The effects of cultivation and hybridization on life-history traits of native plant species used in re-vegetation

Von der Fakultät für Architektur und Landschaft
der Gottfried Wilhelm Leibniz Universität Hannover
zur Erlangung des akademischen Grades

Doktor der Naturwissenschaften (Dr. rer. nat.)

genehmigte Dissertation von
Roland Schröder
geboren am 03.02.1978 in Emsdetten

2014

Contents

Summaries

Executive summary

Keywords: nature conservation, re-vegetation, wild plant species

Native plants are increasingly used for re-vegetation measures (e.g. landscaping, restoration and bioengineering). Collecting plant material directly from wild populations could not meet the demand for plant material needed in re-vegetation. Thus, native plants are cultivated (hereafter cultivars) for re-vegetation measures. Cultivars presumably differ from their wild relatives (hereafter wilds) in life-history traits, because they faced human selection rather than selection by natural environmental conditions. Cultivars mostly derive from distant provenances with environmental conditions that are very different to re-vegetation sites. Therefore, cultivars are presumably adapted to entirely different environmental conditions than their wilds.

Introducing vast quantities of cultivars into the landscape is viewed as problematic by nature conservationists, soil bioengineers, and re-vegetation companies. The life-history traits developed by cultivation may not provide suitable abilities for survival at re-vegetation sites, and, therefore threaten the re-vegetation success. Otherwise, life-history traits developed by cultivation may enhance the fitness of cultivars. If cultivars establish and survive at re-vegetation sites, they might spread their range and may have undesirable effects on the existing native plant communities. It is most likely that cultivars will hybridize with their wilds. The effects of such hybridization on life-history traits of wilds and the significance for nature conservation are largely unknown. The risk of a cryptic invasion of cultivars (wilds, cultivars, and hybrids are difficult to distinguish and the invasion is therefore not detected), especially through hybridization is a concern. Due to these uncertainties a regionalized seed production of wild plant species has been developed in some countries to mitigate suspected problems by applying a precautionary principle. It has not been tested so far, whether this approach can also result in unintended and undesirable cultivation effects.

Above mentioned problems, which may occur due to plant use in hitherto form are based mainly on assumptions. The overall aim of the PhD thesis, therefore, is to investigate whether the large scale introductions of native plant cultivars for re-vegetation represents both a problem for nature conservation and re-vegetation success. Another aim is to give first indications whether a regionalized seed production might mitigate these problems.

By using cultivars, wilds, and artificially produced wild x cultivar hybrids (hereafter hybrids) of *Plantago lanceolata* L. (ribwort plantain) and *Lotus corniculatus* L. (birds-foot trefoil), two species frequently used in re-vegetation in Central Europe, the fol-

lowing objectives were tested: I addressed the questions whether cultivars used in re-vegetation differ in life-history traits from their wilds and whether life-history traits in wilds change through hybridization with cultivars. I tested whether life-history traits in cultivars and hybrids represent advantages or disadvantages for performance under natural climatic conditions of a wild's habitat and whether cultivars and hybrids have the ability to outperform their wilds. Finally, I examined whether a regional-ized seed production can supply appropriate methods to minimize cultivation effects in propagation of wilds. All objectives were tested experimentally using incubators, common garden experiments over a period of two growing seasons and greenhouse experiments over a period of one growing season.

I detected significant differences in life-history traits between cultivars and their wilds, which most likely are a result of cultivation efforts. Cultivars exhibited sig-nificant faster and more abundant germination behavior, indicating human selection against seed dormancy during cultivation. Cultivars began to flower significantly later (*P. lanceolata*) or earlier (*L. corniculatus*) than their wilds. Cultivars showed gi-gantism characteristics, like vigorous and erect growth, combined with higher vege-tative and generative biomass production than their wilds, if grown under permanent human care (greenhouse conditions with sufficient supply of water and nutrients). This behavior of cultivars can be interpreted as fitness advantage over their wilds at least under stress-less environmental conditions.

In a common garden experiment over two growing seasons, cultivars suffered from fitness losses due to the complete mortality of the *L. corniculatus* cultivar and re-duced vegetative biomass production in the case of *P. lanceolata* cultivars in the sec-ond growing season. I assume a trade-off; human selection towards high biomass production in cultivars potentially occurs at the expense of tolerating stressful envi-ronmental conditions (i.e. exceptionally cold winter between the two growing sea-sons). Considering also a reduced seed dormancy in cultivars, a life-history trait maintaining long-term survival of plant populations, I conclude that cultivars seem to be not well adapted to climatic conditions of a wild's habitat. That situation can subsequently threaten the re-vegetation success over the long-term.

Other than cultivars, I showed that evolving hybrids between cultivars and their wilds can establish and perform well (incl. heterosis for generative biomass production in *L. corniculatus* hybrids) under common garden conditions. Hybrids likely inherited both adaptations to the local climatic conditions from their wild parents as well as gigantism characteristics from their cultivated parents. Additionally, I showed that hybrids were competitively superior over their wilds in both studied growing seasons in a common garden-competition experiment. Hybrids are potentially able to out-

perform their wilds. Survival and successful reproduction of hybrids as shown in the presented study will multiply the propagule pressure from individuals with altered life-history traits. Therefore, I suggest that the risk of a cryptic invasion is high or has already taken place for some species whose cultivars have already been used for decades in re-vegetation.

Otherwise, it is also possible that following generations of hybrids may suffer from outbreeding depression due to backcrosses with parental cultivars and wilds (hybrid breakdown); or evolving hybrids directly inherit more maladaptive life-history traits or maladaptive trade-offs from parental cultivars. Both scenarios will reduce their fitness and may lead to natural selection against hybrids over the long-term. Assuming permanent hybridization, such selection subsequently might threaten the existence of "wild populations", because re-evolving towards wilds' life-history traits will be countered by the vast amounts of permanently introduced cultivars.

Using the example of germination behavior, I showed that collecting seeds of wild plants, as done by a tested regionalized seed producer, seemed to be an adequate method to preserve the life-history traits of wilds. There were no significant differences in germination behavior between pure wild seeds and declared wild seeds collected by the regionalized seed producer. Otherwise, the results indicate that propagation efforts presumably need improvements in order to prevent or minimize effects of unintended human selection on life-history traits like germination behavior.

My studies strongly indicate that the use of cultivars of native plant species in re-vegetation does represent both a problem for re-vegetation success as well as nature conservation. The outlined scenarios of permanent hybridization and the risk of a cryptic invasion are not desirable from nature conservation perspective, aiming to conserve intra- and interspecific diversity of local ecosystems. I give implications for the practice of re-vegetation in order to mitigate these problems. It should be thoroughly proved whether it is necessary to carry out re-vegetation via planting or sowing. It may be more advantageous for both re-vegetation success and nature conservation to allow re-vegetation by natural succession rather than by introducing (possibly non-suitable) plant material. If re-vegetation by introducing plant material is needed, the use of cultivars should be avoided and the use of wild plants is recommended. If wild plant material is used, the geographic distance and difference of edaphic conditions between the seed source and site of introduction should be kept to a minimum. If wild plant material needs to be propagated for use in re-vegetation, the implementation of strategies to reduce cultivation effects in life-history traits is needed.

Despite my findings on the effects of cultivation and hybridization on life-history

traits of native plant species and the resulting effects on wild plant populations, there are still knowledge gaps to fill. It is necessary to get reliable data about the distributions and abundances of cultivars and hybrids in the landscape in order to take conservation measures of remnant wild populations. Further studies should concentrate on genetic diversity as well as phenotypic variation as they are assumed to be lower in cultivars compared to their wilds. If this assumption holds true, adaptability to changing environmental conditions can be reduced and may be transferred into wilds by hybridization. Further research should evaluate whether further life-history strategies, such as flower phenology, plant performance, or genetic diversity are negatively affected, both by cultivation in standard seed production as well as in regionalized seed production. This knowledge is essential, in order to develop measures, aiming sustainable re-vegetation success as well as conservation of native plant's biodiversity and local ecosystems. The presented PhD study provides solid arguments in order to enhance nature conservation efforts in the practice of re-vegetation.

Kurzzusammenfassung

Schlagworte: Naturschutz, Begrünungsmaßnahmen, Wildpflanzen

Bei Begrünungsmaßnahmen in der freien Landschaft wird zunehmend Pflanzenmaterial aus heimischen Herkünften eingesetzt. Da das Sammeln von Pflanzenmaterial in Wildpflanzenbeständen den Bedarf z.B. an Saatgut für Begrünungsmaßnahmen bei weitem nicht decken kann, werden zunehmend auch heimische Pflanzen kultiviert und in großen Mengen für Begrünungsmaßnahmen eingesetzt. Die Kulturformen entstammen dabei überwiegend aus Regionen mit anderen Umweltbedingungen (teilweise aus Übersee) als dem Ort der Begrünungsmaßnahme. Wild- und Kulturformen sind demnach vermutlich an völlig unterschiedliche Umweltbedingungen angepasst. Durch die Kultivierung der Pflanzen ist es zudem wahrscheinlich, dass fitnessrelevante Pflanzenmerkmale und Pflanzenverhalten (im Folgenden *life-history traits*) verändert werden, da die Kulturformen nicht der natürlichen, sondern einer menschlichen Selektion unterliegen.

