7	1.64	0.44	27.1

F-test: **total leaves:** N: *** C: *** N x C: **
dropped leaves : N: *** C: ** N x C: *
leaf loss %: N: * C: ** N x C: n.s.

Year: 2000	**Leaf N content [kg N ha^{-1}]**								
Cultivar	**Total N0**	**Drop N0**	**Loss N0%**	**Total N1**	**Drop N1**	**Loss N1%**	**Total N2**	**Drop N2**	**Loss N2%**
Apex	20.7 a	0.9 a	4.4 a	55.4 b	6.0 b	11.0 a	75.7 c	7.4 a	10.1 a
Bristol	25.8 a	1.5 a	5.8 ab	44.2 a	3.8 a	8.9 a	58.7 a	6.4 a	10.9 ab
Capitol	23.7 a	1.9 a	7.7 ab	45.0 a	5.5 b	12.4 a	63.0 ab	7.5 a	12.2 ab
Lirajet	19.1a	1.9 a	10.0 b	47.0 a	4.7 ab	9.9 a	69.0 bc	10.1 b	14.7 b
Mean	22.3	1.6	7.0	47.9	5.0	10.6	66.6	7.9	12.0

F-test: **total leaves:** N: *** C: * N x C: *
dropped leaves: N: *** C: ** N x C: **
leaf loss %: N: * C: * N x C: n.s.

Table III-3: Total leaf dry matter and leaf N content at the beginning of flowering and dry matter and N content of dropped leaves of 5 oilseed rape cultivars at different N rates (N0: soil mineral N, N1: 120 kg N ha^{-1}, N2: 240 kg N ha^{-1}) at Zuchtgarten in 2001. Statistics: Analysis of variance. Means with the same letter are not significantly different at $\alpha = 0.05$ within each N rate.

Year: 2001	**Leaf dry matter [t ha^{-1}]**								
Cultivar	**Total N0**	**Drop N0**	**Loss %**	**Total N1**	**Drop N1**	**Loss %**	**Total N2**	**Drop N2**	**Loss %**
Apex	0.80	0.61 a	79.76	1.49	0.59 a	39.97	1.57	0.76 ab	65.57
Bristol	0.89	0.57 a	62.93	1.39	0.54 a	39.24	1.85	0.66 a	37.43
Capitol	0.92	0.62 a	71.52	1.40	0.77 ab	55.66	1.80	0.97 b	53.53
Lirajet	0.83	0.36 a	43.61	1.38	0.73 ab	54.49	1.80	0.72 ab	40.39
Mohican	0.92	0.59 a	68.34	1.51	1.00 b	66.32	1.89	1.00 b	52.56
Mean	0.87	0.55	65.23	1.43	0.73	51.14	1.78	0.82	49.90

F-test: **total leaves:** N: *** C: n.s. N x C: n.s.
dropped leaves : N: n.s. C: ** N x C: n.s.
leaf loss %: N: n.s. C: n.s. N x C: n.s.

Year: 2001	**Leaf N content [kg N ha^{-1}]**								
Cultivar	**Total N0**	**Drop N0**	**Loss N0%**	**Total N1**	**Drop N1**	**Loss N1%**	**Total N2**	**Drop N2**	**Loss N2%**
Apex	21.35	4.54 a	22.04 a	55.63	7.12 a	12.58 ab	76.22	13.81 b	25.67 b
Bristol	24.47	4.18 a	16.07 a	54.84	5.66 a	10.49 a	82.04	9.82 a	12.93 a
Capitol	24.99	4.09 a	17.94 a	49.19	7.44 ab	15.57 ab	87.83	14.11 b	16.07 ab
Lirajet	24.54	3.35 a	13.63 a	52.15	9.96 bc	19.39 ab	84.28	14.82 b	17.72 ab
Mohican	23.80	3.97 a	18.14 a	50.12	11.49 c	22.92 b	81.12	19.33 c	24.03 ab
Mean	23.83	4.03	17.56	52.39	8.33	16.19	82.30	14.38	19.28

F-test: **total leaves:** N: *** C: n.s. N x C: n.s.
dropped leaves: N: *** C: *** N x C: **
leaf loss %: N: n.s. C: n.s. N x C: n.s.

4.2.4 Nitrogen Harvest Index, Seed and Straw Nitrogen Uptake in Relation to Cumulative Nitrogen Content in Dropped Leaves

The N harvest index (NHI) of oilseed rape cultivars was calculated including the cumulative N content of dropped leaves from beginning of flowering until maturity in the field experiment in 2000 and 2001 (Tab. III-4 A, B). Besides NHI, seed and straw N uptake were determined in both field experiments (see Chapter I). The results indicated that NHI, seed and straw N uptake were significantly affected by N supply in the first field experiment (Tab. III-4 A). Averaged over N rates cultivars differed significantly in NHI, seed and straw N uptake but no interaction between N and cultivar occurred for any trait. NHI decreased with increasing N supply and amounted to 0.87, 0.80 and 0.74 at N0, N1 and N2 supply, respectively. On the other hand, seed and straw N uptake increased when the N supply increased from N0 to N1 or N2. Plants translocated 57, 102 and 130 kg N ha^{-1} to the seeds, while 7, 24 and 37 kg N ha^{-1} remained in the straw. This corresponds to 13, 20 and 26% of the total N uptake at maturity not translocated to the seeds at N0, N1 and N2 supply, respectively, in 2000.

In 2000 the cultivars did not differ in NHI, seed and straw N uptake at N0. However, significant differences in NHI, seed and straw N uptake occurred at N1 and N2 among the four rape cultivars. Both at N1 and N2, Bristol had the highest NHI whereas Apex had the lowest NHI at both N rates. However, in spite of its low NHI, Apex had the highest seed N uptake at N1, but also the highest straw N content. Also under limiting N supply (N0) Apex tended to have high straw N contents. This reflects the high N uptake capacity of Apex compared to other cultivars.

In 2001 NHI, seed and straw N uptake were significantly affected by N supply (Tab. III-4 A). Similar as in the 2000 field trial the NHI decreased with increasing N supply and ranged between 0.80, 0.79 and 0.73 at N0, N1 and N2 supply, respectively. However, seed and straw N uptake increased with increasing N supply. Plants translocated about 74, 117 and 157 kg N ha^{-1} to the seeds while 14, 23 and 45 kg N ha^{-1} remained in the straw. This means that 20, 21 and 27% of total N uptake at maturity were not translocated to the seeds at N0, N1 and N2 supply, respectively.

Table III-4: Nitrogen harvest index and N contents in seeds and straw (without dropped leaves) at maturity of oilseed rape cultivars at different N supply (N0: soil mineral N, N1: 120 kg N ha^{-1}, N2: 240 kg N ha^{-1}) at Zuchtgarten in 2000 (A) and 2001 (B). Statistics: Separate analysis of variance for different experimental years. Means with the same letter are not significantly different at $\alpha = 0.05$ within each N rate.

			Treatment				
	Year/ Measurements	**Cultivar**	**N0**	**N1**	**N2**	**Mean**	**F test**
2000 (A)	**N harvest index** (including dropped leaves)	Apex	0.86 a	0.74 a	0.69 a	0.76	N : **
		Bristol	0.88 a	0.84 b	0.78 b	0.83	Cult: *
		Capitol	0.87 a	0.77 ab	0.77 b	0.80	N x Cult: n.s.
		Lirajet	0.87 a	0.83 b	0.73 ab	0.81	
		Mean	0.87	0.80	0.74		
	N content seeds [kg N ha^{-1}]	Apex	58.36 a	117.26 b	129.12 ab	101.6	N: ***
		Bristol	58.34 a	99.35 a	137.81 b	98.50	Cult: *
		Capitol	54.82 a	91.81 a	117.49 a	88.04	N x Cult:
		Lirajet	56.12 a	98.54 a	135.08 b	96.58	
		Mean	56.91	101.74	129.88		
	N content straw [kg N ha^{-1}]	Apex	9.09 a	37.65 b	50.02 b	32.25	N: ***
		Bristol	5.98 a	15.42 a	33.13 a	18.18	Cultivar: **
		Capitol	6.36 a	25.84 ab	26.45 a	19.55	N x Cult:
		Lirajet	6.27 a	15.40 a	38.34 ab	20.00	
		Mean	6.93	23.58	36.99		
2001 (B)	**N harvest index** (including dropped leaves)	Apex	0.81 a	0.77 a	0.70 a	0.76	N: **
		Bristol	0.81 a	0.82 c	0.78 b	0.80	Cult: ***
		Capitol	0.79 a	0.80 bc	0.76 b	0.78	N x Cult: ***
		Lirajet	0.80 a	0.77 a	0.70 a	0.76	
		Mohican	0.81 a	0.78 ab	0.69 a	0.76	
		Mean	0.80	0.79	0.73		
	N content seeds [kg N ha^{-1}]	Apex	77.86 a	118.85 a	160.02 bc	118.9	N: ***
		Bristol	66.93 a	116.51 a	169.59 c	117.7	Cult: n.s.
		Capitol	77.28 a	118.00 a	152.99 ab	116.1	N x Cult: n.s.
		Lirajet	73.02 a	109.23 a	156.30 ac	112.9	
		Mohican	76.04 a	122.67 a	143.74 a	114.2	
		Mean	74.23	117.05	156.53		
	N content straw [kg N ha^{-1}]	Apex	13.97 a	28.18 b	55.77 c	32.64	N: ***
		Bristol	11.38 a	19.07 a	39.00 ab	23.15	Cult: ***
		Capitol	16.36 a	21.02 a	34.08 a	23.82	N x Cult: ***
		Lirajet	15.21 a	22.84 ab	51.41 c	29.82	
		Mohican	14.19 a	23.56 ab	44.62 b	27.46	
		Mean	14.22	22.93	44.98		

Averaged over N rates cultivars differed significantly in NHI, seed and straw N uptake and the interaction between N and cultivar was significant for NHI and straw N uptake, indicating that the genotypic differences were not the same for each N rate. At N0 cultivars did not differ in NHI, seed and straw N uptake in 2001. However, significant differences in NHI and straw N uptake but not in seed N uptake occurred at N1. At high N (N2), the five rape cultivars differed in NHI, seed and straw N uptake. At medium N (N1), Bristol had a significantly higher NHI than Apex, Lirajet and Mohican. The highest NHI of Bristol at N1 was not associated with a high seed N uptake because no significant differences were found among cultivars at this N rate. At high N (N2), Bristol and Capitol had a significantly higher NHI compared to the other three cultivars. The highest NHI of Bristol at N2 might be explained by the highest seed N uptake at N2. However, this relationship was not true for Capitol. Furthermore, significant differences among cultivars occurred in straw N uptake at N1 and N2. Apex had the significantly highest straw N uptake compared to Bristol and Capitol at N1. At high N (N2) supply Apex and Lirajet had the highest straw N uptake whereas the lowest was shown by Capitol at this N rate.

4.3 Effect of Defoliation on the Seed Yield, Dry Matter Production and Nitrogen Uptake

To assess the importance of leaves for genotypic differences in nitrogen efficiency of oilseed rape cultivars, plants were defoliated at the beginning of flowering in the field experiments in 2000 and 2001 at Zuchtgarten. Harvest of control and defoliated plants was carried out at early maturity in both field experiments. Table III-5 shows seed yield, shoot dry matter and shoot N uptake of four rape cultivars as affected by defoliation at different N rates in the first field experiment (2000). Results indicated that significant differences in seed yield occurred between N rates and defoliation reduced seed yield significantly compared to control plants. At low N (N0) supply, except Apex, all cultivars significantly reduced their seed yield when they were defoliated. However, Apex and Lirajet reduced their seed yield due to defoliation while no significant differences in seed yield were shown by Bristol and Capitol at medium N (N1) supply. All four cultivars responded similar in seed yield with and without defoliation at high N (N2) supply.

Table III-5: Seed yield, shoot dry matter and shoot N uptake of 4 oilseed rape cultivars as affected by defoliation (Control: without defoliation; Def.: half of the leaves were removed at the beginning of flowering) at different N rates (N0: soil mineral N, N1: 120 kg N ha^{-1}, N2: 240 kg N ha^{-1}) at Zuchtgarten in 2000. Statistics: Analysis of variance over N rates and within each N rate. Cultivars effects were tested within each N rate. Means with the same letter represent defoliation effects that were not significantly different at $\alpha = 0.05$ within each cultivar.

Year: 2000			**Seed yield [t ha^{-1}]**				
	Control	**Def.**	**Control**	**Def.**	**Control**	**Def.**	
Cultivar	**N0**	**N0**	**N1**	**N1**	**N2**	**N2**	**F-test**
Apex	1.96 a	1.87 a	3.53 b	2.95 a	3.75 a	3.54 a	N: ***
Bristol	1.82 b	1.45 a	3.74 a	3.73 a	4.42 a	3.97 a	Def: ***
Capitol	1.85 b	1.58 a	3.74 a	3.41 a	4.67 a	3.81 a	N x Def: n.s.
Lirajet	1.95 b	1.69 a	3.40 b	2.95 a	3.99 a	3.65 a	
Mean	1.90 A	1.64 A	3.60 A	3.26 A	4.21 B	3.74 A	
F-test	C: * Def: ***		C: n.s. Def: *		C: n.s. Def: n.s.		
	C x Def: n.s.		C x Def: n.s.		C x Def: n.s.		

Year: 2000			**Shoot dry matter [t ha^{-1}]**				
	Control	**Def.**	**Control**	**Def.**	**Control**	**Def.**	
Cultivar	**N0**	**N0**	**N1**	**N1**	**N2**	**N2**	**F-test**
Apex	8.84 a	8.52 a	13.80 b	11.47 a	15.84 a	15.14 a	N: ***
Bristol	8.64 b	7.14 a	13.81 a	14.36 a	16.35 a	14.52 a	Def: ***
Capitol	8.57 a	8.27 a	13.68 a	13.21 a	15.78 a	13.97 a	N x Def: n.s.
Lirajet	8.35 a	7.63 a	12.82 a	12.13 a	15.89 b	13.54 a	
Mean	8.60 A	7.89 A	13.53 A	12.79 A	15.97 B	14.29 A	
F-test	C: n.s. Def: **		C: n.s. Def: n.s.		C: n.s. Def: *		
	C x Def: n.s.		C x Def: n.s.		C x Def: n.s.		