Das Ausbringen von Kulturformen heimischer Pflanzen in die freie Landschaft wird von Naturschützern, Ingenieurbiologen und ausführende Unternehmen häufig als problematisch beurteilt. Die durch die Kultivierung entstandene *life-history traits* könnten das langfristige Überleben der ausgebrachten Pflanzen verhindern und letztlich den Erfolg der Begrünungsmaßnahmen gefährden. Aus Naturschutzsicht stellt das regelmäßige Ausbringen großer Mengen an Kulturformen innerhalb des Verbreitungsgebietes ihrer Wildformen möglicherweise ebenfalls ein Problem dar. Die aus der Kultivierung hervorgegangenen *life-history traits* könnten den Kulturformen auch Fitnessvorteile verschaffen. Falls sich Kulturformen an ihren Einsatzorten erfolgreich etablieren und überleben, ist es denkbar, dass sie sich von dort ausbreiten mit evtl. ungewünschten Folgen für ihre Wildformen und heimische Lebensgemeinschaften. Es ist zudem davon auszugehen, dass die Kulturformen mit ihren Wildformen hybridisieren. Die Auswirkungen derartiger Hybridisierungsereignisse auf *life-history traits* der Wildformen und dessen Bedeutung für den Naturschutz sind aber weitestgehend unbekannt. Insbesondere durch den Mechanismus der Hybridisierung ist das Risiko einer kryptischen Invasion zu befürchten: Wild-, Kulturformen und deren Hybriden sind morphologisch vermutlich kaum zu unterscheiden, eine Invasion ist somit schwer auszumachen. Um den befürchteten Problemen entgegenzutreten, zeichnen sich in einigen Staaten im Sinne eines Vorsorgeprinzips Entwicklungen in Richtung einer regionalen Saatgutproduktion von Wildpflanzen ab. Ob ein derartiger Lösungsansatz ebenfalls zu unbeabsichtigten und ungewünschten Selektionseffekten führt, ist derzeit noch unklar.

Die aufgezeigten Probleme beruhen meist nur auf Annahmen. Das Ziel der vorliegenden Arbeit ist, das Wissen darüber zu verbessern, ob das großflächige Ausbringen von Kulturformen heimischer Pflanzen bei Begrünungsmaßnahmen tatsächlich ein Problem für den Naturschutz und für den Erfolg von Begrünungsmaßnahmen darstellt. Ein weiteres Ziel ist es, erste Anhaltspunkte zu liefern, ob der Ansatz einer regionalen Pflanzenproduktion geeignet ist, diese Probleme zu reduzieren.

Es wurde der Frage nachgegangen, inwiefern sich die für Begrünungsmaßnahmen genutzten Kulturformen in ihren *life-history traits* von ihren Wildformen unterscheiden und ob sich *life-history traits* der Wildformen durch Hybridisierung mit ihren Kulturen verändern. Weiterhin wurde in dieser Arbeit untersucht, ob die *life-history traits* der Kulturformen und Hybride von Vorteil oder Nachteil für ein Überdauern unter den klimatischen Bedingungen der Wuchsorte ihrer Wildformen sind und ob die Kulturformen und Hybride ihren Wildformen in Konkurrenzsituationen überlegen sind. Abschließend wurden die Methoden einer regionalen Pflanzenproduktion dahingehend betrachtet, ob sie ungewünschte Selektionseffekte in der Pflanzenvermehrung minimieren.

Für die Beantwortung der Forschungsfragen wurden Experimente mit mehreren Kulturformen, Wildformen und künstlich erzeugten Wild x Kultur-Hybriden von *Plantago lanceolata* L. (Spitz-Wegerich) und *Lotus corniculatus* L. (Gewöhnlicher Hornklee) durchgeführt. Beide Arten werden sehr häufig bei Begrünungsmaßnahmen in Mitteleuropa eingesetzt. Die Experimente erfolgten in Inkubatoren und im Freiland über zwei Vegetationsperioden, sowie in Gewächshäusern über eine Vegetationsperiode.

In den Untersuchungen zeigten sich signifikante Unterschiede in *life-history trait*s zwischen Kulturformen und ihren Wildformen, die höchstwahrscheinlich auf die Kultivierung selbst zurückzuführen sind. Die Kulturformen zeigten ein signifikant schnelleres und üppigeres Keimungsverhalten, das vermutlich auf eine bewusste Selektion gegen Samendormanz im Kultivierungsprozess zurückzuführen ist. Die Kulturformen blühten signifikant später (*P. lanceolata*) oder früher (*L. corniculatus*) als ihre Wildformen. Unter ständiger menschlicher Obhut (Gewächshausbedingungen mit ausreichendem Wasser- und Nährstoffangebot) zeigten Kulturformen im Vergleich zu ihren Wildformen Merkmale eines Gigantismus mit sehr kräftigem und aufrechtem Wachstum - kombiniert mit stärkerer vegetativer und generativer Biomasseproduktion. Das Verhalten der Kulturformen kann, zumindest unter derartig stressfreien Umweltbedingungen, als Fitnessvorteil gegenüber ihren Wildformen interpretiert werden.

In einem zwei Jahre andauernden Experiment unter Freilandbedingungen erlitten die Kulturformen hingegen deutliche Fitnesseinbußen mit einem Komplettausfall der *L. corniculatus* Kulturform und verminderter Produktion vegetativer Biomasse bei *P. lan-*

ceolata Kulturformen in der zweiten Vegetationsperiode. Dies ist vermutlich Folge eines *trade-off*. Die menschliche Selektion in Richtung erhöhter Biomasseproduktion während der Kultivierung erfolgte dabei vermutlich auf Kosten der Toleranz gegenüber stressigen Umweltbedingungen, in diesem Fall der besonders strenge Winter zwischen den beiden Vegetationsperioden. Unter Einbeziehung einer reduzierten Samendormanz, ein das Langzeitüberleben einer Pflanzenpopulation sichernder *life-history trait*, ist demnach von einer schlechten Anpassung der Kulturformen an die klimatischen Lebensraumbedingungen ihrer Wildformen auszugehen. Diese Situation kann letztlich den Erfolg der Begrünungsmaßnahme gefährden.

Andererseits zeigte sich, dass Hybriden aus Wild- und Kulturformen sich unter Freilandbedingungen sehr wohl etablieren und sehr gut entwickeln können (inkl. Heterosis-Effekt in der generativen Biomassproduktion bei *L. corniculatus*-Hybriden). Die Hybriden haben vermutlich sowohl die Anpassung an lokale klimatischen Bedingungen von ihren Wildformen als auch Gigantismus-Merkmale von ihren Kulturformen geerbt. Desweiteren zeigten die Hybriden in direkter Konkurrenz gegenüber ihren Wildformen in einem Freiland-Konkurrenzexperiment eine Überlegenheit in beiden Versuchsjahren. Demzufolge sind Hybriden potentiell in der Lage, ihre Wildformen auszukonkurrieren. Das Risiko einer kryptischen Invasion ist auf Grundlage dieser Ergebnisse relativ hoch bzw. für Arten, deren Kulturformen seit vielen Jahren für Begrünungsmaßnahmen eingesetzt werden, bereits erfolgt.

Es ist allerdings nicht auszuschließen, dass künftige Generationen von Hybriden Auskreuzungsdepression entweder durch Rückkreuzungen mit Kultur- und Wildformen erfahren (*hybrid breakdown*) oder Hybriden direkt für das Überleben ungeeignete *life-history traits* von ihren Kulturformen erben. Beide Szenarien führen zu Fitnessverlusten, was auf lange Sicht auch zu einer natürlichen Selektion gegen Hybride führen könnte. Davon ausgehend, dass derartige Hybridisierungsereignisse aber permanent stattfinden, dürfte dies zu einer Gefährdung der Existenz der Wildformen führen, da das permanente Ausbringen großer Mengen an Kulturformen einer potentielle Rückentwicklung in Richtung des Verhaltens der Wildformen entgegensteht.

Am Beispiel des Keimungsverhaltens konnte in dieser Arbeit gezeigt werden, dass die Sammelmethoden der untersuchten regionalen Saatgutproduktion für die Erhaltung von *life-history traits* von Wildformen geeignet zu sein scheinen. Es gab keine signifikanten Unterschiede zwischen dem Keimungsverhalten von reinen Wildformen und deklarierten Wildformen aus Basissammlungen des regionalen Saatgutproduzenten. Andererseits deuten die Ergebnisse Optimierungsbedarf bei der Vermehrung von Wildpflanzenmaterial an, um ungewünschte Selektionseffekte in *life-history traits* (wie z.B. Änderungen im Keimungsverhalten) zu verhindern bzw. zu reduzieren.

Die Ergebnisse der vorliegenden Arbeit weisen deutlich darauf hin, dass der Einsatz von Kulturformen heimischer Pflanzen bei Begrünungsmaßnahmen sowohl ein Problem für den Begrünungserfolg als auch für den Naturschutz darstellt. Die skizzierten Szenarien einer permanenten Hybridisierung und die Gefahr einer kryptischen Invasion sind aus der Sicht des Naturschutzes, dessen Ziel u. a. der Erhalt der inner- und zwischenartlichen Diversität lokaler Lebensgemeinschaften ist, nicht akzeptabel. Um in Zukunft die genannten Probleme, die aus der Pflanzenverwendung in bisheriger Form resultieren, zu lindern, werden in dieser Arbeit Handlungsempfehlungen für die Durchführung von Begrünungsmaßnahmen in der freien Landschaft formuliert.

Es sollte zukünftig sorgfältig geprüft werden, ob eine Begrünungsmaßnahme tatsächlich durch Ansaat oder Anpflanzung durchgeführt werden muss. Sowohl für den Begrünungserfolg als auch für den Naturschutz kann die Begrünung durch natürliche Sukzession vorteilhafter sein als durch den Einsatz von nicht geeignetem Pflanzenmaterial. Falls jedoch eine Begrünung durch Ansaat oder Anpflanzung notwendig ist, sollte auf die Verwendung von Kulturformen heimischer Arten zugunsten der Verwendung von Wildformen verzichtet werden. Falls Wildpflanzenmaterial eingesetzt wird, sollten die Ernteflächen und der Einsatzort der Wildpflanzen geographisch so nah wie möglich beieinander liegen und möglichst ähnliche edaphische Faktoren aufweisen. Falls Wildpflanzenmaterial für Begrünungsmaßnahmen vermehrt werden muss, sollten Methoden entwickelt und angewandt werden, um mögliche Selektionseffekte zu reduzieren.