Year: 2000			**Shoot N uptake [kg N ha^{-1}]**				
	Control	**Def.**	**Control**	**Def.**	**Control**	**Def.**	
Cultivar	**N0**	**N0**	**N1**	**N1**	**N2**	**N2**	**F-test**
Apex	74.6 a	69.9 a	147.5 a	119.6 a	220.9 a	195.2 a	N: ***
Bristol	71.0 b	53.4 a	152.5 a	142.6 a	213.4 a	177.4 a	Def: ***
Capitol	67.3 a	65.4 a	143.5 a	130.1 a	228.4 b	176.9 a	N x Def: n.s.
Lirajet	71.5 a	62.0 a	135.8 a	120.3 a	212.9 a	173.0 a	
Mean	71.1 A	62.7 A	144.8 B	128.1 A	218.9 B	180.6 A	
F-test	C: n.s. Def: **		C: n.s. Def: n.s.		C: n.s. Def: *		
	C x Def: n.s.		C x Def: n.s.		C x Def: n.s.		

Similar to seed yield shoot dry matter was significantly different between N rates, and the rape plants significantly reduced their shoot dry matter when they were defoliated. Only Bristol, but not the other cultivars significantly reduced their shoot dry matter when they were defoliated at N0. Only Apex reduced its shoot dry matter at N1 and Lirajet significantly reduced its shoot dry matter at N2 in response to defoliation.

Results indicated that shoot N uptake was significantly different between N rates, and defoliation significantly reduced shoot N uptake of rape plants. Similar to shoot dry matter, only Bristol significantly reduced its shoot N uptake due to defoliation at N0. No cultivar responded significantly in shoot N uptake when they were defoliated at N1. Only Capitol reduced its shoot N uptake when it was defoliated at N2.

Table III-6 shows shoot dry matter, shoot N uptake and leaf area indices before defoliation at the beginning of flowering and dry matter, N contents and leaf area indices of cut leaves at the time of defoliation in 2000. Before defoliation shoot dry matter was significantly different between N rates. Cultivars differed significantly in shoot dry matter and the interaction between N and cultivars was also significant. Dry matter of cut leaves also differed between N rates and cultivars, but there was no N rate by cultivar interaction. Averaged over cultivars shoot dry matter was in the range of 3.8, 4.6 and 5.1 t ha^{-1} at N0, N1 and N2 supply, respectively. From these amounts of dry matter about 12% (N0: 0.45 t ha^{-1}), 16% (N1: 0.76 t ha^{-1}) and 17% (N2: 0.86 t ha^{-1}) was removed with cut leaves. The highest shoot dry matter was produced by Bristol and Capitol at N0 and N1. The lowest shoot dry matter was produced by Apex at N0 and Lirajet at N1. Apex and Capitol had highest shoot dry matter at N2 whereas the lowest was shown by Bristol. However, no significant differences occurred among cultivars in cut leaf dry matter at N0 and N1, while the significantly highest cut leaf dry matter was shown by Apex at N2.

Results indicated that shoot N uptake was significantly different between N rates before defoliation in 2000 (Table III-6). Cultivars differed significantly in shoot N uptake and the interaction between N and cultivars was also significant. The N content in cut leaves was significantly different between N rates. However, averaged over N rates no significant difference among cultivars occurred in total N uptake and no interaction between N and cultivar was found. The shoot N uptake was in the range of 51, 99 and 139 kg N ha^{-1} at N0, N1 and N2 supply, respectively.

Table III-6: Shoot dry matter, shoot N uptake and leaf area indices before defoliation and dry matter, N uptake and leaf area index of cut leaves of 4 oilseed rape cultivars at different N rates (N0: soil mineral N, N1: 120 kg N ha^{-1}, N2: 240 kg N ha^{-1}) at Zuchtgarten in 2000. Statistics: Analysis of variance. Means with the same letter are not significantly different at $\alpha = 0.05$ within each N rate.

Year: 2000	**Total dry matter [t ha^{-1}]**					
	Shoot			**Cut leaf**		
Cultivar	**N0**	**N1**	**N2**	**N0**	**N1**	**N2**
Apex	3.35 a	4.53 b	5.44 b	0.47 a	0.79 a	0.96 b
Bristol	4.21 b	4.83 bc	4.72 a	0.43 a	0.71 a	0.82 a
Capitol	4.59 b	5.14 c	5.29 b	0.47 a	0.80 a	0.81 a
Lirajet	3.10 a	4.01 a	4.95 ab	0.41 a	0.76 a	0.86 a
Mean	3.81	4.63	5.10	0.45	0.76	0.86
F-test	N: ** C: *** N x C: ***			**F-test**	N: *** C: ** N x C: n.s.	

Year: 2000	**Total N uptake [kg N ha^{-1}]**					
	Shoot			**Cut leaf**		
Cultivar	**N0**	**N1**	**N2**	**N0**	**N1**	**N2**
Apex	46.06 a	108.84 b	160.93 c	10.14 a	29.18 b	35.15 a
Bristol	52.85 a	87.63 a	108.80 a	9.41 a	22.97 a	29.37 a
Capitol	59.53 a	96.73 ab	138.86 b	10.02 a	25.22 ab	31.58 a
Lirajet	45.16 a	102.91 ab	146.70 bc	9.29 a	25.17 ab	33.65 a
Mean	50.90	99.03	138.82	9.71	25.64	32.44
F-test	N: *** C: ** N x C: **			**F-test**	N: *** C: n.s. N x C: n.s	

Year: 2000	**Leaf area index [m^2 m^{-2}]**					
	Leaf before defoliation			**Cut leaf**		
Cultivar	**N0**	**N1**	**N2**	**N0**	**N1**	**N2**
Apex	1.33 n.s.	2.41 b	3.07 c	0.73 n.s.	1.93 n.s.	2.04 n.s.
Bristol	1.22 n.s.	1.55 a	2.02 a	0.58 n.s.	1.44 n.s.	1.53 n.s.
Capitol	1.33 n.s.	2.18 b	2.63 b	0.73 n.s.	1.81 n.s.	1.78 n.s.
Lirajet	1.19 n.s.	2.19 b	3.11 c	0.60 n.s.	1.55 n.s.	2.03 n.s.
Mean	1.27	2.08	2.71	0.66	1.68	1.84
F-test	N: *** C: *** N x C: *			**F-test**	N: *** C: n.s. N x C: n.s	

From these amounts of total shoot N around 19% (N0: 10 kg N ha^{-1}), 26% (N1: 26 kg N ha^{-1}) and 24% (N2: 32 kg N ha^{-1}) was removed with the cut leaves. Cultivars did not differ in total shoot N uptake at N0. The highest shoot N uptake was shown by Apex at N1 and N2 supply whereas the lowest was shown by Bristol at both N rates. Cultivars did not differ in N content of cut leaves at N0 and N2 rates but significant differences occurred among cultivars at N1. The highest leaf N content in cut leaves was shown by Apex while the lowest N content was shown by Bristol at N1.

Leaf area index (LAI) was significantly different between N rates at the beginning of flowering. Cultivars differed significantly in LAI and the interaction between N and cultivars was also significant. Leaf area of cut leaves was significantly different between N rates. However, averaged over N rates no significant difference among cultivars occurred in LAI and no interaction between N rate and cultivar was found. The total shoot LAI was in the range of 1.3, 2.1 and 2.7 m^2 m^{-2} at N0, N1 and N2 supply, respectively. From these amounts about 52% (N0: 0.7 m^2 $m^{-2)}$, 81% (N1: 1.7 m^2 m^{-2}) and 68% (N2: 1.8 m^2 m^{-2}) was removed by defoliation. Cultivars did not differ in LAI at N0. The highest LAI at N1 was developed by Apex, Capitol and Lirajet as compared to Bristol. At N2 supply the highest LAI was shown by Apex and Lirajet whereas the lowest was developed by Bristol. The cultivars did not differ in LAI of the cut leaves at N0, N1 and N2 supply.

Table III-7 shows seed yield, shoot dry matter and shoot N uptake of two rape cultivars as affected by defoliation at different N rates in the 2001 field experiment. Results indicated that significant differences in seed yield occurred between N rates and defoliation reduced seed yield significantly compared to control plants. When both cultivars were defoliated at low N (N0) supply, Capitol significantly reduced its seed yield whereas Apex did not reduce its seed yield. After defoliation no significant grain yield reductions were shown by the two cultivars at medium N (N1) supply. However, cultivars differed significantly at high N (N2), and Apex significantly reduced its seed yield while no reduction in grain yield was shown by Capitol at this N rate. Although no significant differences at all N rates occurred in terms of reduction in shoot dry matter under defoliation treatment, cultivars differed significantly at N0. Similar to seed yield shoot dry matter was significantly reduced by Capitol at N0 while no significant reduction in shoot dry matter was shown by Apex.

Table III-7: Seed yield, shoot dry matter and shoot N uptake of 2 oilseed rape cultivars as affected by defoliation (Control: without defoliation; Def.: half of the leaves were removed at the beginning of flowering) at different N rates (N0: soil mineral N, N1: 120 kg N ha^{-1}, N2: 240 kg N ha^{-1}) at Zuchtgarten in 2001. Statistics: Analysis of variance over N rates and within each N rate. Cultivars effects were tested within each N rate. Means with the same letter represent defoliation effects that were not significantly different at $\alpha = 0.05$ within each cultivar.

Year: 2001			**Seed yield [t ha^{-1}]**				
	Control	**Def.**	**Control**	**Def.**	**Control**	**Def.**	
Cultivar	**N0**	**N0**	**N1**	**N1**	**N2**	**N2**	**F-test**
Apex	2.57 a	2.37 a	4.03 a	3.67 a	5.12 b	4.18 a	N: ***
Capitol	2.82 b	2.23 a	3.81 a	3.77 a	4.95 a	4.60 a	Def: **
Mean	2.69 A	2.30 A	3.92 A	3.72 A	5.03 B	4.39 A	N x Def: n.s.
F-test	C: n.s. Def: *		C: n.s. Def: n.s.		C: n.s. Def: *		
	C x Def: n.s.		C x Def: n.s.		C x Def: n.s.		

Year: 2001			**Shoot dry matter [t ha^{-1}]**				
	Control	**Def.**	**Control**	**Def.**	**Control**	**Def.**	
Cultivar	**N0**	**N0**	**N1**	**N1**	**N2**	**N2**	**F-test**
Apex	8.69 a	8.16 a	12.84 a	11.60 a	13.00 a	13.35 a	N: n.s.
Capitol	8.93 b	7.87 a	11.19 a	11.56 a	13.30 a	12.62 a	Def: **
Mean	8.81 A	8.01 A	12.01 A	11.58 A	13.15 A	12.99 A	N x Def: n.s.
F-test	C: n.s. Def: *		C: n.s. Def: n.s.		C: n.s. Def: n.s.		
	C x Def: n.s.		C x Def: n.s.		C x Def: n.s.		

Year: 2001			**Shoot N uptake [kg N ha^{-1}]**				
	Control	**Def.**	**Control**	**Def.**	**Control**	**Def.**	
Cultivar	**N0**	**N0**	**N1**	**N1**	**N2**	**N2**	**F-test**
Apex	75.35 a	71.73 a	155.93 b	127.16 a	220.14 b	183.46 a	N: ***
Capitol	79.19 a	68.96 a	128.82 a	122.23 a	203.72 a	180.8 a	Def: **
Mean	77.27 A	70.35 A	142.37 A	124.69 A	211.93 B	182.13 A	N x Def: n.s.
F-test	C: n.s. Def: n.s.		C: n.s. Def: n.s.		C: n.s. Def: *		
	C x Def: n.s.		C x Def: n.s.		C x Def: n.s.		

Cultivars responded similar at N1 and N2 and showed no dry matter reductions at these N rates under defoliation. In contrast to shoot dry matter, shoot N uptake of the two cultivars was significantly affected by defoliation at different N supplies. Results indicated that shoot N uptake of both cultivars was not negatively influenced in response to defoliation at N0. However, shoot N uptake was significanty reduced by Apex at N1 and N2. By contrast, no significant reduction in shoot N uptake was shown by Capitol at N1 and N2.

Table III-8 shows shoot dry matter, shoot N uptake and leaf area indices of the two cultivars before defoliation at the beginning of flowering and dry matter, N contents and leaf area indices of cut leaves at the time of defoliation in 2001. Before defoliation shoot dry matter was not significantly different between N rates. Cultivars differed significantly in total shoot dry matter but no interaction between N and cultivars was found. Dry matter of cut leaves also differed between N rates and among cultivars, but there was no N rate by cultivar interaction. Averaged over cultivars shoot dry matter was in the range of 3.6, 4.9 and 5.3 t ha^{-1} at N0, N1 and N2 supply, respectively. From these amounts of dry matter about 13% (N0: 0.48 t ha^{-1}), 14% (N1: 0.70 t ha^{-1}) and 15% (N2: 0.80 t ha^{-1}) was removed with cut leaves. Capitol had higher shoot dry matter than Apex at N0 and N2 rates. Both cultivars did not differ in shoot dry matter at N1. However, no significant differences occurred among both cultivars in cut leaf dry matter at N0 and N1, while the significantly higher cut leaf dry matter was shown by Apex than by Capitol at N2.

Shoot N uptake was significantly different between N rates before defoliation in 2001 (Table III-8). Cultivars did not differ significantly in shoot N uptake and the interaction between N and cultivars was not significant. The N content of cut leaves was significantly different between N rates and among cultivars but no interaction between N and cultivar was found. The shoot N uptake was in the range of 58, 115 and 173 kg N ha^{-1} at N0, N1 and N2 supply, respectively. From the total shoot N uptake around 20% (N0: 12 kg N ha^{-1}), 20% (N1: 23 kg N ha^{-1}) and 19% (N2: 33 kg N ha^{-1}) was removed with the cut leaves. Cultivars did not differ in total shoot N uptake at any N rate. Although no significant differences among both cultivars at N0 and N1 were found in N content of cut leaves, cultivars differed only at N2. Apex had a significantly higher leaf N content than Capitol at N2.