Trotz der Erkenntnisse aus der vorliegenden Arbeit über die Auswirkungen von Kultivierung und Hybridisierung auf *life-history traits* heimischer Pflanzenarten und erste Anzeichen von möglichen Auswirkungen auf betroffene Wildpflanzenpopulationen, gibt es noch große Kenntnisdefizite. Es ist dringend notwendig, belastbare Daten über die Verbreitung und Häufigkeit des Vorkommens von Kulturformen und Wild x Kultur Hybriden in der freien Landschaft zu gewinnen, um Maßnahmen zum Schutz von Restpopulationen der Wildformen zu entwickeln. Weitere Forschungen sollten sich zudem auf die Themenfelder genetische Diversität und phänotypische Plastizität konzentrieren. Es wird angenommen, dass beide Eigenschaften in Kulturformen im Vergleich zu ihren Wildformen reduziert sind, mit negativen Folgen für die Anpassungsfähigkeit an sich ändernde Umweltbedingungen. Diese reduzierte Anpassungsfähigkeit könnte sich weiterhin durch Hybridisierung auf ihre Wildformen übertragen und somit deren Überlebensfähigkeit reduzieren. Weitere Forschungen sollten sich zudem darauf konzentrieren, ob weitere als die hier untersuchten *life-history traits* sowohl durch die konventionelle Kultivierung als auch durch die regionale Saatgutproduktion von Wildpflanzen in unerwünschter Weise beeinflusst werden. Dieses

Wissen ist zwingend notwendig, um Maßnahmen zu entwickeln, die den Zielen eines nachhaltigen Begrünungserfolges und den Zielen des Naturschutzes zum Schutz intra- und interspezifischer Diversität der Landschaft gerecht werden. Die Ergebnisse der vorliegenden Arbeit liefern dabei belastbare Argumente, die naturschutzfachlichen Bemühungen in der Praxis von Begrünungsmaßnahmen weiter auszubauen.

Chapter 1

Introduction

1.1 Background

1.1.1 Changes in life-history traits of plant species by cultivation

Humans have been cultivating plants for thousands of years (e.g. Renfrew 1969, according to Ladizinsky 1985), which has modified wild plants' life-history traits according to human interests. For instance, studies with crop species have shown that cultivated plant varieties (referred to as cultivars) are often selected to allocate more resources to vegetative growth than their wild relatives (referred to as wilds) and, thus, they often show a more vigorous and sometimes a more erect vegetative growth (gigantism, examples in Evans 1996). Furthermore, cultivars are sometimes bred for higher seed production (McGrath et al. 2010), larger and heavier seeds (Evans 1996), as well as larger flowers (van Gaal et al. 1998). Seeds of cultivars often exhibit lower dormancy and a faster, more abundant germination than their wilds (Harper & Mc-Naughton 1960; Hilu & Dewet 1980; Adler et al. 1993; Kitchen & Monsen 1994; Meyer & Kitchen 1994; Snow et al. 1998; Rojas-Arechiga et al. 2001; Wilson & Mecca 2003; Mercer et al. 2006; Maass & Usongo 2007). Flowering phenology of cultivars often differs from that of their wilds, starting either earlier or later and exhibiting longer or shorter flowering duration (e.g. Evans 1996; Meek et al. 2004 according to Walker et al. 2004a). The abovementioned changes of life-history traits caused by plant cultivation are often described as "domestication syndrome" (Harlan 1992, according to Frary & Doganlar 2003).

These changes in life-history traits that occur during cultivation increase revenue in agriculture and horticulture. For instance, a more vigorous vegetative growth may increase pasture or crop yields. Erect growth habits and vigorous growth of grasses may also facilitate cutting as a hay crop (Akeroyd 1994). Lower seed dormancy in cultivars is desired to facilitate high germination rates. Additionally, this kind of selection is often promoted by legislation. For instance, the European Seed Regulations (EEC 1966) require a fast and abundant germination for cultivars to be certified and permitted to be sold as fodder plants. Changes in flower phenology often occur in plant species cultivated as ornamentals, e.g. to improve their showy appearance. As constant uniformity of certain life-history traits is required for certification (e.g. EEC 1994), the changes acquired in life-history traits of cultivars can be assumed as genetically fixed. Besides the desired changes for economic reasons, other changes in life-history traits, as a result of physiological trade-offs, may occur. The theory of physiological trade-offs is based on the assumption of a proportional distribution of resources to the allocation for competing traits (Lloyd 1988; Thiele et al. 2009). Resources that are invested in one trait are therefore not available for other traits. For

instance, a selection for leaf gigantism traits in cultivars of *Trifolium repens* is negative correlated with flower-head production (Annicchiarico & Piano 1997, further examples in Obeso 2002).

In addition to specific selections for economically important life-history traits and linked trade-offs, cultivars presumably differ from their wilds in their adaptation to environmental conditions of their habitat. Contrary to their wilds, cultivars are grown under permanent human care without suffering from resource limitation, such as nutrients or water deficiency. Additionally, cultivars often derive from far distant provenances, sometimes even from another continent, which exhibit considerably different climatic conditions compared to habitats of their wilds. In conclusion, cultivars are often adapted to entirely different environmental conditions than their wilds and are subjected to human selection rather than selection by natural environmental conditions.

1.1.2 Cultivated varieties intended for use in re-vegetation

For several decades cultivars have not only been produced for agriculture and horticulture, but also for re-vegetation measures (in this term I include all kinds of greening measures in landscaping, restoration and soil-bioengineering). Generally, native plants are assumed to be well-adapted to the environmental conditions of the re-vegetation sites (e.g. Smith et al. 2007) and, therefore, the demand for native plants intended for use in re-vegetation has been increasing. However, the demand for native seeds for re-vegetation could not be met by collecting seeds of local wild plants, at least in Central Europe. Cultivation and mass-production of native plants are often more cost effective than collecting seeds from wild habitats. Thus, a commercial native plant production (i.e. cultivars of wild plant species) and seed market has been established in Central Europe and continues to grow where cultivars of native plants have been used for several decades in re-vegetation (cf. Posselt 2000).

The amount of annually introduced cultivars of native plant species for re-vegetation is largely unknown. However, during 2007 and 2008, approximately 13.700 tons of cultivated grass seeds and 280 tons of cultivated herb seeds were imported to Germany from both EU and non-EU countries (German Federal Office for Agriculture and Food, personal communication) and subsequently released into the environment. In the USA 2.9 million ha of cultivars of native grass species were established on former cropland in 2007 through the USDA Conservation Reserve Program (USDA 2007 according to Lambert et al. 2011). This situation may nationally be intensified by legislation concerning the trading of plant material. For instance, up to now, the Ger-

man Seed Directive has restricted the trade of a large number of native plant species to their cultivars only in order to ensure high quality of seeds and to protect certified plant variety rights (However, this regulation has been loosened recently, allowing the trade of small quantities of wilds, see BMELV 2011). Consequently, vast amounts of cultivars are annually released into the semi-natural range of their wild relatives (Lambert et al. 2011). From a plant ecology perspective, this situation can be regarded as a permanent and strong propagule pressure by human inducted "seed rain".

Introducing vast quantities of non-native plants (such as cultivars of native plants) into the landscape is considered undesirable by nature conservationists, soil bioengineers, and companies involved in re-vegetation (Rogers & Montalvo 2004; Broadhurst et al. 2008; Laikre et al. 2010; Vander Mijnsbrugge et al. 2010; Byrne et al. 2011). This kind of plant use can probably represent both a problem for the re-vegetation success and a problem for nature conservation.

Central European soil-bioengineers observed already decades ago that plants from different origins or from nurseries often seemed poorly adapted to the environmental conditions they encountered after being released (e.g. Stiny 1908, and later Hiller 1999 according to Hiller & Hacker 2001; Molder 2000; Krautzer et al. 2011). Assuming that natural selection selects for the best traits for surviving in a particular environment, human selection during cultivation focuses only on a few traits, if not only on a single trait. The abovementioned domestication syndromes in plants produced for agricultural or ornamental purposes are of minor relevance, as these plants are kept under more or less constant human supervision. Undesirable effects such as that appeared as trade-off for economically desirable life-history traits could be accounted for by human care. On the contrary, plant material used for re-vegetation should survive without constant or regular human treatment. For the long-term survival of these plants, changes in life-history traits by cultivation might be maladaptive and, therefore, can threaten the re-vegetation success. For instance, the life-history trait of seed dormancy is seen as a bet-hedging strategy that allows plant populations to spread the risk of extinction over time (Slatkin 1974; Venable & Brown 1988; Rees 1994; Evans & Dennehy 2005; Satterthwaite 2010). A reduction of seed dormancy will probably reduce the ability of a population to maintain its long-term existence.

In addition to being a potential threat to the re-vegetation success, introducing vast amounts of cultivars may represent a problem for nature conservation. The amount of introduced cultivar seeds may be as large as or larger than the amount of progenies, which are annually produced by their wilds. This situation may result in a numerical advantage of cultivars over their wilds. Wilds and cultivars likely come into contact

due to the strong "seed rain" of cultivars from re-vegetation projects. The interaction of wilds and cultivars as well as numerical advantages of cultivars might affect populations of wilds, further plant species in native vegetation as well as organisms in higher trophic levels of local ecosystems in undesirable ways.

Life-history changes induced by cultivation may make cultivars less fit or even fitter than wilds. An increased fitness may persist outside the protected environment of a nursery, i.e. the harsher environment of the re-vegetation site. If cultivars are fitter they will invade and take over wild populations of the same species, resulting in undesirable changes in community structures of native vegetation. It has been shown that a fast and abundant germination is linked to invasive occurrence of cultivars in native vegetation outside the natural range of their wild relatives (Chrobock et al. 2011). For example, the Japanese shrub *Ardisia crenata*, bred for ornamental purposes, invaded North-American hardwood forests, likely due to changes in leaf architecture by cultivation efforts, which enhanced its competitive ability (Kitajima et al. 2006). Assuming that cultivars are selected for more vigorous and erect growth, they may outcompete their wilds because tall plants often exhibit greater competitive abilities than smaller plants (Grime 1977; Goldberg 1987). There is already some evidence that invading cultivars can threaten the existence of wilds. For instance, in northern Spain (Galicia) cultivars of *Dactylis glomerata*, introduced for hay production in the 1970's and hybrids with their wilds have displaced the wild populations of this species (Lumaret 1990). A similar phenomenon has been assumed for *Lolium perenne* in Britain (Warren et al. 1998) and *L. multiflorum* in Switzerland (Peter-Schmid et al. 2008), whose cultivars have been introduced due to grassland melioration for several decades. The numerical advantage of introduced genotypes over conspecific local relatives is generally known as cryptic invasion (e.g. Saltonstall 2002). The invasion is a cryptic one, because the introduced genotypes (such as cultivars) and the local wilds are often difficult to separate from another and the invasion is therefore not detected immediately (Hufford & Mazer 2003). Hence, a cryptic invasion can derive due to replacements of wilds by cultivars exhibiting fitness advantages (e.g. larger competitive abilities); or the numerical dominance of cultivars over their wilds is a result of the permanent and strong "seed-rain" from re-vegetation activities.