Table III-8: Shoot dry matter, shoot N uptake and leaf area indices at the time of defoliation and dry matter, N uptake and leaf area index of cut leaves of 2 oilseed rape cultivars at different N rates (N0: soil mineral N, N1: 120 kg N ha^{-1}, N2: 240 kg N ha^{-1}) at Zuchtgarten in 2001. Statistics: Analysis of variance. Means with the same letter are not significantly different at $\alpha = 0.05$ within each N rate.

Year:2001	**Total dry matter [t ha^{-1}]**					
	Shoot			**Cut leaf**		
Cultivar	**N0**	**N1**	**N2**	**N0**	**N1**	**N2**
Apex	3.02 a	4.62 n.s.	4.81 a	0.50 n.s.	0.73 n.s.	0.86 b
Capitol	4.22 b	5.12 n.s.	5.86 b	0.46 n.s.	0.66 n.s.	0.73 a
Mean	3.62	4.87	5.34	0.48	0.70	0.80
F-test	N: n.s.	C: **	N x C: n.s.	**F-test**	N: **	C: ** N x C: n.s.

Year: 2001	**Total N uptake [kg N ha^{-1}]**					
	Shoot			**Cut leaf**		
Cultivar	**N0**	**N1**	**N2**	**N0**	**N1**	**N2**
Apex	47.96 n.s.	118.42 n.s.	165.29 n.s.	12.59 n.s.	23.86 n.s.	35.07 b
Capitol	67.53 n.s.	112.42 n.s.	179.73 n.s.	10.31 n.s.	22.62 n.s.	30.67 a
Mean	57.75	115.42	172.51	11.45	23.24	32.87
F-test	N: **	C: n.s.	N x C: n.s.	**F-test**	N: ***	C: * N x C: n.s.

Year: 2001	**Leaf area index [m^2 m^{-2}]**					
	Leaf before defoliation			**Cut leaf**		
Cultivar	**N0**	**N1**	**N2**	**N0**	**N1**	**N2**
Apex	0.98 n.s.	2.12 n.s.	2.82 n.s.	0.75 n.s.	1.45 b	1.72 n.s.
Capitol	1.24 n.s.	1.96 n.s.	2.92 n.s.	0.63 n.s.	1.18 a	1.54 n.s.
Mean	1.11	2.04	2.87	0.69	1.32	1.63
F-test	N: ***	C: n.s.	N x C: n.s.	**F-test**	N: ***	C: ** N x C: n.s.

Before defoliation the leaf area index (LAI) was significantly different between N rates at the beginning of flowering. Cultivars did not differ significantly in LAI and the interaction between N and cultivars was not significant. Leaf area of cut leaves was significantly different between N rates and among cultivars but no interaction between N rate and cultivar was found. The total shoot LAI was in the range of 1.1, 2.0 and 2.9 m^2 m^{-2} at N0, N1 and N2 supply, respectively. From these amounts about 62% (N0: 0.7 m^2 $m^{-2)}$, 65% (N1: 1.3 m^2 m^{-2}) and 57% (N2: 1.6 m^2 m^{-2}) was removed by defoliation. Both cultivars differed only at N1 and LAI of cut leaves was higher by Apex than by Capitol.

5. Discussion

The aim in this chapter was to investigate the role of leaves for genotypic differences in N efficiency of winter oilseed rape. Ideally, to achieve maximum yield, cultivars should retain a high leaf area for a long time to assimilate carbon and then efficiently retranslocate the N from the leaves to support seed growth and minimize N losses.

5.1 Significance of Leaf Characteristics under Varying Nitrogen Supply

Nitrogen availability during growth and development plays a major role in establishing and maintaining a photosynthetic active canopy (Rathke et al., 2006). Several studies demonstrated that an increase in external N supply substantially increased the leaf area index (LAI) of the crops (Porter and Remkes, 1990; Muchow and Sinclair, 1994; Kappen et al., 1998). In agreement with these studies, our results demonstrated that averaged over cultivars LAI increased significantly when the N supply increased from low (N0) to medium N (N1) or to high N (N2) rates either at the beginning of flowering or end of flowering in all three field experiments (2000, 2001 and 2002) at Zuchtgarten (Tab. III-1). As a result of enhancement in LAI, the shoot dry matter and grain yield was significantly increased (Chap. I, Tab. I-1, 2, 3, 5). This is in agreement with several studies which demonstrated a positive correlation between LAI and dry matter and grain yield in various crop species (Booij et al., 1996; Mae, 1997; Gardner et al., 1994; Lafitte and Edmeades, 1994b).

Generally, development of maximum leaf area of oilseed rape is reached until beginning of flowering (Kappen et al., 1998) while a substantial decline in leaf area occurs during reproductive growth (Tayo and Morgan, 1975; Diepenbrock and Grosse, 1995). At the beginning of flowering the decline in leaf area is triggered initially by shading of flowers and later by shading of pods (Gabrielle et al., 1998a). Leach et al. (1989) demonstrated that during flowering almost 60-65% of incoming radiation was absorbed and reflected by the flowers which may result in a decline in photosynthesis up to 40% (Diepenbrock , 2000). In agreement with theses studies, our results clearly indicated that rape plants reached maximum LAI at the beginning of flowering whereas substantial reduction in LAI occurred at the end of flowering in three field experiments (Tab. III-1 A, B, C).

Compared to the 2000 and 2002 field experiments absolute and relative declines in LAI between beginning of flowering and end of flowering were considerably lower in the 2001

field experiment at all N rates. Probably shoot dry matter (Chap. I, Fig. I-1) and grain yield (Chap. I, Fig. I-5) was, therefore, considerably higher in 2001 compared to 2000 and 2002 at all N rates, because assimilate availability at this stage substantially affects seed yield formation, and so the leaves play a major role in determining ultimate number of pods and seeds (Evans, 1984). Differences between experimental years can be explained by the unfavourable weather conditions in 2000 (warm and dry season, low rainfall: 591 mm) and 2002 (heavy rainfall: 863 mm) compared to favourable weather conditions in 2001 (optimal temperature and sufficient rainfall: 647 mm) (Chap. I, Fig. MM I-1).

From beginning until end of flowering the relative decline in LAI was substantially higher at N0 than at N1 and N2. This may be due to leaf senescence, and thus retranslocation of assimilates and N compounds from leaves to the sink organs started earlier at limiting N (N0) than at non-limiting N conditions (N1 and N2). This is in agreement with other studies reporting that the chlorophyll degradation in oilseed rape started almost one week after beginning of flowering at low N and three weeks after flowering under high N conditions (Ogunlela et al., 1989; Sharma and Ghildiyal 1992; Ahmad and Abdin, 2000). Since shading is less under low N conditions compared to high N conditions due to a lighter canopy, leaf losses are most probably induced by decreasing N contents of the leaves due to insufficient N uptake of the roots (Rood et al., 1984; Rossato et al., 2002a).

The significance of leaves for the development of pods and seeds of oilseed rape during reproductive growth was demonstrated in several studies, but also questioned in others. Source limitation starts usually with the beginning of flowering (Grosse, 1989; Diepenbrock, 2000). Allen et al. (1971) supposed that the contribution of leaves to final seed yield of oilseed rape is minor because, leaves senesce during the time of rapid pod growth. Thus, green pods provide a major portion of assimilates for seed growth (Allen and Morgen, 1972). This was also confirmed by Brar and Thies (1977) who found that pods were a source of photosynthates for seed growth. The field study of Major et al. (1978) clearly showed that lower rape leaves exported labelled $^{14}CO_2$ assimilates to the roots, whereas upper stems and leaves exported C primarily to seeds and pods. However, pods did not export labelled assimilates to the other pods or plant parts. Altogether the existing information suggests that the pods are the sinks for assimilates from the leaves and leaves contribute to the final seed yield of rape (Krogman and Hobbs, 1975).

In our study to determine the role of leaves in contributing to the final seed yield of oilseed rape, defoliation via mechanical leaf removal (50% of leaf area) was examined in the 2000 2001 field experiments at low N (N0), medium N (N1) and high N (N2) rates at Zuchtgarten. Results indicated that averaged over cultivars, seed yield, shoot dry matter and shoot N uptake of treated plants were significantly negatively affected by the mechanical defoliation compared to control plants in both field experiments (Tab. III-5, 6). However, influence of defoliation was surprisingly small and different between plant parameter. The relative decline in seed dry matter (14-15% at N0, 5-9% at N1 and 11-13% at N2) was higher than in shoot dry matter (8-9 at N0, 4-6% at N1 and 1-11% at N2), indicating that the defoliation caused a decline in harvest index.

Similar results on defoliation of rape were found by several researchers. Clarke (1978) reported about 30% relative seed yield reduction when the rape plants were defoliated at the beginning of flowering under field conditions. Freyman et al. (1973) found that defoliation at the end of the flowering reduced seed yield by about 35% compared to control plants. Another field study conducted with four *Brassica* species demonstrated that the highest relative yield reduction due to defoliation at late flowering stage varied in between 44-54% among species under high N (315 kg N ha^{-1}) supply (Ramana and Ghildiyal, 1997). Compared to our results in seed yield reduction (5-15%) substantial grain yield reduction (30-54%) under defoliation demonstrated by various other studies might be the result of removing all leaves and also newly formed leaves on the plant instead of an only partly defoliation (50%) which was applied in our study. Clark (1978) demonstrated that leaf removal at the beginning of flowering had a substantial influence on yield components, so that sink capacity was decreased. This finding explains why seed yield was stronger decreased than total shoot dry matter in our study (Tab. III-5, 6).

The relative decline in shoot N uptake due to defoliation was 9-12% at N0, 12-12% at N1 and 14-18% at N2. The absolute decline in shoot N uptake corresponded to the N content of the cut leaves (Tab. III-6, 8). Thus in spite of almost 50% leaf defoliation, the N uptake of rape plants was less strongly influenced compared to shoot and seed dry matter. This means that N uptake was not decreased under defoliation. However, without continuous assimilate allocation from the leaves root growth and activity cannot be maintained (Jackson et al., 1986). Therefore, it appears that the remaining leaves and new developed leaves, which are generally formed on the upper lateral braches after flowering (Major et al., 1978; Diepenbrock

and Geisler, 1985), may be corroborated by a decreasing demand for assimilates of the pods, have been able to allocate sufficient assimilates to the roots to allow them maintaining growth and N uptake. Also the remaining leaves may have had a higher assimilation rate because of a better illumination under the less dense canopy.

Besides N-uptake dynamics and allocation processes, the reason for the low N recoveries in harvested organs of oilseed rape have been attributed to considerable leaf senescence and leaf dropping occurring during winter and spring periods particularly shortly after flowering which returns a significant amount of N to the soil (Lickfett and Przemeck, 1997; Malagoli, 2005). Corroborating these studies our results in two field experiments (2000 and 2001) at Zuchtgarten clearly demonstrated that from beginning of flowering up to maturity substantial leaf losses via dropping occurred at all levels of N supply (Fig. III-1). This explains the absolute reductions in LAI occurring at the end of flowering in 2000 and 2001 at all N rates (Tab. III-1).

Averaged over N rates the cumulative dry matter of dropped leaves was considerably higher in the second field experiment (0.70 t ha^{-1} in 2001) compared to first field experiment (0.34 t ha^{-1} in 2000). This might be due again to the favourable weather condition in 2001 which contributed to enhancement in LAI compared to unfavourable weather condition in 2000 (Chap. I, Fig. MM I-1). In general leaf dropping stopped during seed filling at low N (N0) while leaf dropping continued until maturity at medium N (N1) and high N (N2) supply in both experimental years. This can be explained by earlier onset of leaf senescence and thus retranslocation of assimilates and N compounds from leaves to other sink organs at limiting N (N0) than at non-limiting N supplies (N1 and N2).

The cumulative dry matter of dropped leaves varied in between 0.19-0.55 t ha^{-1} at N0, 0.38-0.73 t ha^{-1} at N1 and 0.44-0.82 t ha^{-1} at N2 in two field trials. Our results corroborated the study of Behrens (2002) who demonstrated between 0.8 and 1.1 t ha^{-1} cumulative dropped leaf dry matter at 240 kg N ha^{-1} fertilization in long-term field studies. Another study indicated that leaf dropping varied not only according to weather conditions, since between 0.6 and 2.8 t ha^{-1} leaf dry matter can be lost at different sites (Macdonald et al., 1997). Similar to dropped leaf dry matter, the N content of dropped leaves was considerably higher in 2001 (8.9 kg N ha^{-1}) than in 2000 (4.8 kg N ha^{-1}). The N content of dropped leaves was substantially lower at N0 than at N1 and N2 supply. However, our result disagree with some

studies demonstrating maximal N contents of dropped leaves between 40-60 kg N ha^{-1} during spring (Hocking et al., 1997; Lickfett and Przemeck, 1997; Gosse et al., 1999). High N content of dropped leaves demonstrated by these authors could be the results of the differences in the period of dropped leaves collection and also applied N fertilizer level. On the other hand, our results confirmed the studies by Aniol (1993), Schjoerring et al. (1995) and Behrens (2002), who reported 18, 20 and 21 kg N ha^{-1} in dropped leaves, respectively, in N-fertilized plots. It thus seems that the N contents lost by dropped leaves quantitatively only play a minor role for the N harvest index (Table III-4) and the N balance of the crop.

5.2 Genotypic Differences in Leaf Characteristics and Its Contribution to Nitrogen Efficiency

It was assumed that higher N efficiency may be achieved by those cultivars which are able to sustain high N uptake rates during reproductive growth because of a better assimilate availability to the roots. Our results (Chapter 2) with the core method in three field experiments (2000, 2001 and 2002) and with the rhizotron method in two field experiment (2000 and 2002) clearly indicated that the "N-efficient" cultivar Apex had a vigorous root growth which was usually associated with a higher root length density and a higher root turn over (new fine root formation) than for the "N-inefficient" cultivar Capitol. Therefore, during reproductive growth the N uptake differences among two cultivars amounted to almost 20 kg N ha^{-1} in 2000, 18 kg N ha^{-1} in 2001 and 28 kg N ha^{-1} in 2002 (Tab. I-12, 13, 14).

A better assimilate availability during reproductive growth to the roots of Apex might be associated with a lower reduction in LAI n between beginning and end of flowering under limiting (N0) N conditions. Despite of the same (in 2000) or a lower (2001 and 2002) LAI at the beginning of flowering, Apex usually tended to have a higher LAI than Capitol at the end of flowering (Tab. III-1). Therefore, a longer leaf area duration (LAD) of Apex might contribute to the assimilate supply of the roots.

However, despite of playing a significant role in assimilate availability during reproductive growth to the roots for the "N-efficient" cultivar, no significant reduction in grain yield was shown by Apex compared to Capitol under almost 50% defoliation at N0 (Tab. III-5, 7). This can be explained by sustained N uptake by Apex even under defoliation compared to Capitol. This might be due to the fact that Apex already had an extensive root system before flowering or because Apex could better compensate for the reduction in leaf area by increasing the

photosynthetic rate of the remaining leaves due to a better illumination under the less dense canopy (Chapman et al., 1984; Zhaou and Lin, 1997).

Although a continued high N uptake activity and thus possibly prolonged LAD during reproductive growth under low (N0) N supply of Apex, the result of dropping leaves examined in two field experiments (Fig. III-2) indicated very small amounts of cumulative dry matter of dropped leaves compared to other cultivars. Actually averaged over cultivars the cumulative leaf N content at both low N (N0) and high N (N2) were very low (1.6-7.9 kg N ha^{-1} in 2000 and 4.0-14.0 kg N ha^{-1} in 2001). Therefore, these losses play a negligible role on the genotypic differences in N harvest index (NHI) compared to genotypic differences in N remaining in the straw (7.0-37.0 kg N ha^{-1} in 2000 and 14.0-45.0 kg N ha^{-1} in 2001) (Tab. III-4).

In conclusion, the result of the present study indicate that, the N-efficient cultivars could be characterized by a lower reduction in LAI and longer leaf area duration (LAD) and thus by an ongoing photosynthetic activity. This clearly indicates a delayed N retranslocation process from the vegetative organs, especially from the stay green leaves, to the seeds of N-efficient cultivars. Furthermore, defoliation experiment indicated that the seed yield of N-efficient cultivars did not significantly influenced and therefore could be also characterized by a better illumination under the less dense canopy to compensate the reduction of LAI by increasing the photosynthetic rate of the remaining leaves.

CHAPTER IV

GENOTYPIC DIFFERENCES IN RADIATION USE EFFICIENCY OF OILSEED RAPE (*BRASSICA NAPUS* L.)

1. Abstract

It was found that maintaining a high N uptake activity during reproductive growth is an important characteristic of N-efficient rape cultivars (Chapter I). This was associated with an efficient and vigorous root growth (Chapter II) owing to adequate assimilate supply from the leaves which is sustained by a greater leaf area and longer leaf area duration (Chapter III). Due to delayed leaf senescence and high leaf area index (LAI) the photosynthetic capacity of the leaves is maintained at a high level during reproductive growth and thus interception of solar radiation and radiation use efficiency (RUE) of N-efficient rape cultivars may be increased. To check this hypothesis, genotypic differences in radiation interception and RUE of two oilseed rape cultivars differing in N efficiency and N uptake during reproductive growth was studied in two field experiments (2001, 2002) at two N rates (N0: soil mineral N, N2: 240 kg N ha^{-1}) at Zuchtgarten, near Göttingen. The cumulative intercepted radiation and RUE was usually higher under N non-limiting (N2) than N-limiting (N0) conditions. The cultivars differing in N efficiency varied also significantly in intercepted radiation and RUE at different growth intervals. Generally the N-efficient cultivar was able to achieve a high light interception than the N-inefficient cultivar at N0. This may be related to a better leaf orientation or advantageous canopy architecture and to delayed leaf senescence of the N-efficient cultivar during reproductive growth. Despite of a high cumulative radiation interception, the N-efficient cultivar had a lower RUE at vegetative stage compared to the N-inefficient cultivar. This may be related to a high assimilate allocation to the roots which was not included into the calculation of RUE. It thus seems that it is not possible to achieve both, high radiation interception and high RUE during vegetative growth. A high crop growth rate during vegetative growth may be achieved with a high crop N uptake. The N-efficient cultivar could be characterized by a high investment in root growth during vegetative growth, which reduced RUE during vegetative growth, but enhanced RUE during reproductive growth due to a high N uptake.

Key words: Solar radiation, light interception, RUE, genotypic variation, cultivar, canopy, *Brassica napus* L.

2. Introduction

Nitrogen supply can affect plant growth and productivity by altering both leaf area and photosynthetic capacity (Novoa and Loomis, 1981; Sinclair and Horie, 1989). At the crop level, photosynthetic capacity can be expressed as radiation use efficiency (RUE) (Muchow and Sinclair, 1994) which is usually defined as conversation efficiency of solar energy into crop biomass (Monteith, 1972). The radiation used may be either: i) the total short wave radiation (intercepted or absorbed radiation) or ii) the photosynthetically active radiation (PAR intercepted or absorbed) (Muchow and Sinclair, 1994). In general, the RUE is defined as the quantity of dry biomass (DM) produced per unit of radiation (MJ) intercepted or absorbed by the crop. The value of the RUE is expressed in grams of aerial dry matter or total dry matter (shoot and root) per mega joule of radiation (g MJ^{-1}). Monteith (1977) presented an analysis of the relationship between the accumulation of crop dry matter and intercepted solar radiation, and concluded that radiation-use efficiency is ≈ 1.4 g MJ^{-1} for many crops.

In terms of solar radiation, oilseed rape (*Brassica napus* L.) has a natural advantage compared to the other annual field crops, because it has the longest growing period, about 350 days from sowing to maturity which allows a long radiation interception of the canopy. However, many authors have shown that the radiation use efficiency of the oilseed rape crop varies within a wide range, from 1.0 to 4.0 g MJ^{-1} according to developmental stage and environmental conditions (Leach et al., 1989; Mendham et al., 1991; Mendham and Salisbury, 1995; Habekotté, 1996, 1997). Justes et al. (2000) reported that N deficiency in oilseed rape caused a significant reduction in the leaf area index (LAI), pod area index (PAI) and thus total absorbed PAR.

The working hypothesis of this study was that N-efficient oilseed rape cultivars may be characterized by maintaining a high N uptake activity during reproductive growth via efficient and vigorous root growth due to adequate assimilate supply from the leaves which sustain a high leaf area and long leaf area duration (delayed leaf senescence). Due to delayed leaf senescence and high leaf LAI, the photosynthetic capacity of the leaves is maintained at a high level during reproductive growth and thus interception of solar radiation and RUE of N-efficient oilseed rape cultivars may be increased. To check this hypothesis, genotypic differences in radiation interception and use efficiency of two oilseed rape cultivars differing in N efficiency and N uptake during reproductive growth was studied in this chapter.

3. Materials and Methods

3.1 Description of the Experimental site

Light interception and radiation use efficiency of oilseed rape cultivars were assessed within the field experiments conducted in the 2000/2001 and 2001/2002 cropping periods at Zuchtgarten by the Institute of Plant Nutrition, Leibniz University of Hannover in cooperation with the Institute of Agronomy and Plant Breeding, University of Göttingen. The experimental station Zuchtgarten is located near to Göttingen (51.32° northern latitude and 09.56° eastern longitude). A detailed description of the field experimental site, soil characteristics and weather conditions can be found in Chapter I.

3.2 Treatments and Experimental Design

Two contrasting oilseed rape cultivars, Apex as "N-efficient" and Capitol as "N-inefficient" , were compared for light interception and radiation use efficiency at low (N0) and high (N2) N supply (N0: soil mineral N, N2: 240 kg N ha^{-1}) in 2001 and 2002. The field experiments were designed as split-plots with N supply as main plots and cultivars as sub plots. Four replications were randomized in a block arrangement. A detailed description of the experimental design of these experiments is given in Chapter I. The incoming global radiation above canopy level and the fractional radiations (reflected, intercepted and transmitted radiation) were measured continuously from the beginning of shooting till maturity. Harvests were performed at the beginning of shooting, beginning and end of flowering and at maturity.

3.3 Measurements and Analyses

3.3.1 Solar Radiation Measurements by Tube and Dome Solarimeters

A solar system was installed on the field to measure continuously the incoming global radiation above canopy level and the fractional radiations (reflected, intercepted and transmitted radiation) at canopy and soil level using tube and dome solarimeters. The solarimeters were installed into four neighbouring plots, two supplied with high N (N2) and two with limiting N (N0), while within each N rate, one plot was cropped with the cultivar Apex and the other with Capitol. The tube solarimeters (TSL, Delta-T Devices, Cambridge, U.K) were 979 mm long and 26 mm in diameter. In 2001, three tube solarimeters were installed into each plot. One tube was placed above canopy level and directed to the sky to

measure the global incoming radiation, and the second one was placed below the canopy at soil level and directed to the sky to measure the transmitted radiation through the canopy. The third tube was placed also above canopy level but directed towards the canopy to measure the reflected radiation from canopy and soil surface. In 2002, two tube solarimeters were placed into each plot at soil level to measure transmitted radiation, one tube solarimeter per plot was used to measure reflectance, and one tube solarimeter was installed above the canopy to measure total incoming radiation as reference for all four plots. Besides the tube solarimeters, as a reference measure of incoming global radiation, a dome solarimeter (Pyranometer-GS1, 36mm in diameter, Delta-T Devices, Cambridge, UK) was placed above canopy level during the plant growing season in both years. Additionally, to convert the transmission measurements into quantum units, a reference PAR Quantum Sensor (Quantum Sensor-QS2, Delta-T Devices, Cambridge, UK) was also placed above the canopy level throughout the plant growing season.

3.3.2 Data Collection

In order to collect the continuously measured solar radiation data from the tube solarimeters, 1 dome solarimeter and 1 PAR quantum sensor the measurement devices were connected to a data logger (Delta-T logger, DL2e, Delta-T Devices, Cambridge, UK). Mean solar measurement values (kW m^{-2} s^{-1}) were recorded every 30 minutes. All the logged data was downloaded weekly to a notebook.

3.3.3 Calculation of Intercepted Radiation

Continuously measured radiation of the tube solarimeters were summed up by converting the 30 minutes recorded mean values of kilowatt (kW m^{-2} s^{-1}) into the unit of kilo joule (kJ) by multiplying by 1800 (30 minutes = 1800 seconds). To convert from kJ into Mega joule (MJ), the value was divided by 1000. After that conversion the radiation data was summed up for 24-hours periods and subsequently for three different growth intervals: i) Beginning of shooting –Beginning of flowering (BS-BF), ii) Beginning of flowering – End of the flowering (BF-EF), iii) End of the flowering – Maturity (EF-MA). The fractions of transmitted, reflected and intercepted radiation were calculated by dividing the sums of each radiation by total incoming radiation as measured by three (2001) or one (2002) tube solarimeters. To consider that PAR is preferentially taken up by the canopy compared to total radiation, the fraction of transmitted PAR was corrected according to Monteith (1993) as:

Fraction of transmitted PAR = Fraction of total transmitted radiation[1.35]

The fraction of intercepted radiation by the canopy was derived as:

Fraction of Intercepted Radiation = (1 – (Fraction of Transmitted PAR + Fraction of Reflected Radiation)

To achieve the absolute amounts of intercepted radiation, the fractions were then multiplied by total global radiation. Before this calculation, total global radiation was converted into photosynthetic active radiation (PAR) by multiplying the data by the factor 0.5 (Sinclair and Muchow, 1999).

3.3.4 Calculation of Radiation Use Efficiency (RUE)

The efficiency of conversation of solar energy into biomass by a crop is usually represented by a synthetic value which is the conversation efficiency of intercepted radiation or radiation use efficiency (RUE) (Monteith, 1972). The RUE is defined as the quantity of dry biomass (g m^{-2}) produced per unit of radiation intercepted or absorbed (MJ m^{-2}) by the crop. In the present study, the incoming global radiation above canopy level and the fractional radiations (transmitted, reflected and intercepted) of two oilseed rape cultivars were measured continuously from beginning of shooting until maturity individually in two field experiments (2001 and 2002). The intercepted radiation was calculated cumulatively for three growth intervals (BS-BF, BF-EF and EF-MA) and for the complete growth period from beginning of shooting until maturity (BS-MA). To calculate the RUE (g MJ^{-1}) for each growth interval the dry matter production (g m^{-2}) was determined for each growth interval and divided into cumulative intercepted radiation calculated at the same growth interval. Dry matter data from the harvests performed on four replications from the same field experiment (Chapter I, Table I-2, I-3) were used for RUE calculations in this study. No harvests were performed in the plots, in which the solarimeters were installed.

In all calculations, the seeds were considered as dry matter (g m^{-2}) like the straw. However, seed dry matter was corrected by an oil factor which is generally proposed in various studies. For calculating RUE for oil plants, it should be considered that the formation of oil in the seeds require higher energy amounts compared to the remaining dry matter. Bange et al. (1997b) calculated the RUE of sunflowers by multiplying each gram of oil by a factor of 2.24 units. This concept was adopted in the current study by calculating an oil correction factor of 2.17 units according to the data reported by Habekotte (1997).