Hybridization between wilds and cultivars has been observed frequently (Ellstrand et al. 1999; Ellstrand 2003) and can create further weaken of wild populations. Intraspecific crossings and back-crossings between cultivars and their wilds have been demonstrated mainly for crop species (e.g. Ellstrand 2003; Magnussen & Hauser 2007). The same phenomenon may occur in species used for re-vegetation measures. There is a high probability of hybridization between cultivars and their wilds as vast amounts

of cultivars are released into the environment each year. These hybridizations are certainly not a single event. Gene flows over long time periods in both directions, both from cultivars to their wilds and vice versa, are likely. The effects of such hybridizations on the existence of wilds have been shown for a woody species in Central Europe. Large scale and long-term hybridizations between wilds of *Populus nigra* and introduced cultivars (e.g. *Populus* x *canadensis*) have threatened the existence of the wild genotype (example from Belgium: Vanden Broeck et al. 2004). Meanwhile, pure stands of wild *Populus nigra* individuals are difficult to detect in large areas of Central Europe.

However, the ultimate effect of cultivars on their wilds depends on how cultivars affect the fitness of the related wild populations (Ellstrand 2003). Carry-over of maladaptive life-history traits or trade-offs developed by cultivation towards wilds by hybridization might result in reduced fitness and potentially reduced survival. This phenomenon, called outbreeding depression, is already known from studies on intraspecific hybridization between wild plants used in re-vegetation, which originated from geographically distant populations (Waser & Price 1994; Keller et al. 2000; Montalvo & Ellstrand 2000; Cremieux et al. 2010). Outbreeding depression is caused by two principle mechanisms: the environmental component and the physiological component. The mechanism of the environmental component is represented by the dilution of local adaptation. This dilution is caused by inheritance of life-history traits or occurring trade-offs, which do not provide a suitable adaptation to local environmental conditions. Outbreeding depression by physiological mechanisms is known as hybrid breakdown due to disruption of co-adapted gene complexes via recombination with parental genotypes (Lynch 1991; Hufford & Mazer 2003). Hence, if introduced cultivars and local wilds are adapted to different environments, the fitness of hybrid progeny could decrease because of a 50% dilution of the genome of the local wild population following hybridization (Hufford & Mazer 2003). Over the long-term this permanent fitness reduction by hybridization will likely threaten the existence of affected wild populations.

Otherwise, hybrids of cultivars and their wilds may be fitter than their wild parents. This has been shown in hybrids of crop species and their wild progenitors (e.g. *Raphanus sativus*: Klinger & Ellstrand 1994; *Oryza sativa*: Langevin et al. 1990; *Helianthus annuus*: Mercer et al. 2006; Mercer et al. 2007). Fitness advantages over their wilds have already been assumed in wild x cultivar hybrids detected in a restored prairie-grassland in North-America, which was established with seeds i.a. from a cultivar of *Andropogon geradii* (Gustafson et al. 2004). The underlying mechanism of an enhanced fitness of hybrids is often a heterosis effect. Heterosis can occur

if hybridization occurs between individuals from populations, which are genetically impoverished because of drift or inbreeding (Hufford & Mazer 2003). As there is some evidence that cultivars are genetically impoverished due to selection by breeding (Bennett 1970; Ladizinsky 1985), similar effects of heterosis may be suspected in hybrids with their wilds. Whether such evolved enhanced fitness in hybrids between cultivars for re-vegetation and their wilds might really occur has not been studied before. Such research is essential to evaluate whether heterosis in hybrids will result in increased competitive abilities. Similar to cultivars, wild x cultivar hybrids can threaten the existence of wild populations or lead to undesirable changes in native vegetation.

Assuming that cultivars and evolving hybrids differ in life-history traits and assuming that they will survive at the re-vegetation sites and probably will increase their range; cultivars and hybrids may not only have undesirable effects on populations of wilds and native plant community structure, but also may have effects on organisms of higher trophic levels of local ecosystems. Different flower onset of cultivars has been observed for cultivars used in agriculture as well as cultivars used in re-vegetation. Often cultivars flower earlier or later than their wild relatives (e.g. *Trifolium repens*, Meek et al. 2004 according to Walker et al. 2004a). Changes in flower phenology by cultivation might result in temporal mismatch between main occurrences of pollinator taxa and flower onset. This may result in lower reproductive output of affected plant species (Rafferty & Ives 2012) and/or shifting in affected invertebrate communities.

1.1.3 Initial approaches in the practice of re-vegetation to mitigate indicated problems

Despite the uncertainties regarding unintended and undesirable effects that may develop from carrying out re-vegetation with cultivars, some effort in the conservation of wild plant species and in order to increase the re-vegetation success have been done yet by applying a precaution. Seed provenance zones were developed mainly in Australia, North America and Europe to avoid the re-introduction of poorly adapted plant material (e.g. Waters 2001; Johnson et al. 2010; Prasse et al. 2010; Malaval et al. 2010). These zones are defined as geographic areas within which plant material can be moved freely with little disruption of genetic patterns or loss of local adaptation (Miller et al. 2011). While seed zones represent a practice that has been used in forestry for several decades, the application of this approach for re-vegetation measures involving herbaceous plants and grasses began only a few years ago (McKay et

al. 2005; Vander Mijnsbrugge et al. 2010; Miller et al. 2011). For instance, in Germany 22 seed provenance zones have been delineated based on natural regions, climatic and geological criteria (Prasse et al. 2010). In these seed zones, regionalized propagation of common wild plant species occurs (in addition to the direct transfer of wild plants from a donor- towards a re-vegetation site). Thereby, seeds are collected from wild plant populations, propagated for a few generations on farms and subsequently used for re-vegetation measures within the particular seed zone. A regionalized seed production aims to minimize cultivation effects in the propagation of wilds. However, it is likely that human invention like collection and propagation will still change the life-history traits. For instance, it is known from ex situ conservation efforts in botanic gardens (Ensslin et al. 2011) and seed banks (Schoen & Brown 2001) that unintended selection against dormant seeds might occur. Similar effects of unintended human selection can therefore also be assumed in a regionalized seed production.

1.2   Objectives and structure of thesis

The relevance of the origin of plant material for re-vegetation success and nature conservation has been studied for several years (e.g. Keller et al. 2000; McKay et al. 2005; Bischoff et al. 2006b; Bischoff et al. 2008). These studies predominantly focused on the provenance effect on life-history traits of native plants originated from different pure wild populations. Surprisingly, hardly any study addressed the effect of the introduction of cultivars in re-vegetation on populations of their wild relatives and tested for these effects in-situ (but see Gustafson et al. 2004). Similarly, an evaluation of the relevance of such effects for nature conservation and the practice of re-vegetation has not been carried out. Abovementioned changes of life-history traits of native plant species by cultivation as well as the effects of cultivars on their wilds are based mainly on assumptions as these effects have primarily been studied for crops and garden varieties. Research is urgently needed to identify whether negative effects on wild relatives might really occur and whether the use of cultivars may threaten the re-vegetation success in order to develop approaches to mitigate possible problems. Additionally, no studies have been found, which test whether the regionalized seed production may also have undesirable effects on life-history traits of wild plants. This knowledge is essential to develop collection and propagation strategies, which will minimize cultivation effects in a regionalized seed production for re-vegetation.

Thus, the overall aim of the PhD thesis was to improve knowledge on whether the large-scale introduction of cultivars of native plant species in re-vegetation is a problem for nature conservation and re-vegetation success. Another aim was to inves-

tigate whether a regionalized seed production might mitigate undesired cultivation effects. The main objectives of the presented PhD thesis are as follows:

- Do cultivars used in re-vegetation differ from their wilds in life-history traits?

- Do life-history traits of wilds change through hybridization with cultivars?

- Do life-history traits in cultivars and hybrids represent advantages or disadvantages for the performance under natural climatic conditions of a wild's habitat?

- Do cultivars and hybrids have the ability to outcompete their wilds?

- Does regionalized seed production apply appropriate methods to minimize cultivation effects in the propagation of wilds?

The results of the thesis are presented in four articles, of which two are already published in or accept to peer-reviewed international journals.

Chapter 2 (article I) addresses the question whether cultivars and their wilds differ in germination behavior, as this life-history trait is known to be one of the most important characteristics securing long-term existence. I tested whether assumed differences may be transferred into the next generation and whether such changes in cultivars may be transferred into wilds by hybridization.

In Chapter 3 (article II) differences in morphological traits and flower onset between cultivars, their wilds, and evolving hybrids are presented. I tested whether cultivars are selected towards high vegetative and generative yield, which may enhance their fitness. I tested whether wild x cultivar hybrids show effects of outbreeding depression or heterosis. I furthermore investigated whether assumed enhanced fitness due to enhanced biomass production in cultivars might also persist outside the favorable environmental conditions of a nursery under local climatic conditions of a typical wild's habitat in Central Europe.

Chapter 4 (article III) addresses the question whether cultivars as well as wild x cultivar hybrids have the ability to outperform their wilds, driving the assumption that human selection in cultivars towards larger biomass allocation with vigorous and erect growth habits may result in competitive superiority over their wilds.

Chapter 5 (article IV) addressed the question whether regionalized seed production can affect germination behavior of wilds by selecting towards fast and abundant germination. Using seeds from a regionalized seed production, I investigated whether collecting seeds of wilds and propagating them for one generation may be an effective

measure to preserve wilds' germination behavior. Additionally, I tested whether there are differences in germination behavior between seeds propagated by a regionalized seed producer and cultivar seeds derived from standard commercial seed production.

Chapter 6 presents a synthesis of the main results of the study, which are subsequently discussed in chapter 7. Finally, chapter 8 draws conclusions, including implications for the practice of re-vegetation as well as an outlook towards further necessary research.