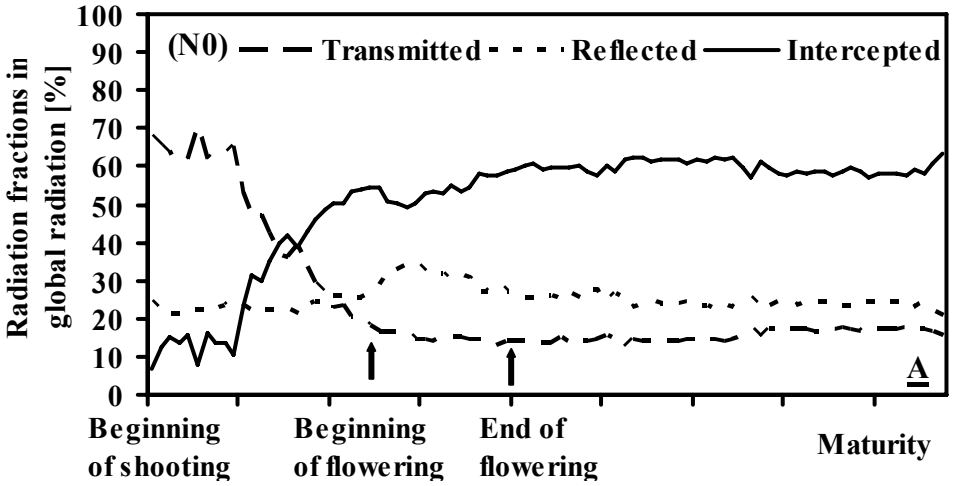
4. Results

4.1 Intercepted Radiation and Radiation Use Efficiency as Affected by Different Nitrogen Rates

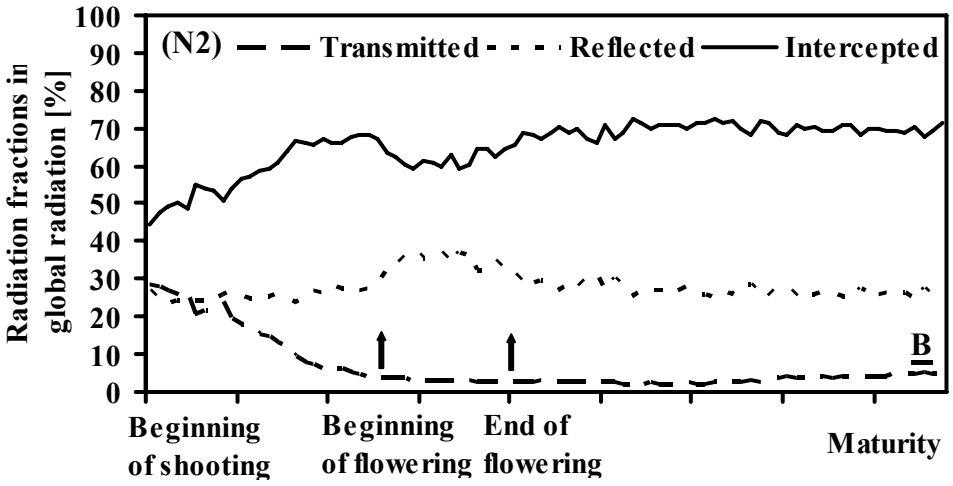
Figure IV-1 shows the percentage of transmitted, reflected and intercepted radiation of global incoming radiation as mean value of two oilseed rape cultivars as affected by low N (A) and high N (B) supply in the field experiment in 2001 at Zuchtgarten. Results indicate that the ratio of transmitted radiation in global incoming radiation was high (68%) at the beginning of shooting at N0 (Fig. IV-1 A). This might be due to the light plant canopy developed at the beginning of shooting under limiting N (N0) supply. Therefore, a very low percentage of radiation (7%) was intercepted while 25% of the total solar radiation was reflected to the atmosphere.

On the other hand, compared to N0 the transmitted fraction of global incoming radiation was considerably lower (29%) at the beginning of shooting at N2 (Fig. IV-1 A). This might be due to a quickly developed crop canopy at non-limiting N (N2) supply. Thus, the ratio of intercepted radiation in global incoming radiation was substantially higher (44%). However, almost 27% of the total solar radiation was reflected to the atmosphere at N2 which is nearly similar to N0. As a result of an increase in leaf area index (LAI) at later growth stages (Chap. III Tab. III-1), a sharp decline in transmitted radiation was found from beginning of shooting until beginning of flowering at both N rates (Fig. IV-1 A, B). On the other hand, intercepted radiation continuously increased from beginning of shooting due to an increase in plant canopy size until beginning of flowering at N0 and N2.

From beginning of shooting up to beginning of flowering (BS-BF) cumulative global incoming radiation amounted to about 170 MJ m^{-2} (Fig. IV-1 A). At N0, plants used about 33% of this global radiation for dry matter production while the remaining global radiation was either transmitted to the soil or reflected to the atmosphere. At this N rate the cumulative transmitted radiation was higher than the cumulative reflected radiation. However, the opposite was found at high N (N2) (Fig. IV-1 B). Nearly similar percentages of reflected radiation were found at N0 and N2, although the transmitted radiation was considerably lower at N2 than at N0 (Fig. IV-1 A, B). This indicates a dense plant canopy at the beginning of shooting at non-limiting N (N2) supply. Thus, rape plants intercepted almost 61% of the global incoming radiation from beginning of shooting until beginning of flowering at N2.



(N0)	Growth interval			Total
Radiation [MJ m^{-2}]	BS-BF	BF-EF	EF-MA	(BS-MA)
Global	170.26	150.48	452.33	773.07
Transmitted	74.41	22.92	70.82	162.69
Reflected	40.40	47.03	111.00	198.17
Intercepted	55.46	80.52	270.52	412.20
RUE [g MJ^{-1}]	**2.91**	**4.16**	**0.91**	**1.80**



(N2)	Growth interval			Total
Radiation [MJ m^{-2}]	BS-BF	BF-EF	EF-MA	(BS-MA)
Global	170.26	150.48	452.33	773.07
Transmitted	23.78	4.92	14.44	40.32
Reflected	44.02	52.01	122.03	217.76
Intercepted	102.46	93.55	315.87	514.98
RUE [g MJ^{-1}]	**2.87**	**5.06**	**1.20**	**2.22**

Figure IV-1: Percentage of radiation fractions of global incoming radiation above canopy level (Figures) and cumulative global radiation and radiation fractions as well as radiation use efficiency (RUE) at three growth intervals (Tables) of oilseed rape cultivars (mean of two cultivars) as affected by N supply (N0: soil mineral N (A), N2: 240 kg N ha^{-1} (B)) at Zuchtgarten in 2001. (BS-BF: Beginning of shooting–Beginning of flowering, BF-EF: Beginning of flowering–End of flowering, EF-MA: End of flowering–Maturity).

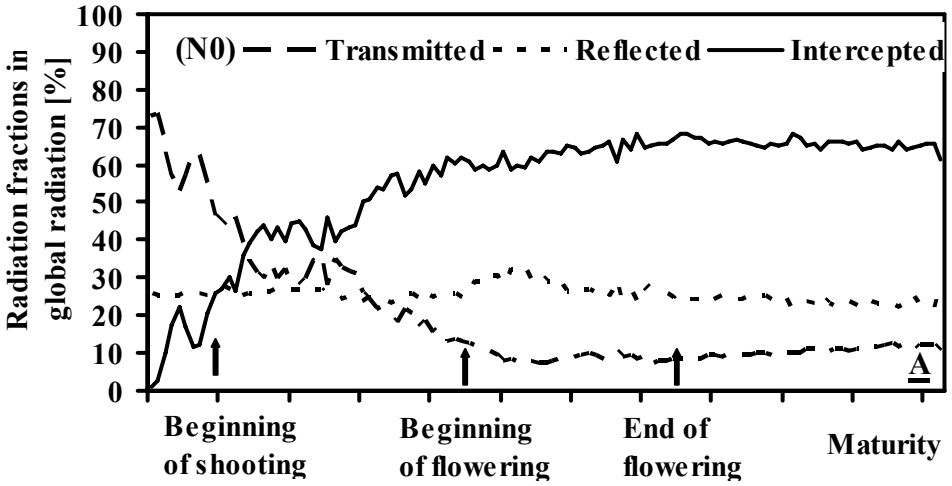
At the beginning of flowering the ratio of transmitted radiation in global incoming radiation was about 18% at N0 and 4% at N2 (Fig. IV-1 A, B). At both N rates the decline in transmitted radiation continued until the end of flowering and remained constant up to maturity. In contrast, intercepted radiation steeply increased until beginning of flowering, and this was followed by a slight reduction between beginning and end of flowering (BF-EF) at both N rates. This was mostly due to the emergence of flowers which caused an increase in reflected radiation during flowering. The rape plants increased the percentage of reflected radiation from 26 to 35% at N0 and from 25 to 34% at N2 during flowering in 2001. Because of a high percentage of reflected radiation during flowering the percentage of the intercepted radiation of global incoming radiation declined for a short time period from 55 to 50% at N0 and from 69 to 59% at N2 (Fig. IV-1 A, B). The results of the cumulative radiation indicated that rape plants intercepted almost 54% and 63% of the global incoming radiation during the BF-EF growth interval at N0 and N2, respectively (Fig. IV-1 A, B).

After the end of flowering (EF-MA) the percentage of intercepted radiation of global incoming radiation increased from 59 to 64% at N0 and from 62 to 71% at N2 supply (Fig. IV-1 A, B). However, the percentage of reflected radiation of global incoming radiation declined from 27 to 21% at N0 and from 31 to 24% at N2. On the other hand, a slight increase from 14 to 17% at N0 and from 3 to 5% at N2 was found for transmitted radiation. Furthermore, due to the long time period the cumulative radiation fractions were substantially higher at EF-MA compared to the other growth intervals at N0 and N2 (Fig. IV-1 A, B). About 59% of the total global incoming radiation (BS-MA) was available for the rape plants during the EF-MA growth interval. From this amount of incoming energy (452 MJ m^{-2}) plants intercepted around 60% and 70% during EF-MA at N0 and N2, respectively. On the other hand, almost 25 and 27% of the global incoming radiation during EF-MA was reflected at N0 and N2, respectively. In conclusion, the results indicated that from beginning of shooting until maturity (BS-MA) almost 773 MJ m^{-2} global incoming radiation was available for the canopy, and plants used almost 53% of the incoming global radiation for interception while 21% was transmitted to the soil and about 21% was reflected to the atmosphere under limiting N (N0) conditions (Fig. IV-1 A). Under non-limiting N (N2) conditions, rape plants intercepted almost 67% of the global incoming ration while almost 5% was transmitted to the soil and about 28% was reflected to the atmosphere (Fig. IV-1 B).

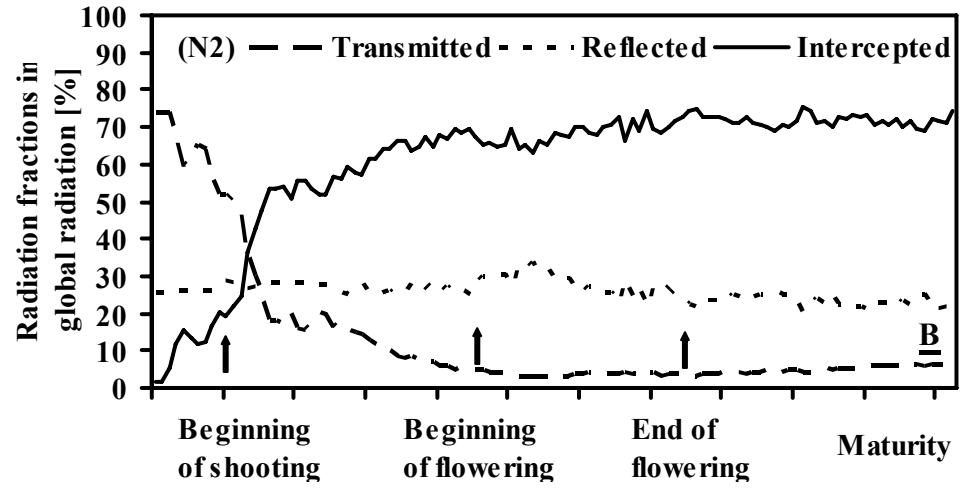
The quantity of dry biomass (g m^{-2}) produced per unit of intercepted radiation (MJ m^{-2}) by the plant, *i.e*. radiation use efficiency (RUE), increased from beginning of shooting until the end of flowering and then sharply declined from end of flowering until maturity at both N rates (Fig. IV-1 A, B). RUE was slightly higher at N0 than at N2 from beginning of shooting until beginning of flowering. However, from beginning of flowering onwards, the opposite result occurred. Regarding the whole growing period from beginning of shooting until maturity, RUE was higher at N2 than at N0 supply. At low N (N0) RUE was in the range of 2.91 g MJ^{-1} at BS-BF, 4.16 g MJ^{-1} at BF-BE and 0.91 g MJ^{-1} at EF-MA growth intervals (Fig. IV-1 A). At high N (N2) supply RUE was in the range of 2.87 g MJ^{-1} at BS-BF, 5.06 g MJ^{-1} at BF-BE and 1.20 g MJ^{-1} at EF-MA growth intervals (Fig. IV-1 B). The low RUE at N0 and N2 after the end of flowering might be the result of low dry matter accumulation during this growth interval (Chapter I, Fig. I-1).

Figure IV-2 shows the percentage of fractional radiation as mean values of two oilseed rape cultivars as affected by N supply in the field experiment in 2002 at Zuchtgarten. Compared to the previous field experiment in 2001 (Fig. IV-1 A) the ratio of transmitted radiation in global incoming radiation was slightly lower (62%) in 2002 at the beginning of shooting at N0 (Fig. IV-2 A). This might be due to slightly higher plant canopy development which may have covered the measurement area at the beginning of shooting under limiting N (N0) conditions. Therefore, the intercepted radiation was slightly higher (12%) while almost similar amount of solar radiation (26%) was reflected to the atmosphere at N0. The transmitted radiation of global incoming radiation at N2 was similar (64%) to N0 at the beginning of shooting (Fig. IV-1 B). Thus, the ratio of intercepted radiation in global incoming radiation (12%) and the total solar radiation reflected to the atmosphere were also same (26%) at N2 and N0.

All these results clearly indicate nearly similar canopy development at the beginning of shooting at N0 and N2. However, due to an increase in leaf area index (LAI) at later growth stages (Chapter III, Tab. III-1), the transmitted radiation sharply declined from beginning of shooting until beginning of flowering at both N rates (Fig. IV-2 A, B). On the other hand, intercepted radiation continuously increased from beginning of shooting as a result of enhancement in canopy development until beginning of flowering at N0 and N2.



(N0)	Growth interval			Total
Radiation [MJ m^{-2}]	BS-BF	BF-EF	EF-MA	(BS-MA)
Global	261.44	222.87	353.29	837.61
Transmitted	74.90	19.69	35.97	125.64
Reflected	67.86	61.74	83.81	213.40
Intercepted	118.69	141.45	233.51	498.57
RUE [g MJ^{-1}]	**1.63**	**2.34**	**0.89**	**1.46**



(N2)	Growth interval			Total
Radiation [MJ m^{-2}]	BS-BF	BF-EF	EF-MA	(BS-MA)
Global	261.44	222.87	353.29	837.61
Transmitted	50.38	8.24	16.66	69.82
Reflected	71.44	61.36	81.13	213.93
Intercepted	139.62	153.27	255.50	553.85
RUE [g MJ^{-1}]	**3.01**	**2.63**	**0.77**	**1.84**

Figure IV-2: Percentage of radiation fractions of global incoming radiation above canopy level (Figures) and cumulative global radiation and radiation fractions as well as radiation use efficiency (RUE) at three growth intervals (Tables) of oilseed rape cultivars (mean of two cultivars) as affected by N supply (N0: soil mineral N (A), N2: 240 kg N ha^{-1} (B)) at Zuchtgarten in 2002. (BS-BF: Beginning of shooting–Beginning of flowering, BF-EF: Beginning of flowering–End of flowering, EF-MA: End of flowering–Maturity).

From beginning of shooting until beginning of flowering (BS-BF) cumulative global incoming radiation amounted to about 261 MJ m^{-2} in 2002 (Fig. IV-2 A). At N0, plants used about 45% of this global radiation for dry matter production while the remaining global radiation was transmitted (29%) to the soil or reflected (26%) to the atmosphere. At this N rate the cumulative transmitted radiation was slightly higher than the cumulative reflected radiation. However, the opposite was found at high N (N2) (Fig. IV-2 B). Nearly similar percentages of reflected ration was found at N0 and N2 rates, although the transmitted radiation was considerably lower (30%) at N2 than N0. This indicates that the development of aboveground biomass at BS-BF was higher at non-limiting N (N2) conditions. Thus, rape plants intercepted almost 54% of the global incoming radiation during the BS-BF growth interval at N2.

At the beginning of flowering the percentage of transmitted radiation of global incoming radiation was about 13% at N0 and 5% at N2 in 2002 (Fig. IV-2 A, B). At both N rates the decline in transmitted radiation continued until end of flowering and then remained constant until maturity. In contrast, the intercepted radiation strongly increased until beginning of flowering, but this was followed by a slight decline between flowering and end of flowering (BF-EF) at both N rates. This is mostly due to the emergence of flowers which caused an increase in reflected radiation. Results indicated that rape plants increased the percentage of reflected radiation from 25 to 33% at N0 and from 25 to 34% at N2 in global incoming radiation during flowering in 2002.

As a result of the high reflection during flowering the percentage of intercepted ration was reduced for a short period from 62 to 59% at N0 and from 69 to 63% at N2 (Fig. IV-2 A, B). The results of cumulative radiation indicated that rape plants intercepted about 63% and 69% of the global incoming radiation during flowering (BF-EF) at N0 and N2, respectively.

After flowering (EF-MA) the percentage of intercepted radiation of global incoming radiation declined from 68 to 62% at N0 whereas an increase from 71 to 75% occurred at N2 (Fig. IV-1 A, B). However, the decline in the percentage of reflected radiation of global incoming radiation was almost similar (24 and 22%) at N0 and N2. On the other hand, a slight increase from 8 to 11% at N0 and 4 to 7% at N2 was found in the percentage of transmitted radiation of global incoming radiation. As well, due to the long growing period the cumulative radiation fractions were substantially higher at EF-MA compared to the other growth intervals

at N0 and N2 (Fig. IV-1 A, B). Almost 42% of the total global incoming radiation (BS-MA) was available for the rape plants at EF-MA. From this amount of incoming energy (353 MJ m^{-2}) plants intercepted about 66% and 72% during EF-MA at N0 and N2, respectively. On the other hand, about 24 and 23% of the global incoming radiation during EF-MA was reflected and about 10 and 5% was transmitted to the soil at N0 and N2, respectively.

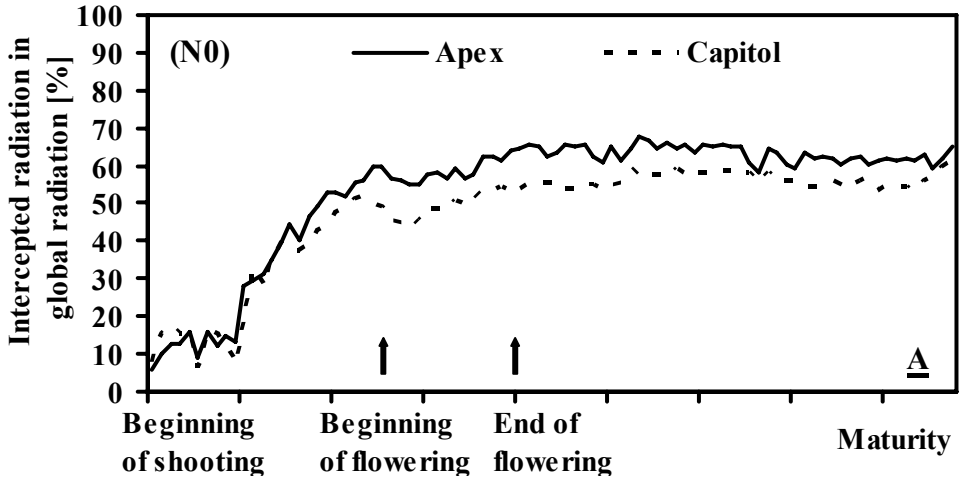
Finally, the results indicated that from beginning of shooting until maturity (BS-MA) 837 MJ m^{-2} global incoming radiation was available for the canopy, and plants used about 60% of the incoming global radiation for interception, while about 15% was transmitted to the soil, and 25% was reflected to the atmosphere under limiting N (N0) conditions (Fig. IV-2 A). Under non-limiting N (N2) conditions, rape plants intercepted about 66% of the global incoming radiation, while 8% was transmitted to the soil and about 26% was reflected to the atmosphere (Fig. IV-2 B).

RUE differed among the two field experiments (2001 and 2002). In 2002, it was lower during each growth interval (except BS-BF at N2) as well as over the whole growing period (Fig. IV-2) compared to 2001 at both N rates. Results calculated for the whole growth interval in 2002 showed that RUE declined by almost 19% at N0 and 17% at N2 compared to RUE in 2001. However, compared to the previous field experiment RUE was substantially lower at BS-BF at N0 in 2002, although slightly higher RUE was found at N2 in 2002. From beginning of shooting until end of flowering RUE increased at N0 while a slight decline occurred at N2. On the other hand, a sharp decline in RUE after the end of flowering (EF-MA) occurred at both N rates. From beginning of shooting the RUE was in the range of 1.63 MJ^{-1} at BS-BF, 2.34 g MJ^{-1} at BF-EF and 0.89 g MJ^{-1} at EF-MA growth intervals under limiting N (N0) conditions. However, at non-limiting N (N2) RUE was in the range of 3.01 MJ^{-1} at BS-BF, 2.63 g MJ^{-1} at BF-EF and 0.77 g MJ^{-1} at EF-MA growth intervals. The low RUE at N0 and N2 after the end of flowering might be the result of substantial dry matter losses occurring during this period (Chap. I. Fig. I-1).

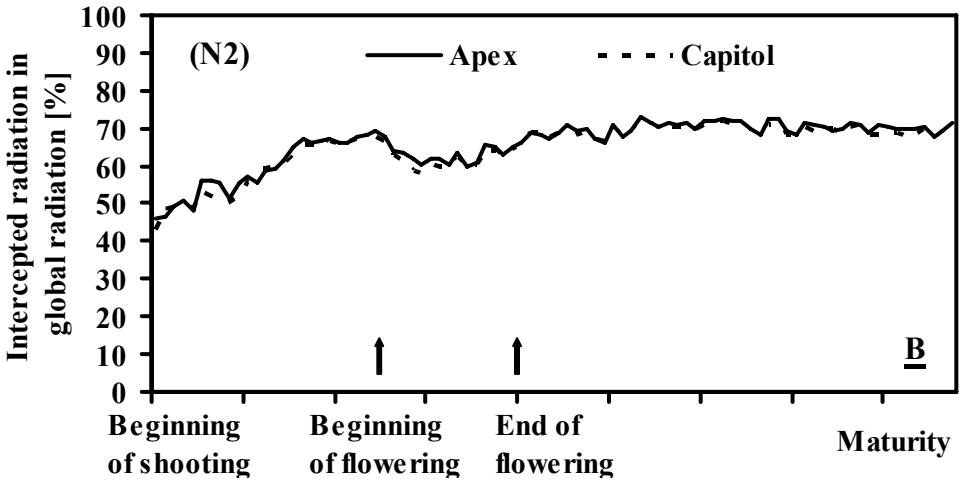
4.2 Intercepted Radiation and Radiation Use Efficiency of Oilseed Rape Cultivars

In the field experiment in 2001, the percentage of intercepted radiation of global incoming radiation among two contrasting rape cultivars (Apex and Capitol) was usually different at low N (N0) supply from beginning of shooting until maturity (Fig. IV-3 A). However, opposite to N0, no major differences in intercepted radiation among two cultivars were found at high N (N2) supply (Fig. IV-3 B). Although Capitol had higher percentage of intercepted radiation than Apex at N0 for a short period at the beginning of shooting, at later growth stages Apex showed higher percentages of intercepted radiation than Capitol even until maturity (Fig. IV-3 A). From beginning of shooting until maturity (BS-MA) the result of the cumulative intercepted radiation indicated that Apex intercepted almost 13% more radiation at N0 than Capitol. Also, the differences in the percentage of cumulative intercepted radiation among the two cultivars varied at all individual growth intervals and thus Apex intercepted 12% at BS-BF, 17% at BF-EF and 12% at EF-MA more radiation than Capitol at N0. Despite of its higher cumulative intercepted radiation at all growth intervals, Apex had almost 17% less RUE than Capitol at total BS-MA at N0 (Fig. IV-3 A). Results of individual growth intervals indicated that Apex had almost 50% less RUE at BS-BF and about 20% less RUE at EF-MA than Capitol at N0. A slightly higher RUE (5%) than Capitol was shown by Apex at BF-EF at N0. A high cumulative intercepted radiation, however, but lower RUE of Apex could be the result of intensive assimilate allocation to the roots under limiting N (N0) condition (Chap. II, Fig. II-10, II-12) which was not considered as a dry matter fraction in the calculation of RUE.

Although no considerable differences in the percentage of intercepted radiation among Apex and Capitol occurred at N2 from beginning of flowering until maturity, the result of the cumulative radiation indicated that Apex intercepted almost 2% more radiation than Capitol over the whole measurement period (BS-MA) at N2 (Fig. IV-3 B). Apex intercepted about 3% more radiation than Capitol at BS-BF, 3% at BF-EF and 1% at EF-MA at this N rate. However, similar to low N (N0) conditions, Apex had an almost 32% lower RUE than Capitol at BS-BF at high N (N2) conditions. On the other hand, different from N0, Apex had an almost 17% higher RUE than Capitol at BF-EF and a 28% higher RUE at EF-MA at N2.



(N0)	Intercepted radiation [MJ m^{-2}]			
	Growth interval			Total
Cultivar	BS-BF	BF-EF	EF-MA	(BS-MA)
Apex	58.87	87.65	287.86	441.43
Capitol	52.04	73.39	253.18	382.98
	RUE [g MJ^{-1}]			
Apex	**1.94**	**4.28**	**0.81**	**1.64**
Capitol	**3.88**	**4.05**	**1.01**	**1.97**



(N2)	Intercepted radiation [MJ m^{-2}]			
	Growth intervals			Total
Cultivar	BS-BF	BF-EF	EF-MA	(BS-MA)
Apex	103.69	94.70	317.65	519.12
Capitol	101.23	92.39	314.08	510.85
	RUE [g MJ^{-1}]			
Apex	**2.31**	**5.54**	**1.39**	**2.32**
Capitol	**3.42**	**4.58**	**1.00**	**2.12**

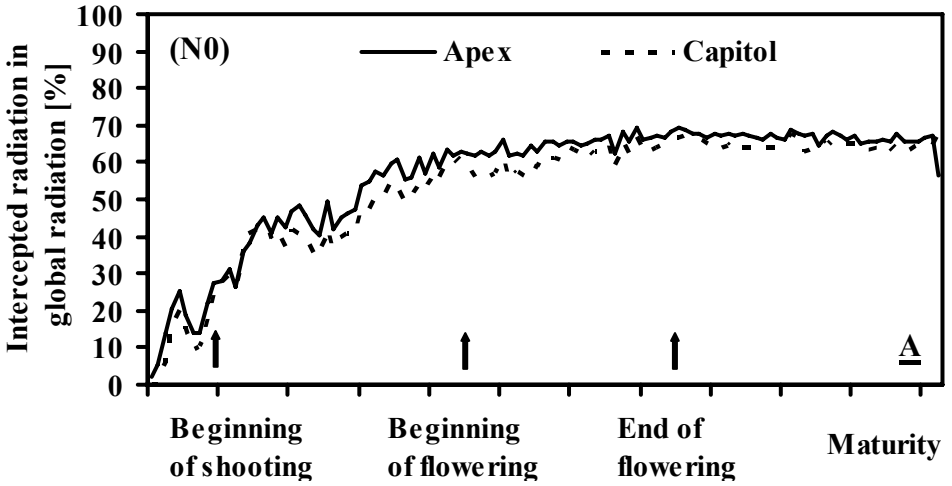
Figure IV-3: Percentage of intercepted radiation of global incoming radiation above canopy level (Figures) and cumulative intercepted radiation and radiation use efficiency (RUE) at three growth intervals (Tables) of two oilseed rape cultivars as affected by N supply (N0: soil mineral N (A), N2: 240 kg N ha^{-1} (B)) at Zuchtgarten in 2001. (BS-BF: Beginning of shooting–Beginning of flowering, BF-EF: Beginning of flowering–End of flowering, EF-MA: End of flowering–Maturity).