1.3   Approach

All objectives were tested experimentally using incubators, common garden, and greenhouse experiments. Two species with different pollination mechanisms and different germination strategies, both commonly propagated in nurseries and used for re-vegetation in Central Europe (i.e. components of frequently used seed mixtures) were selected for the studies. *Plantago lanceolata* L. (ribwort plantain, Plantaginaceae) and *Lotus corniculatus* L. (birdsfoot trefoil, Fabaceae) are both hemicryptophytes, are abundant in a wide range of habitats and are distributed over large parts of the northern hemisphere. *P. lanceolata* is wind-pollinated and self-incompatible (Sagar & Harper 1964; Cavers et al. 1980). *L. corniculatus* is an insect-pollinated and a predominantly outcrossing species (Jones & Turkington 1986). The wild plants of both species exhibit seed dormancy. *P. lanceolata* seeds display a partially non-deep physiological dormancy (Sagar & Harper 1964; Blom 1978; van Groenendael 1985a; Pons 1992, classification of Baskin & Baskin 2004), while for seeds of *L. corniculatus* a physical dormancy is apparent (van Assche et al. 2003).

Chapter 2

Cultivation and hybridization alter the germination behavior of native plants used in re-vegetation and restoration

Author contributions: Conceived the experiments: RS, RP. Designed and performed the experiments: RS. Analyzed the data: RS. Wrote the paper: RS, RP

Abstract

Native plants are increasingly used for re-vegetation and restoration. These plants are cultivated for several generations at plant nurseries and often they are of unknown provenance. Therefore, cultivated plants often differ from their wild progenitors in life-history traits. Using germination behavior as example, we tested the assumption that cultivated plants have different life-history traits than their uncultivated progenitors. Cultivated as well as wild individuals of *Plantago lanceolata* and *Lotus corniculatus*, two species frequently used in re-vegetation, were tested in a common garden experiment as well as in incubators for their germination behavior. We observed significantly faster and more abundant germination in cultivated varieties. Using artificial crossings we found that also hybrids of cultivated varieties and wild relatives germinate faster and more abundant than the wilds. As wild plants acquire their life-history traits by natural selection, we have to assume that they represent the optimal adaptation to the environmental conditions. If these traits are changed by cultivation or by hybridization between cultivated varieties and local populations, the long-term survival probabilities of local populations may be altered. Therefore, the use of cultivated varieties of native plants should be avoided in re-vegetation.

Chapter 3

From nursery into nature: A study on performance of cultivated varieties of native plants used in re-vegetation, their wild relatives and evolving wild x cultivar hybrids

Author contributions: Conceived the experiments: RS, RP. Designed and performed the experiments: RS. Analyzed the data: RS. Wrote the paper: RS, RP

Abstract

Cultivated varieties may have life-history traits which are very different to those of their wild progenitors. Changes in life-history traits due to cultivation may not be desirable for plant material used for re-vegetation, as these plants may be adapted to constant human care and lack the finely tuned trade-off that allows wild plants to cope with the often harsh and heterogeneous environmental conditions outside of nurseries. Research is needed to identify differences in life-history traits between cultivated varieties used in re-vegetation and restoration and their wild relatives. If such traits are changed by cultivation, it is necessary to examine if they will persist also at the re-vegetation site and may be transferred to wild relatives by hybridization as that may reduce their survival or lead to undesirable changes on local ecosystems. In this study we examined whether cultivated varieties of *Plantago lanceolata* and *Lotus corniculatus*, two species frequently used in re-vegetation and restoration projects, differ from their wild relatives in morphology or flower phenology and whether differences could be transferred into wild relatives by hybridization. We tested if cultivated varieties are bred for high vegetative and generative yield in greenhouse studies. In common garden experiments we studied if enhanced biomass production is also persistent under the climatic conditions of the wild plant's natural habitat in Central Europe. Additionally, we tested if hybrids show effects of outbreeding depression or heterosis. The cultivated varieties of both species grew very vigorously and showed a more erect growth pattern than their wild relatives. The cultivated varieties seem to be selected towards high vegetative and generative yield. However, if exposed to local climatic conditions, cultivated varieties suffered a fitness loss with a complete mortality for the *L. corniculatus* cultivar and a reduced vegetative biomass production for *P. lanceolata* cultivars. Otherwise, we detected heterosis effects in hybrids for survival and generative biomass production in *L. corniculatus* and number of leaves in *P. lanceolata*. As it remains unclear whether hybridizations might result in strongly competitive genotypes or disturb the local adaptation of wild plant populations and cultivated varieties may threaten the re-vegetation success, the large-scale use of cultivated varieties of native plants should be avoided in re-vegetation and restoration.

Chapter 4

Do cultivated varieties of native plants have the ability to outperform their wild relatives?

Author contributions: Conceived, designed and performed the experiments: RS. Analyzed the data: RS. Wrote the paper: RS, RP

Abstract

Vast amounts of cultivars of native plants are annually introduced into the semi-natural range of their wild relatives for re-vegetation and restoration. As cultivars are often selected towards enhanced biomass production and might transfer these traits into wild relatives by hybridization, it is suggested that cultivars and the wild x cultivar hybrids are competitively superior to their wild relatives. The release of such varieties may therefore result in unintended changes in native vegetation. In this study we examined for two species frequently used in re-vegetation (*Plantago lanceolata* and *Lotus corniculatus*) whether cultivars and artificially generated intra-specific wild x cultivar hybrids may produce a higher vegetative and generative biomass than their wilds. For that purpose a competition experiment was conducted for two growing seasons in a common garden. Every plant type was growing (a.) alone, (b.) in pairwise combination with a similar plant type and (c.) in pairwise interaction with a different plant type. When competing with wilds cultivars of both species showed larger biomass production than their wilds in the first year only and hybrids showed larger biomass production than their wild relatives in both study years. As biomass production is an important factor determining fitness and competitive ability, we conclude that cultivars and hybrids are competitively superior their wild relatives. However, cultivars of both species experienced large fitness reductions (nearly complete mortality in *L. corniculatus*) due to local climatic conditions. We conclude that cultivars are good competitors only as long as they are not subjected to stressful environmental factors. As hybrids seemed to inherit both the ability to cope with the local climatic conditions from their wild parents as well as the enhanced competitive ability from their cultivars, we regard them as strong competitors and assume that they are able to outperform their wilds at least over the short-term. Therefore, as a precaution it is strongly recommend to avoid the use of cultivated varieties in re-vegetation.

Chapter 5

Testing the effects of a regionalized seed production on the germination behavior of wild plant species.

Author contributions: Conceived and designed the experiments: RS. Performed the experiments: RS, JJ, GR, JS, IT. Analyzed the data: RS. Wrote the paper: RS, MG.

Abstract

Cultivated varieties of native plants are increasingly used for restoration. Life-history traits which are acquired by natural selection in wild plants, like germination, are likely changed when plants are cultivated. Altered life-history traits in introduced cultivated varieties may result in the reduction of long-term viability or enhance their invasion potential. Standard seed production (SSP) frequently uses native seeds from distant provenances and these seeds are cultivated for numerous generations. A regionalized seed production (RSP) aims to preserve wild´s life-history traits. In this study we compared the germination rates of (a) declared wild seeds (F0) and their subsequent propagated generation (F1) from RSP, (b) seeds derived from SSP methods, and (c) seeds collected from the wild in order to test whether RSP methods preserve natural germination rates. We tested the germination behavior of *Plantago lanceolata* and *Lotus corniculatus*, two species frequently used in re-vegetation. F0-seeds of both species from RSP did not differ in germination behavior from wild seeds. Cultivated varieties from SSP germinated significantly faster and had a higher total germination for both species. While F1-seeds of *P. lanceolata* did not differ from their F0-seeds, F1-seeds of *L. corniculatus* germinated significantly faster and were more abundant than their F0-seeds. Whereas RSP methods seemed to preserve natural germination behavior in *P. lanceolata*, we observed unintended selection against seed dormancy and slow germinating seeds during propagation of *L. corniculatus*. Applying appropriate methods in all parts of harvesting and propagation activities (e.g. scarification) is important to preserve life-history traits of wild populations for restoration activities.

Chapter 6

Synthesis of results

Do cultivars used in re-vegetation differ from their wilds in life-history traits?

I detected significant differences in characteristics of life-history traits between cultivars and their wilds in both study species *P. lanceolata* and *L. corniculatus*. Seeds of cultivars germinated significantly faster and more abundantly than seeds of their wilds. These differences in germination behavior were consistent both in the F0-generation as well as the F1-generation of the tested seeds. F0- as well as F1-seeds of *P. lanceolata* cultivars were significantly larger than seeds of their wilds. Seed weight of the wild *L. corniculatus* was significantly larger in the F0-generation, whereas the cultivar seeds showed larger weights in the F1-generation. F0-cultivars of both species exhibited considerable gigantism characteristics. They grew vigorously, showed a strong erect growth pattern with significantly longer leaves (*P. lanceolata*) and shoots (*L. corniculatus*), but lower number of leaves and shoots, respectively, than their wilds. F0-cultivars began to flower significantly later (*P. lanceolata*) or earlier (*L. corniculatus*) than their wilds. In both species F0-cultivars produced significantly more vegetative and generative dry biomass than their wilds if exposed to stress-less environmental conditions and human care (greenhouse conditions in a competitively free environment with sufficient supply of water and nutrients).

Do life-history traits of wilds change through hybridization with cultivars?

By carrying out artificial crossings, I showed that life-history traits of cultivars could be transferred into their wilds by hybridization. F1-seeds of wild x cultivar hybrids (♀= wild, ♂ = cultivar) germinated significantly faster and more abundantly than seeds of "parental" wilds' progeny. Hybrids predominantly showed an intermediate growth habit with less erect growth than their cultivated parents but significantly more erect growth than their wild parents. Heterosis occurred for leaf number per plant in *P. lanceolata* hybrids.

Do life-history traits in cultivars and hybrids represent advantages or disadvantages for the performance under natural climatic conditions of a wild's habitat?