Moreover, between beginning of shooting and maturity (BS-MA) Apex showed almost 9% more RUE than Capitol at this high N rate.

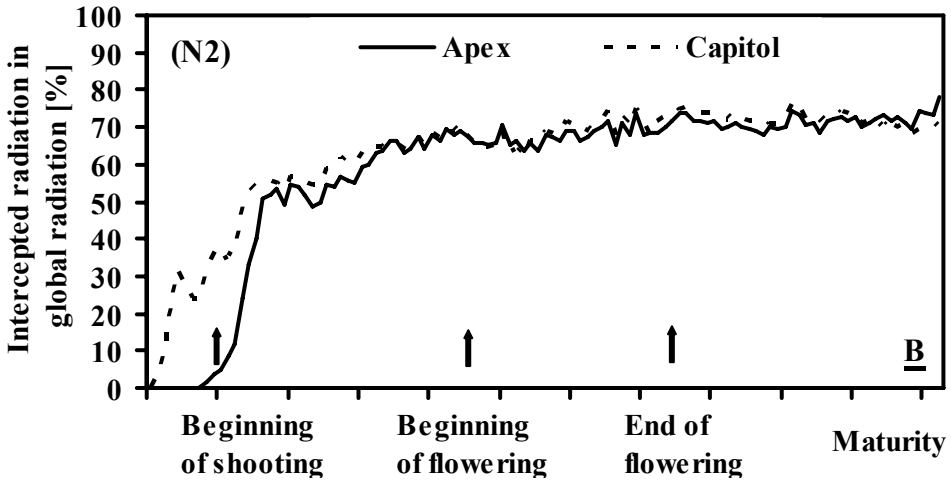
Like in 2001, Apex and Capitol differed in the percentage of intercepted radiation of global incoming radiation from beginning of shooting until maturity at low N (N0) supply also in 2002 (Fig. IV-4 A). Different from the 2001 field experiment, substantial differences among these cultivars in intercepted radiation were also found at high N (N2) supply, particularly from beginning of shooting up to flowering (Fig. IV-4 B).

Under limiting N (N0) supply, Apex showed higher percentage of intercepted radiation than Capitol from beginning of shooting until maturity (Fig. IV-4 A). The cumulative intercepted radiation at BS-MA indicated that Apex intercepted almost 6% more radiation than Capitol at N0. Also, the differences in the percentage of cumulative intercepted radiation among two cultivars varied at the individual growth intervals, At N0 Apex intercepted 9% more radiation than Capitol at BS-BF, 5% at BF-EF and 3% at EF-MA. In addition to a higher cumulative intercepted radiation from beginning of shooting until maturity (BS-MA) Apex had almost 3% more RUE than Capitol at N0. However, cultivar differences in RUE varied considerably during individual growth intervals. Apex had about 56% less RUE than Capitol at BS-BF at N0, while at BF-EF and EF-MA growth intervals at the same N rate Apex showed almost 25% and 28% more RUE, respectively, than Capitol.

Under non-limiting N (N2) supply Capitol had a substantially higher percentage of intercepted radiation than Apex from beginning of shooting until shortly before flowering (Fig. IV-4, B). The differences among two cultivars in intercepted radiation remained up to maturity but they were negligible. The results of cumulative radiation indicated that Capitol intercepted almost 12% more radiation than Apex at BS-BF while the intercepted radiation was only 1% and 2% more than Apex at BF-EF and EF-MA, respectively, at N2. Furthermore, from beginning of shooting up to maturity (BS-MA) Capitol had almost 4% more cumulative intercepted radiation than Apex at this high N rate. Similar to low N (N0) conditions, Capitol had almost 12% more RUE than Apex at BS-BF at high N (N2). By contrast, Apex had almost 15% more RUE than Capitol at BF-EF at N2. After the end of flowering (EF-MA) Capitol had again almost 23% higher RUE than Apex at N2. Moreover, between beginning of shooting and maturity (BS-MA) Capitol had almost 6% more RUE than Apex at this N rate.



(N0)	Intercepted radiation [MJ m^{-2}]			
	Growth intervals			Total
Cultivar	BS-BF	BF-EF	EF-MA	(BS-MA)
Apex	124.41	145.41	237.11	512.54
Capitol	112.97	137.48	229.92	484.59
	RUE [g MJ^{-1}]			
Apex	**1.00**	**2.68**	**1.03**	**1.48**
Capitol	**2.25**	**2.00**	**0.74**	**1.44**



(N2)	Intercepted radiation [MJ m^{-2}]			
	Growth intervals			Total
Cultivar	BS-BF	BF-EF	EF-MA	(BS-MA)
Apex	130.45	152.00	253.64	544.13
Capitol	148.79	154.54	257.36	563.57
	RUE [g MJ^{-1}]			
Apex	**2.82**	**2.85**	**0.67**	**1.78**
Capitol	**3.19**	**2.41**	**0.87**	**1.90**

Figure IV-4: Percentage of intercepted radiation of global incoming radiation above canopy level (Figures) and cumulative intercepted radiation and radiation use efficiency (RUE) at three growth intervals (Tables) of two oilseed rape cultivars as affected by N supply (N0: soil mineral N (A), N2: 240 kg N ha^{-1} (B)) at Zuchtgarten in 2002. (BS-BF: Beginning of shooting–Beginning of flowering, BF-EF: Beginning of flowering–End of flowering, EF-MA: End of flowering–Maturity).

In conclusion, the results clearly indicated that in both field experiments (2001 and 2002), while intercepting more cumulative radiation especially under low N (N0) supply, Apex showed a lower RUE than Capitol particularly at the early groth stage (BS-BF), but had a higher RUE than Capitol particularly during flowering (BF-EF) under both limiting N (N0) and non-limiting N (N2) conditions (Fig. IV-3, IV-4 B).

5. Discussion

The aim in this chapter was i) to determine the relative importance of light interception and radiation use efficiency (RUE) for the decrease in crop growth under limiting N supply, and ii) to determine genotypic differences in light interception or RUE during different growth stages that may explain differences in N efficiency of two oilseed rape cultivars.

5.1 Light Interception and Radiation Use Efficiency under Different Nitrogen Conditions

Primary factors affecting total dry matter yield are the solar radiation intercepted and the efficiency of utilizing that energy for CO_2 fixation (Gardner et al., 1994). To use solar radiation efficiently most of the radiation must be absorbed by green, photosynthetic tissues and thus leaves are the major source organs for the interception of radiation and carbon assimilation of crops (Grosse, 1989; Sinclair, 1994). Although the maximum surface area of the pods is nearly the same as that of the leaves (Allen and Morgen, 1972), the leaf area is the major source of interception of radiation and carbon assimilation of oilseed rape crop from re-growth in early spring up to end of flowering (Grosse et al., 1992b).

In our two field experiments (2001 and 2002), averaged over N rates, the percentage of intercepted radiation increased from beginning of shooting up to beginning of flowering followed by a slight decline during flowering and then remained almost constant until maturity (Fig. IV-1, 2). This may be associated with leaf area development and thus dry matter production of rape particularly until the beginning of flowering. Monteith (1977) showed an almost linear relationship between annual above-ground dry matter and cumulative intercepted solar radiation, while a curvilinear relationship between intercepted radiation and leaf area development was demonstrated in many other studies (Brougham, 1956; Shibles and Weber, 1965; Gardner et al., 1994). The intermittent decline in intercepted radiation at the beginning of flowering at both N rates and in both experimental years (Fig. IV-1, 2) might be the result of flower emergence which caused an increase in reflected radiation during flowering (Fig. IV-1, 2; Leach et al., 1989). After the end of flowering, light interception stayed high, so that the decrease in LAI must have been matched completely by an increase in pod area.

Our results indicated that the ratio of intercepted radiation varied between two N rates and was almost 58% at limiting N (N0) and 69% at non-limiting N (N2) shortly before flowering when averaged over both years (Fig. IV-1, 2). The percentages of the intercepted radiation at both N rates were associated with LAI values that varied in between 1.1 and 1.3 at N0 and 3.0 and 3.5 at N2 in both field experiments (Chap. III, Tab. III-1). Several studies demonstrated that the leaf area index (LAI) is an important parameter in estimating the intercepted radiation in global incoming radiation. For instance, Sinclair and Gardner (1998) from their studies on three different crop species (sugar beet, kale and wheat) calculated that about half of the incoming global radiation (50%) was intercepted with an LAI of only 1.0, and 90% of the global radiation was intercepted at an LAI of 3.3. A defoliation experiment by Brougham (1956) applied on a ryegrass-clover canopy indicated that crop growth rate increased when the LAI increased up to a critical (optimum) value of 5.0, where the canopy intercepted 95% of the solar radiation. However, Watson (1952) demonstrated a critical LAI value of 3.3, with a similar experiment to that of Brougham.

The LAI values at N2 might be sufficient for optimal light interception according to Sinclair and Gardner (1998) or Watson (1952). Radiation interception, however, was very much lower than 95% considered for optimal growth. The dissimilarity might be due to the high percentage of reflected radiation measured in this study, which is frequently not considered in other studies. Our results indicated that only 16% and 4% of global incoming radiation were transmitted to the soil at N0 and N2, respectively, because almost 26% and 27% of the global incoming radiation was reflected at N0 and N2, respectively (Fig. IV-1, 2). Therefore, the LAI reached at N2 can be considered as sufficient for optimum light interception, while at N0 the LAI was insufficient.

Averaged over N rates, the quantity of dry biomass (g m^{-2}) produced per unit of intercepted radiation (MJ m^{-2}) by the rape plant, *i.e*. radiation use efficiency (RUE) started to increase between beginning of shooting and beginning of flowering (BS-BF) and reached the highest value between beginning of flowering and end of the flowering (BF-EF) and then declined sharply between end of flowering and maturity in 2001 and 2002. Differences in RUE at each development stage may be associated directly with the nitrogen uptake and thus leaf nitrogen content of rape. E.g., Bange et al. (1997a) demonstrated that RUE of sunflower was high from bud visible to anthesis while it declined after anthesis due to decline in leaf nitrogen content. Furthermore, Sinclair and Hoire (1989) studying maize, rice and soybean demonstrated that

calculated RUE of different crop species was commonly associated with changes in leaf nitrogen content per unit leaf area. Apart from leaf N content, RUE can also vary with light intensity. At low light conditions, e.g. in a dense canopy, RUE usually increases (Sinclair and Horie, 1989). This might have contributed to the high RUE of the rape plants during flowering (Fig. IV-1, 2), since, the leaves are then shaded by the flowers.

Our results indicated that the RUE varied between two N rates and was almost 1.6 g MJ^{-1} at limiting N (N0) and 2.0 g MJ^{-1} at non-limiting N (N2) averaged over both years over the whole studied growth period (BS-MA) (Fig. IV-1, 2). The result corroborated several other studies which indicated that RUE of oilseed rape can be varied within a wide range, from 1.0 to 4.0 g MJ^{-1} according to developmental stage and environmental conditions (Leach et al., 1989; Mendham et al., 1991; Mendham and Salisbury, 1995; Habekotté, 1996, 1997b). Substantially higher RUE at N2 compared to N0 might be the result of high nitrogen uptake and thus high leaf N contents, since similar positive relationships between RUE and leaf nitrogen content under different soil nitrogen fertility status were found in a number of crop species, including wheat (Fischer, 1993), maize (Muchow and Davis, 1988) sorghum (Muchow and Sinclair, 1994) and oilseed rape (Dreccer et al., 2000).

Finally, our results from two field experiments clearly showed that due to insufficient LAI development at the vegetative stage under limiting N (N0) in 2001, from beginning of shooting up to beginning of the flowering the cumulative intercepted radiation was substantially lower at N0 than N2 and thus limited the crop growth, whereas RUE was increased. In contrast, light interception was less reduced at N0 in 2002 due to a higher LAI at the vegetative stage in that year (Chap. III, Tab. III-1). In this case, however, this was coupled to a strongly reduced RUE as compared to N2. It thus seems that it is not possible to achieve both, high radiation interception and high RUE during vegetative growth. The reason may be that a high leaf area will result in low leaf N contents per unit leaf area so that photosynthesis rate will be strongly reduced (Anten et al., 1995). Therefore, a high crop growth rate during vegetative may only be achieved with a high crop N uptake.

On the other hand, during reproductive growth in 2001 and 2002, intercepted radiation was less reduced at N0 compared to N2, so that it was less limiting for crop growth during this growth phase. Therefore, an increased LAI will hardly enhance radiation interception and crop growth during reproductive growth at limiting N. In contrast, RUE was stronger reduced

at N0 during flowering and particularly after the end of flowering in 2001, probably because of low shoot N concentrations. In contrast, in 2002, RUE was higher at N0 than N2 after the end of flowering, probably due to continuous N uptake during reproductive growth at N0, while N losses occurred at N2 (Chap. I, Fig. I-3). In conclusion, an increased LAI may be of limited advantage for the crop growth of oilseed rape during reproductive growth at N0, while an increase in RUE may be more effective in increasing yield.

5.2 Genotypic Differences in Light Interception and Radiation Use Efficiency of Oilseed Rape

Many studies have been performed comparing various crop species in intercepted radiation and radiation use efficiency (RUE). However, so far not much information is available on genotypic differences in RUE within crop species. A study of Tollenaar and Aguilera (1992) demonstrated the existence of genotypic differences among an old and a new maize hybrid in RUE and they reported that an increased dry matter accumulation after silking was closely associated with an increase in RUE. Another study, which was carried out by Hammer and Vanderlip (1989) on an old and a new sorghum cultivars, indicated that the cultivars differed in RUE under different temperatures (17 and 25°C) and the new cultivar had a higher RUE than the old one at 25°C, but cultivars did not differ significantly at 17°C.

Our results from two field experiments (2001 and 2002) clearly indicated genotypic differences in intercepted radiation and RUE among two oilseed rape cultivars differing in N efficiency (Apex: “N-efficient”, Capitol: “N-inefficient”) at two N rates. Apex always showed a higher cumulative intercepted radiation than Capitol at all three growth intervals under limiting N (N0) supply in 2001 and 2002 (Fig. IV-3, 4 A), although Apex did not have a higher leaf area than Capitol (Chap. III, Tab. III-1). This might be achieved by a better leaf orientation or an advantageous leaf shape of Apex, which avoids better mutual shading within the canopy. However, despite of a higher intercepted radiation at BS-BF, Apex had a substantially lower RUE than Capitol in both field experiments. This might be due to a higher assimilate allocation to the roots than to the shoot during vegetative growth by Apex. The root investigations (Chapter II) demonstrated that from the beginning of vegetative growth in spring until maturity Apex was usually characterized by a higher fine root formation compared to Capitol under low N supply (Chap. II, Fig. II-10, 12).

After the beginning of flowering Apex still intercepted more radiation than Capitol at N0 (Fig. IV-3, 4) This might be related to a slightly lower reduction in LAI during flowering as compared to Capitol (Chap. III, Tab. III-1) or to a higher pod area formation. Apex also achieved a higher RUE than Capitol during reproductive growth in both years (Fig. IV-3, 4). However, despite of continuously high assimilate allocation to the roots even at reproductive growth by Apex, the differences in RUE can be explained by a higher N uptake of Apex compared to Capitol at N0 (Chap. I, Tab. I-13, 14), which might have enabled this cultivar to retain high leaf N contents also during reproductive growth, and thus to achieve high photosynthetic rates.

In contrast to the genotypic differences found at limiting N supply, the cultivar differences were less pronounced at high N supply. In the first experiment (2001) Apex constantly intercepted slighty more radiation than Capitol at all growth intervals at N2. However, in the next field experiment (2002) opposite results were recorded, and Apex constantly intercepted less radiation than Capitol at N2. In contrast to the high difference in LAI among two cultivars at N0 in 2001 (21%), the difference in LAI was negligible (3%) at N2 in 2001 and also in 2002 (Chap. III, III-1). Like at limiting N supply, RUE of Apex was lower compared to Capitol during vegetative growth. This could be the result of the difference in fine root formation which was significantly higher by Apex than Capitol from beginning of shooting up to end of flowering at N2 (Chap. II, Fig. II-10, 12). During reproductive growth, RUE of Apex was partly higher than for Capitol. This was the case, when Apex also achieved a higher shoot N uptake than Capitol (Chap. I, Tab. I-13, 14).

In conclusion, the N-efficient cultivar could be characterized by a high investment in root growth during vegetative growth, which reduced RUE during vegetative growth, but enhanced RUE during reproductive growth due to a high N uptake. Also, the N-efficient cultivar was able to achieve a high light interception at limiting N supply, which might be related to an advantageous canopy architecture and during reproductive growth to delayed leaf senescence.

General Discussion

In this study the relationship between agronomic plant traits and both N efficiency components (N uptake and N utilization) were assessed (Chapter I) at different levels of N supply under field conditions. To understand the interrelated mechanisms of N efficiency, the morphological (Chapter II) and physiological (Chapter III and IV) plant traits contributing to N efficiency were investigated. The most important results and conclusions of these field experiments are discussed in the following section.

A genotype can be characterized as N-efficient either when realizing a yield above average under conditions suboptimal N supply or when converting N fertilizer efficiently into yield under conditions of high N supply (Sattelmacher et al., 1994). In this work, "N-efficient" cultivars were defined as those realizing an above-average yield under suboptimal N supply (Graham, 1984), while cultivars having a high yield under optimum N supply were called "responsive". The result of the present study indicated that averaged over three experimental years (2000, 2001 and 2002) and two sites, highly significant ($P<0.001$) genotypic variation in grain yield among 12 rape genotypes (cultivars and DH lines) existed (Chapter I). Yield response to supplied N, i.e. the interaction between N and genotype, was also highly significant ($P<0.001$). This indicates that the interrelated mechanisms of the N efficiency under limiting N (N0) are functioning differently from those under non-limiting N (N1 and N2) conditions. In agreement with several studies (Yau and Thurling, 1987b; Lafitte and Edmeades, 1994b; Sattelmacher et al., 1994) our results demonstrate that a low yielding "N-inefficient" genotype at low N (N0) can be highly responsive to applied N and hence converts the fertilizer N more efficiently into grain yield at medium N (N1) or high N (N2) supply. By contrast, a high yielding "N-efficient" genotype at N0 can produce a high grain yield also at N1 and N2 rates indicating a high responsiveness to the N fertilization. This is in agreement with the results of Möllers et al. (1999) with oilseed rape and Anbessa et al. (2009) with barley who reported that the same cultivars were superior in grain yield at both low N and high N conditions. Consequently, all types of cultivars were present in our study: efficient or inefficient cultivars and responsive and non-responsive cultivars, whereby responsive cultivars could be efficient or inefficient. This suggests that breeding for N efficiency is highly promising (Bänziger et al., 2000).

Improved grain yield (high N efficiency) under low N (N0) conditions significantly correlated with N uptake (2000, 2001) and N utilization (2002) efficiencies indicating that both N efficiency components play a role in N efficiency. Generally, high grain yield and thus high N efficiency under limiting N (N0) supply was achieved by that cultivars which maintained a high N uptake activity particularly during reproductive growth. The difference in N uptake between two rape cultivars from beginning of flowering up to maturity amounted to 25 kg N ha^{-1} in 2000, 18 kg N ha^{-1} in 2001 and 28 kg N ha^{-1} in 2002 (Chapter I). This is in agreement with the field studies of Wiesler et al. (2001b) who demonstrated that high grain yield under conditions of low N supply was significantly correlated with differences in N uptake during reproductive growth which varied among genotypes (25 kg N ha^{-1} for maize and 41 kg N ha^{-1} for oilseed rape). Another study by Worku et al. (2007) clearly demonstrated that high grain yield of maize hybrids under low N were consistently positively related with higher post-anthesis N uptake, whereas there was no correlation between N uptake before anthesis and grain yield.

On the other hand, high grain yield and thus high N efficiency was associated strongly with high N utilization among newly introduced DH lines under low N (N0) conditions (Chapter I). Generally the N utilization-efficient genotype was characterized by high biological production efficiency at N0 owing to low N concentrations in shoots and seeds (Chapter I). This is in agreement with the study of Yau and Thurling (1987b) who demonstrated among 40 rape genotypes highly significant genotypic differences in N utilization related to biological production efficiency at low N. Also, Sinebo et al. (2004) reported a negative correlation between grain yield and seed N concentration of barley genotypes. The study further revealed that the grain N concentration was negatively correlated with N utilization which is consistent with our results.

According to our results the main strategy to improve N efficiency in oilseed raps is a high N uptake during reproductive growth. N-efficient cultivars should be characterized by maintaining a high N uptake activity during reproductive growth via a more efficient and vigorous root growth (Chapter II) due to adequate assimilate supply from the leaves which sustain a high leaf area and long leaf-area duration (delayed leaf senescence) under limiting N (N0) supply (Chapter III). Due to delayed leaf senescence and high leaf area index (LAI), the photosynthetic capacity of the leaves is maintained at a high level during reproductive growth

and thus interception of solar radiation and radiation use efficiency (RUE) of N-efficient oilseed rape cultivars may be increased (Chapter IV).

Both root methods clearly showed that the N-efficient cultivars were characterized by higher root-length densities (core) and higher new fine root formation (rhizotron) than the N-inefficient cultivars particularly in the top-soil layers (Chapter II). This is in agreement with the studies of Wiesler and Horst (1992) and Schenk and Barber (1980) who demonstrated genotypic differences among maize hybrids in root growth associated with high N uptake during the reproductive growth under low N conditions. However, our results indicated that high N-uptake efficiency under limiting N (N0) supply was associated not only with greater root growth during reproductive growth. A high N-uptake efficiency was achieved by the cultivars which had a generally vigorous root growth during the whole vegetation period and irrespective of the level of N supply.

However, without continuous assimilate allocation from the leaves, root growth and thus N uptake activity cannot be maintained during reproductive growth. Morphological leaf characteristics (Chapter III) may be responsible for higher root growth and high N uptake of N-efficient cultivars. The study of Bänziger et al. (2002) revealed that preventing N remobilization from vegetative parts or delayed leaf senescence during early stages of grain filling is desirable for continued photosynthesis of leaves particularly under low N (N0) conditions. In agreement with this study, our result indicated that the N-efficient cultivars generally had a lower LAI reduction between beginning of flowering and end of flowering (Chapter III) which might contribute to a better assimilate availability during reproductive growth to the roots of N-efficient cultivars (Chapter II). The prolonged leaf area duration (LAD) and thus maintained photosynthetic capacity of the leaves at a high level during reproductive growth (Chapter III) might result in a better harvest index (HI) in the N-efficient cultivars under limiting N (N0) conditions compared to the N-inefficient cultivars (Chapter I).

The defoliation experiment clearly showed that the grain yield of the N-efficient cultivars was not significantly reduced by the removal of leaves at N0 supply (Chapter III) thus sustaining N uptake even under defoliation. This might be due to the fact that N-efficient cultivars already had an extensive root system before flowering (Chapter II), or because they could better compensate for the reduction in leaf area by increasing the photosynthetic rate of the

remaining leaves due to a better illumination (Chapter IV) under a less dense canopy (Chapman et al., 1984; Zhaou and Lin 1997).

The dropping leaves constitute a substantial proportion of crop residues which return a significant amount of N to the soil (Malagoli, 2005) and may thus contribute to the low N recoveries in harvested organs of oilseed rape (Lickfett and Przemeck, 1997; Lickfett et al., 2001). Some of these studies demonstrated maximal N contents of dropped leaves which varied in between 40-60 kg N ha^{-1} during spring (Hocking et al., 1997; Lickfett and Przemeck, 1997; Gosse et al., 1999). Inconsistent with these results, in our field study the cumulative N content of dropped leaves varied in between 1.6 and 14.0 kg N ha^{-1} at low N (N0) and high N (N2) rates, respectively (Chapter III).

High N contents of dropped leaves demonstrated by the above cited studies could be the results of the differences in the period of dropped leaves collection and also applied N fertilizer level. On the other hand, our results clearly corroborated the studies by Aniol (1993) and Schjoerring et al. (1995) who reported 18, and 20 kg N ha^{-1} in dropped leaves, respectively, in N-fertilized plots. Generally, the N-efficient cultivars showed a lower dropped leaves dry matter and leaf N content than N-inefficient cultivars under limiting N (N0) conditions. Thus they play a negligible role in genotypic differences in N harvest index (NHI) and the N balance of the crop compared to genotypic differences in remaining N in the straw which varied between 7.0 and 45 kg N ha^{-1}.

Our results demonstrated a close positive relationship between LAI development and intercepted incoming radiation while RUE was negatively correlated with LAI at the vegetative stage (Chapter IV). Due to insufficient LAI development at the vegetative stage under limiting N (N0) from beginning of shooting up to beginning of the flowering, the cumulative intercepted radiation was substantially lower at N0 than at N2 and thus limited crop growth, whereas RUE was increased. However, contrasting results were found when the LAI was increased at the vegetative stage. It thus seems that it is not possible to achieve both, high radiation interception and high RUE during vegetative growth. The reason may be that a high leaf area will result in low leaf N contents per unit leaf area so that the rate of photosynthesis will be strongly reduced (Anten et al., 1995). Therefore, a high crop growth rate during vegetative growth may only be achieved with a high crop N uptake. This was not possible with our N-efficient cultivar which was characterized by a comparatively slow

growth (Chapter I) due to high investment of assimilate in root growth during the vegetative stage (Chapter II) and comparatively low N uptake rates until flowering (Chapter I). However, due to a continued vigorous root growth and continued N-uptake activity during reproductive growth leaf senescence was delayed, LAD was prolonged, and the photosynthetic capacity of the leaves was maintained at a high level (Chapter III) during reproductive growth, and thus interception of solar radiation RUE of N-efficient rape cultivars was higher compared to the N-inefficient cultivar (Chapter IV).

It seems that comparatively slow shoot growth due to high investment of assimilated in vigorous root growth at the vegetative stage (Chapter II), maintained vigorous root growth and thus maintained N uptake during reproductive growth (Chapter I), slow leaf senescence (stay green), low LAI reduction, and sustained high photosynthetic capacity (Chapter III), high radiation interception, and high RUE during reproductive growth (Chapter IV) are the significant plant traits contributing to the N-efficient rape ideotype.

In conclusion, our results from three field studies suggest that N uptake and crop growth during the reproductive growth phase are more important for N efficiency than N retranslocation from vegetative plant parts to the seeds. Hence, our results clearly confirm that the N-efficient rape cultivars can be assigned to the “alternative ideotype” due to comparatively slow growth and N-uptake rates until flowering, which continue during reproductive growth as hypothesized by Wiesler et al. (2001a). A significance of the “improved traditional ideotype” with vigorous growth and high N uptake until flowering and efficient N retranslocation into the seeds during reproductive growth as hypothesized by the same authors could be not confirmed by our study.

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Erklärung

Hiermit erkläre ich, dass ich diese Dissertation selbstständig verfasst und die benutzten Hilfsmittel und Quellen sowie gegebenenfalls die zu Hilfeleistungen herangezogenen Institutionen vollständig angegeben habe.

Die vorliegende Dissertation wurde nicht schon als Masterarbeit, Diplomarbeit oder ähnliche Prüfungsarbeit verwendet.