The results showed that cultivars of the F1-generation exhibited higher biomass production in the first growing season of the common garden experiment, but wilds exhibited higher biomass production in the second growing season. Similar to tested F0-plants in the greenhouse, F1-cultivars of both species produced significantly more biomass than F1-wilds if exposed to natural climatic conditions of their wild's habitat in the first growing season of the common garden experiment. However, F1-cultivars

showed worse performance in the second year of study with a 100% mortality of the *L. corniculatus* cultivar and reduced vegetative biomass production in *P. lanceolata* cultivars compared to their wilds. Survival of *P. lanceolata* cultivars and wilds of both species was 100%. Other than parental cultivars, hybrids of both species completely survived and did not show a reduction in biomass production. In contrast, I detected strong heterosis effects for *L. corniculatus* hybrids for survival and generative biomass production in the first growing season. Heterosis in hybrids of this species was also assumed for vegetative biomass production in the second growing season of the common garden experiment. There were no indications of outbreeding depression in hybrids of both study species.

Do cultivars and hybrids have the ability to outperform their wilds?

In competition with their wilds (between-type competition), cultivars of both study species performed better than their wilds in the first season of the common garden-competition experiment, but did not in the second growing season. In competitive interactions with their wilds cultivars of both species produced more vegetative and generative biomass in the first growing season. There was no difference in biomass production of *P. lanceolata* cultivars and their wilds in the second growing season. Survival in *P. lanceolata* wilds and cultivars was >90% regardless of the identity of competing neighbors. *L. corniculatus* cultivar individuals showed a high mortality (83%), regardless of the presence or identity of competing neighbors in the second growing season. In competition with their wilds (between-type competition), hybrids of both species performed better than their wild relatives. Hybrids of both species tended to produce more vegetative and generative biomass than their wild relatives in both growing seasons. Additionally, hybrids in competition with their wilds (between-type competition) produced more biomass than in competition with hybrids (within-type competition, *P. lanceolata* in the second growing season, for *L. corniculatus* in both growing seasons). In both species survival of hybrids was larger than 90%.

Does regionalized seed production apply appropriate methods to minimize cultivation effects in the propagation of wilds?

Testing the effects of a regionalized seed production on the germination behavior of native plants the results showed that seeds of both study species collected from the regionalized seed producer (in this chapter, hereafter F0-seeds) did not differ in germination behavior from pure wild seeds. F0-seeds showed a significantly slower and

less abundant germination than seeds from cultivars from standard seed production. Results of the germination behavior of F0-seeds and seeds from the following plant generation propagated by the regionalized seed producer (in this chapter, hereafter F1-seeds) differed between the species. For *P. lanceolata* the F1-seeds did not differ significantly from their F0-seeds. F1-seeds of *L. corniculatus* germinated more quickly and abundantly than the F0-seeds and did not differ from fast and abundantly germinating seeds of cultivars from standard seed production.

Chapter 7

Synthesis of discussion

The results of my studies showed considerable differences between wilds of native plant species and their cultivars in characteristics of life-history traits. The fast and abundant germination behavior (indicating reduction of seed dormancy), gigantism characteristics such as erect and vigorous growth as well as enhanced biomass production with larger leaves (*P. lanceolata*) and shoots (*L. corniculatus*) in cultivars are most likely a result of selection by cultivation rather than a function of environmental effects of their geographical origin (i.e. maternal effects). I minimized possible maternal effects by testing also F1-individuals whose parental F0-generation was grown under identical environmental conditions. Therefore, changes in life-history traits by cultivation are considered to be genetically fixed.

I interpret these gigantism characteristics including enhanced vegetative and generative biomass production as fitness advantage of cultivars over their wilds under conditions of human care and at least temporarily under local climatic conditions of a wild's habitat. Cultivars were fitter than their wilds in the first growing season of the experiment under local climatic conditions in a competition-free environment. However, cultivars suffered fitness losses compared to their wilds by the end of the experiment in the second growing season. Especially the complete mortality of the *L. corniculatus* cultivar during winter between studied seasons indicated very poor adaptation to local climatic conditions. Cultivars most likely suffered from strong frost events in this winter with exceptionally high number of days of temperature permanently below 0°C. In contrast, all wild individuals of *L. corniculatus* survived. Local climatic conditions had no effect on the survival of *P. lanceolata* cultivars. However, the strong winter might be seen as a reason for the reduction of vegetative biomass production of *P. lanceolata* cultivars during the second growing season compared to their wilds. Especially for the *L. corniculatus* cultivar I assume a trade-off in life-history trait manifestation. Human selection towards large biomass production may in this case have included a selection against the ability to tolerate stressful environmental conditions due to changes in resource allocation. A similar reduction of frost resistance has been shown in cultivated *Daucus carota* ssp. *sativus* in comparison to parental wild *Daucus carota* ssp. *carota* (Hauser 2002). Such trade-offs can also result in loss of resistance to pests (e.g. *Lolium multiflorum*, Boller et al. 2009).

These results indicate that life-history traits of cultivars can provide characteristics for a successful re-vegetation; but only over the very short-term. Fast and abundant germination, combined with fast and vigorous growth enhance the development of re-vegetation sites (e.g. development of a sward or greening at roadside verges). However, a reduction of seed dormancy by cultivation and the occurrence of further maladaptive trade-offs can decrease the ability of long-term survival under environ-

mental conditions without human care. I suggest that wild plant species most likely cope better with local climatic conditions than their cultivars over the long-term. Thus, cultivars are not appropriate for long-term re-vegetation success.

The results of the competition experiment showed that cultivars in competition with wilds (between-type competition) produced higher biomass than their wilds over the short-term. Gigantism characteristics developed by cultivation therefore resulted in a competitive superiority over their wilds, at least in the first growing season. Fitness losses in cultivars (up to nearly complete mortality in *L. corniculatus* cultivar during winter) by the end of the second growing season occurred regardless of competition treatments, both with and without competition as well as regardless of the type of competing neighbors (wild, cultivar or hybrid). Hence, similar to the performance in a competition-free environment, cultivars may be fitter and may be competitively superior over their wilds until the occurrence of stressful environmental factors.

Other than cultivars, hybrids tended to exhibit fitness advantages over their wilds in both growing seasons under local climatic conditions, regardless of the existence of competing neighbors. I assume that hybrids inherited both tolerances to local climatic conditions from their wild parents as well as the ability to enhanced biomass allocation from their cultivated parents. As hybrids in competition with their wilds (between-type competition) were fitter than wilds and between-type competition always tended to be lower than within-type competition (hybrid vs. hybrid) it can be suggested that hybrids are competitively superior to their wilds. Thus, from a theoretical perspective I assume that especially hybrids have the ability to outperform their wilds, potentially resulting in competitive exclusion of the latter over the long-term. Otherwise, it is also possible that following generations of hybrids may suffer from outbreeding depression due to backcrosses with parental cultivars and wilds (hybrid breakdown, Hufford & Mazer 2003), which will result in fitness reduction. Alternatively, outbreeding depression can occur if evolving hybrids directly inherit more maladaptive life-history traits or maladaptive trade-offs from parental cultivars, probably resulting in reduced fitness (Hauser 2002) and reduced competitive abilities. This situation may lead to natural selection against hybrids over the long-term. Assuming permanent hybridization, such selection subsequently might threaten the existence of "wild populations", because re-evolving towards wilds' behavior (see Levin 2001) will be countered by the vast amounts of permanently introduced cultivars.

The results of my studies showed that some relevant traits for a successful invasion are produced during cultivation and may be handed over into future plant generations. Although it is not possible to predict the ultimate fate of cultivars and hybrids

within the semi-natural range of their wilds, I assume that over the long-term the risk of cryptic invasion of cultivars, especially by the mechanisms of hybridization is high or already has happened. The survival, successful reproduction (especially heterosis for generative biomass production in *L. corniculatus* hybrids) and competitive superiority of hybrids as shown in in the presented studies will multiply the human inducted "seed rain" of undesirable plant material and therefore increase the probability of cryptic invasion or result in undesirable changes in native vegetation. These scenarios represent a fundamental problem for nature conservation aiming at the conservation of intra- and interspecific diversity of local ecosystems (Laikre et al. 2010; Byrne et al. 2011).

Another problem for nature conservation might occur, if large scale establishment of cultivars and evolving hybrids will affect organisms on higher trophic levels. I detected changes in flower phenology of both study species by cultivation and hybridization. Cultivars started flowering about two weeks earlier (*L. corniculatus*) or about three weeks later (*P. lanceolata*) than their wilds and this behavior could partially be transferred into wilds by hybridization. Whether a shifting in flower phenology is persistent in future plant generations and whether this situation has undesirable effects on plant-pollinator interactions is highly speculative. Mismatches in pollinator interactions and their demographic consequences on both the pollinator species and affected plant populations can be assumed. For instance, it has been shown that changes towards earlier flowering may have reproductive cost for plants due to temporal mismatch of pollinator taxa and flower onset (Rafferty & Ives 2012). Research is urgently needed to test for these effects and to test whether shifting in flower phenology by cultivation and hybridization may have undesirable effects on e.g. invertebrate species and communities.

A regionalized seed production may be an approach in order to reduce cultivation effects in native plant species propagated for use in re-vegetation. The results out of my studies, testing the effect of a regionalized seed production on the germination behavior of wilds, indicate that this approach partially seems to be appropriate for conserving life-history traits of wild plant species. In both species I did not detect a significant difference in germination behavior between pure wild seeds (from own collections) and declared wild seeds (F0-seeds) from regionalized seed production. I conclude that collecting and storing of wild seeds as carried out by the regionalized seed producer seemed to preserve germination behavior of wild plants. Otherwise, the findings of the study indicate that the propagation of wild seeds as carried out by the regionalized seed producer seemed to affect germination behavior at least in *L. corniculatus.* Already after just one generation, F1-seeds from regionalized seed

production germinated as fast and abundantly than cultivar seeds from standard seed production. This different behavior of F1-seeds compared to the F0-seed germination behavior is probably a result of unintentional selection against late germinating and potential dormant seeds during the propagation process. Hence, propagation efforts presumably need improvement in order to prevent or minimize effects of unintended human selection on life-history traits.

Chapter 8

Conclusions and outlook

The results of my studies strongly indicate that the use of cultivars of native plant species in re-vegetation does represent both a problem for re-vegetation success as well as nature conservation. I draw the following implications for the practice of re-vegetation in order to mitigate these problems:

- It should be thoroughly proved whether it is necessary to carry out re-vegetation via planting or sowing. It may be more advantageous for both the re-vegetation success and nature conservation to allow re-vegetation by natural succession rather than by introducing (possibly non-suitable) plant material. Re-vegetation by natural succession will be more cost effective than introducing plant material, which possibly has to be done several times, because of re-vegetation failure by the use of non-suitable plant material.

- If re-vegetation by introducing plant material is needed, the use of cultivars should be avoided. The use of wild plants is recommended because it is desirable for planted or sown vegetation to be self-sustaining and able to cope with the normal periodic stress events in heterogeneous environments (Society for Ecological Restoration International Science & Policy Working Group 2004).

- If wild plant material is used, the geographic distance and difference of edaphic conditions between the seed source and site of introduction should be kept to a minimum as environmental factors are the major driving force for natural selection (home-site advantage, e.g. Montalvo & Ellstrand 2000; Bischoff et al. 2006a,b; Bischoff et al. 2008).

- If wild plant material needs to be propagated in order to supply the vast amounts of seeds needed for re-vegetation, the implementation of strategies to reduce cultivation effects in life-history traits is needed. The strategies are as follows:

  - In all parts of harvesting and propagation activities, selections against certain genotypes, e.g. stronger or weaker vegetatively growing or flowering plants, early or late germinating plants, dormant seed fractions or smaller or larger seeds should be avoided (Prasse et al. 2010). By appropriate methods like stratification, scarification, or treatment with e.g. gibberellic acid or potassium nitrate (ISTA 2006) germination of dormant seeds should be facilitated. This will be especially true in species with well-known and partially deep dormancy behavior (e.g. physical dormancy in many species of Fabaceae). Propagation of wilds should be done under nearly natural environmental conditions (e.g. without adding lots of nutrients and water) to prevent selection towards highly productive genotypes.

    – To further minimize risks of unintended selection, the propagation of wild seed collections should be carried out as short as possible for only a very few generations. Afterwards, a new harvest from the wild population is necessary.

    – Generally, for the propagation of wild plant species for re-vegetation, many genotypes from the harvested wild population should be used (» 50 individuals, Broadhurst et al. 2008; Prasse et al. 2010; Vander Mijnsbrugge et al. 2010).

• In re-vegetation measures by using wild seeds it may be necessary to increase sowing seed densities in order to comply with the customer's demand for rapid success and to reduce the minimum germination success requested by the European and national seed directives, as it is desirable that the propagated wild plant material used for re-vegetation retains its dormancy strategy (Schröder & Prasse 2010).

Outlook

Despite my findings on the effects of cultivation and hybridization on life-history traits of native plant species and the resulting effects on wild relatives, there are still knowledge gaps. We need to evaluate the significance and magnitude of these effects and potentially further occurring undesirable effects on local ecosystems and the mechanisms behind them in order to develop further and improve already existing mitigation measures.

Knowledge about the effects of introducing cultivars within the semi-natural range of their wilds is still very limited. Up to now we hardly have any information about the magnitudes of permanent gene flow from cultivars into their wilds. Considering the vast amount of annually introduced individuals of cultivars and the long-time practice of such plant use, the existence of (remnant) pure wild populations is questionable. The present results are conflicting. For instance, it has been assumed that the lack of genetic differentiation between wilds and cultivars of *Lolium perenne* and *L. multiflorum* in grasslands is due to conventional plant usage in Britain (Warren et al. 1998) and Switzerland (Peter-Schmid et al. 2008). Otherwise, such distinguishable patterns of genetic diversity could be found in *L. perenne*, *Trifolium repens* and *Poa pratensis* in the Netherlands (van Treuren et al. 2005; van Treuren 2008). As there is a real threat that populations of wilds whose cultivars have been frequently used for e.g. grassland melioration as well as restoration are no longer available (Walker et al. 2004b), it is necessary to get reliable data about the distributions and abundances

of cultivars and wild x cultivar hybrids in the landscape in order to take measures in conservation of remnant wild populations. The results of my studies concerning differences in morphological and phenological life-history traits may give an impetus for further studies with a focus on biometrical differences between wilds and their cultivars in order to facilitate the detection of cultivars and hybrids in the landscape (see Bonnemaison & Jones 1986). Strategies should be developed to carry out inventories of remnant wild plant populations of common native plants, e.g. within "old grasslands" in Central Europe.

Within the framework of the PhD thesis it was only possible to test the effects of cultivation and hybridization on a selection of life-history traits of two native species. It can be assumed that further life-history traits and further species are affected, possibly also resulting in undesired effects on wild plants and other ecosystem compartments on higher trophic levels. Cultivation and hybridization may alter phyto-chemical contents in wilds. Toxic phytochemicals might be reduced as a function of trade-offs during selection of cultivars towards e.g. higher nutrient content or yield (Evans 1996). For instance, less glycoside contents (catalpol and aucubin) have been found in cultivars of *P. lanceolata* compared to their wilds (Al-Mamun et al. 2008). Reduced toxic phytochemicals and increased nutrient contents may enhance the palatability of cultivars to herbivores (Benrey et al. 1998). Enhanced palatability to herbivores might be transferred to wilds by hybridization, potentially disturbing local adaptation of affected species, because a low palatability can be a mechanism of local adaptation in wilds (e.g. Keller et al. 1999; Cremieux et al. 2008). Considerable differences in the colonization of herbivore insect communities between cultivars of grasses, frequently used for re-vegetation, and their wilds had already been observed (Wesserling & Tscharntke 1993) possibly resulting in removing or reducing the survival of affected insect taxa (Neugebauer & Tscharntke 1997). Further studies have to concentrate on changes in phytochemicals in native plants by cultivation and hybridization and if such changes have undesirable effects on species of higher trophic levels (e.g. invertebrates).

Genetic diversity as well as phenotypic variation of cultivars is assumed to be lower in comparison to their wilds (Williams 2001; van Treuren et al. 2005). Presumably, only a small fraction of the genetic spectrum of their wilds has been used in cultivation efforts (Ladizinsky 1985) and therefore the genetic basis of modern cultivars may be limited compared to their wild progenitors (Bennett 1970). If this assumption holds true, adaptability to changing environmental conditions might be reduced (Bennett 1970) because phenotypic variation due to genotypic variation or phenotypic plasticity seems to be important for adaptation abilities (Booy et al. 2000; Rice & Emery

2003; Pertoldi et al. 2007; Jump et al. 2009). Furthermore, founder effects or inbreeding depression may be effective, as already observed in the (re-)establishment of wild plant populations where material came from limited sources of wild populations (e.g. founder effect: *Zostera marina*, Williams 2001; inbreeding depression: *Sarracenia flava*, Sheridan & Karowe 2000). New insights into adaptation abilities of cultivars versus wild relative are not only a topic for restorationists who are interested in sustainable population development. This should be a major topic for agricultural plant breeding as well. In light of changing environments, genetic diversity and adaptation abilities of wild plant species as a source for developing new cultivars for grassland melioration will become more important (Maxted et al. 2007).

More research on the effects of collection and propagation methods in regionalized seed production on the germination behavior of wilds is needed to evaluate the generality of my findings because I tested only two species from one regionalized seed producer. Further studies should evaluate the number of generations that can be propagated without occurrence of strong selection effects. Whether frequent replenishment of propagation stocks with new seed collections from wild populations is an appropriate method to minimize unintentional selection should be studied. More research is needed to evaluate whether further life-history strategies, such as flower phenology, plant performance, or genetic diversity (Aavik et al. 2012) are negatively affected by regionalized seed production.

References

Aavik, T., P.J. Edwards, R. Holderegger, R. Graf, and R. Billeter. 2012. Genetic consequences of using seed mixtures in restoration: A case study of a wetland plant *Lychnis flos-cuculi*. *Biological Conservation* 145:195–204.

Adler, L.S., K. Wikler, F.S. Wyndham, C.R. Linder, and J. Schmitt. 1993. Potential for persistence of genes escaped from canola - Germination cues in crop, wild, and crop-wild hybrid *Brassica rapa*. *Functional Ecology* 7:736–745.

Akeroyd, J.R. 1994. Some problems with introduced plants in the wild. In A. R. Perry, R. G. Ellis (eds.): The Common ground of wild and cultivated plants: introductions, invasions, conservation, vol. 22 (Conference Report / Botanical Society of the British Isles)31–40.

Al-Mamun, M., D. Abe, H. Kofujita, Y. Tamura, and H. Sano. 2008. Comparison of the bioactive components of the ecotypes and cultivars of plantain (*Plantago lanceolata* L.) herbs. *Animal Science Journal* 79:83–88.

Annicchiarico, P., and E. Piano. 1997. Effect of selection under cultivation on morphological traits and yield of Ladino white clover landraces. *Genetic Resources and Crop Evolution* 44:405–410.

Baskin, J.M., and C.C. Baskin. 2004. A classification system for seed dormancy. *Seed Science Research* 14:1–16.

Bennett, E. 1970. Adaptation in wild and cultivated plant populations. In: Frankel, O.H. , and E. Bennett (eds.): Genetic Resources in Plants - Their Exploration and Conservation. Blackwell Scientific Publications. Oxford and Edinburgh

Benrey, B., A. Callejas, L. Rios, K. Oyama, and R. Denno. 1998. The Effects of domestication of *Brassica* and *Phaseolus* on the interaction between phytophagous insects and parasitoids. *Biological Control* 11:130–140.

Bischoff, A., L. Cremieux, M. Smilauerova, C.S. Lawson, S.R. Mortimer, J. Dolezal, V. Lanta, A.R. Edwards, A.J. Brook, M. Macel, J. Leps, T. Steinger, and H. Muller-Scharer. 2006a. Detecting local adaptation in widespread grassland species - the importance of scale and local plant community. *Journal of Ecology* 94:1130–1142.

Bischoff, A., B. Vonlanthen, T. Steinger, and H. Muller-Scharer. 2006b. Seed provenance matters - Effects on germination of four plant species used for ecological restoration. *Basic and Applied Ecology* 7:347–359.

Bischoff, A., T. Steinger, and H. Müller-Schärer. 2008. The Importance of plant provenance and genotypic diversity of seed material used for ecological restoration. *Restoration Ecology*.

Blom, C. 1978. Germination, seedling emergence and establishment of some *Plantago* species under laboratory and field conditions. *Acta Botanica Neerlandica* 27:257–271.

BMELV. 2011. Erhaltungsmischungsverordnung (ErMiV) vom 6. Dezember 2011 (BGBl. I S. 2641).

Bolker, B.M., M.E. Brooks, C.J. Clark, S.W. Geange, J.R. Poulsen, M.Henry H. Stevens, and J.-S.S. White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution* 24:127–135.

Boller, B., M.K. I. Peter-Schmid, E. Tresch, P. Tanner, and F.X. Schubiger. 2009. Ecotypes of Italian ryegrass from Swiss permanent grassland outperform current recommended cultivars. *Euphytica* 170:53–65.

Bonnemaison, F., and D.A. Jones. 1986. Variation in Alien *Lotus corniculatus* L.1. Morphological Differences between Alien and Native British Plants. *Heredity* 56:129–138.

Booy, G., R.J.J. Hendriks, M.J.M. Smulders, J.M. van Groenendael, and B. Vosman. 2000. Genetic diversity and the survival of populations. *Plant Biology* 2:379–395.

Broadhurst, L.M., A. Lowe, D.J. Coates, S.A. Cunningham, M. McDonald, P.A. Vesk, and C. Yates. 2008. Seed supply for broadscale restoration: maximizing evolutionary potential. *Evolutionary Applications* 1:587–597.

Brown, R.F., and D.G. Mayer. 1988. Representing cumulative germination. 2. The use of the Weibull function and other empirically derived curves. *Annals of Botany* 61:127–138.

Bundesregierung. 2005. Bereitstellung von gebietsheimischem Wildkräutersaatgut im Konflikt zwischen Bestimmungen des Saatgutverkehrsgesetzes und des Bundesnaturschutzgesetzes (Drucksache 15/5087).

Byrne, M., L. Stone, and M.A. Millar. 2011. Assessing genetic risk in revegetation. *Journal of Applied Ecology* 48:1365–1373.

Casper, B.B., and R.B. Jackson. 1997. Pant competition underground. *Annual Review of Ecology and Systematics* 28:545–570.

Cavers, P.B., I.J. Bassett, and C.W. Crompton. 1980. The biology of Canadian weeds.47. *Plantago lanceolata* L. *Canadian Journal of Plant Science* 60:1269–1282.

Chrobock, T., A. Kempel, M. Fischer, and M. van Kleunen. 2011. Introduction bias: Cultivated alien plant species germinate faster and more abundantly than native species in Switzerland. *Basic and Applied Ecology* 12:244–250.

Connolly, J., and P. Wayne. 1996. Asymmetric competition between plant species. *Oecologia* 108:311–320.

Cremieux, L., A. Bischoff, H. Muller-Scharer, and T. Steinger. 2010. Gene flow from foreign provenances into local plant populations: Fitness consequences and implications for biodiversity restoration. *American Journal of Botany* 97:94–100.

Cremieux, L., A. Bischoff, M. Smilauerova, C.S. Lawson, S.R. Mortimer, J. Dolezal, V. Lanta, A.R. Edwards, A.J. Brook, T. Tscheulin, M. Macel, J. Leps, H. Muller-Scharer, and T. Steinger. 2008. Potential contribution of natural enemies to patterns of local adaptation in plants. *New Phytologist* 180:524–533.

Dawson, W., M. Fischer, M. van Kleunen, and K. Suding. 2012. Common and rare plant species respond differently to fertilisation and competition, whether they are alien or native. *Ecology Letters* 15:873–880.

Ellstrand, N. C. 2003. Dangerous Liaisons? When cultivated plants mate with their wild relatives. The John Hopkins University Press. Baltimore

Ellstrand, N.C., H.C. Prentice, and J.F. Hancock. 1999. Gene flow and introgression from domesticated plants into their wild relatives. *Annual Review of Ecology and Systematics* 30:539–563.

Ensslin, A., T.M. Sandner, and D. Matthies. 2011. Consequences of ex situ cultivation of plants: Genetic diversity, fitness and adaptation of the monocarpic *Cynoglossum officinale* L. in botanic gardens. *Biological Conservation* 144:272–278.

Etterson, J.R., S.R. Keller, and L.F. Galloway. 2007. Epistatic and cytonuclear interactions govern outbreeding depression in the autotetraploid *Campanulastrum americanum. Evolution* 61:2671–2683.

EEC (European Economic Community). 1966. Council Directive of 14 June 1966 on the marketing of fodder plant seed. *Official Journal of the European Community* 109:1757–1764.

EEC (European Economic Community). 1994. Council Directive of 27 July 1994 on Community plant variety rights. (EC) No. 2100/941–38.

Evans, L.T. 1996. Crop evolution, adaptation, and yield. Cambridge University Press. New York

Evans, M.E.K., and J.J. Dennehy. 2005. Germ banking: Bet-hedging and variable release from egg and seed dormancy. *Quarterly Review of Biology* 80:431–451.

Frary, A., and S. Doganlar. 2003. Comparative genetics of crop plant domestication and evolution. *Turkish Journal of Agriculture and Forestry* 27:59–69.

Freckleton, R.P., and A.R. Watkinson. 2001. Asymmetric competition between plant species. *Functional Ecology* 15:615–623.

Gelman, A.; Hill, J. 2007. Data analysis using regression and multilevel/hierarchical models. Cambridge University Press.

Gelman, A., S. Yu-Sung, M. Yajima, J. Hill, M.G. Pittau, J. Kerman, and T. Zheng. 2012. arm: Data analysis using regression and multilevel/hierarchical models. R package version 1.5-05. Available online at http://CRAN.R-project.org/package=arm.

Goldberg, D.E. 1987. Neighborhood competition in an old-field plant community. *Ecology* 68:1211–1223.

Goldberg, D.E., and L. Fleetwood. 1987. Competitive effect and response in 4 annual Plants. *Journal of Ecology* 75:1131–1143.

Grime, J.P. 1977. Evidence for existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* 111:1169–1194.

Gustafson, D.J., D.J. Gibson, and D.L. Nickrent. 2004. Competitive relationships of *Andropogon gerardii* (Big Bluestem) from remnant and restored native populations and select cultivated varieties. *Functional Ecology* 18:451–457.

Harper, J.L., and I. McNaughton. 1960. The inheritance of dormancy in inter- and intraspecific hybrids of *Papaver. Heredity* 15:315–320.

Hauser, T.P. 2002. Frost sensitivity of hybrids between wild and cultivated carrots. *Conservation Genetics* 3:75–78.

Heberich, E., and T. Hothorn. 2012. Dunnett-type inference in the frailty Cox model with covariates. *Statistics in Medicine* 31:45–55.

Hierro, J., E. Özkan, D. Villarreal, and M. Chiuffo. 2012. Non-native conditions favor non-native populations of invasive plant: demographic consequences of seed size variation? *Oikos* 122:583-590.

Hiller, A., and E. Hacker. 2001. Ingenieurbiologie und die Vermeidung von Florenverfälschung. *Mitteilungen der Gesellschaft für Ingenieurbiologie e.V.* 18:16–42.

Hilu, K.W., and J.M.J. Dewet. 1980. Effect of artificial selection on grain dormancy in *Eleusine* (Gramineae). *Systematic Botany* 5:54–60.

Hothorn, T., F. Bretz, and P. Westfall. 2008. Simultaneous inference in general parametric models. *Biometrical Journal* 50:346–363.

Hufford, K.M., and S.J. Mazer. 2003. Plant ecotypes: genetic differentiation in the age of ecological restoration. *Trends in Ecology & Evolution* 18:147–155.

Humphrey, L.D., and E.W. Schupp. 2002. Seedling survival from locally and commercially obtained seeds on two semiarid sites. *Restoration Ecology* 10:88–95.

Huxel, G.R. 1999. Rapid displacement of native species by invasive species: effects of hybridization. *Biological Conservation* 89:143–152.

ISTA. 2006. Chapter 5: The germination test. In International Seed Testing Association (Ed.): International rules for seed testing, Edition 2006/1.

Johnson, R.C., V.J. Erickson, N.L. Mandel, J.B. St Clair, and K.W. Vance-Borland. 2010. Mapping genetic variation and seed zones for *Bromus carinatus* in the Blue Mountains of eastern Oregon, USA. *Botany* 88:725–736.

Jones, D.A., and R. Turkington. 1986. Biological flora of the British-Isles - *Lotus corniculatus* L. *Journal of Ecology* 74:1185–1212.

Jump, A.S., R. Marchant, and J. Penuelas. 2009. Environmental change and the option value of genetic diversity. *Trends in Plant Science* 14:51–58.

Keddy, P.A., and B. Shipley. 1989. Competitive hierarchies in herbaceous plant communities. *Oikos* 54:234–241.

Keller, M., J. Kollmann, and P.J. Edwards. 1999. Palatability of weeds from different European origins to the slugs *Deroceras reticulatum* Muller and *Arion lusitanicus* Mabille. *Acta Oecologica-International Journal of Ecology* 20:109–118.

Keller, M., J. Kollmann, and P.J. Edwards. 2000. Genetic introgression from distant provenances reduces fitness in local weed populations. *Journal of Applied Ecology* 37:647–659.

Kitajima, K., A.M. Fox, T. Sato, and D. Nagamatsu. 2006. Cultivar selection prior to introduction may increase invasiveness: evidence from *Ardisia crenata*. *Biological Invasions* 8:1471–1482.

Kitchen, S.G., and S.B. Monsen. 1994. Germination rate and emergence success in Bluebunch Wheatgrass. *Journal of Range Management* 47:145–150.

Klinger, T., and N.C. Ellstrand. 1994. Engineered genes in wild populations - Fitness of weed-crop hybrids of *Raphanus sativus*. *Ecological Applications* 4:117–120.

Klopf, R.P., and S.G. Baer. 2011. Root dynamics of cultivar and non-cultivar population sources of two dominant grasses during initial establishment of Tallgrass Prairie. *Restoration Ecology* 19:112–117.

Krautzer, B., W. Graiss, G. Peratoner, C. Partl, S. Venerus, and B. Klug. 2011. The influence of recultivation technique and seed mixture on erosion stability after restoration in mountain environment. *Natural Hazards* 56:547–557.

Ladizinsky, G. 1985. Founder effect in crop-plant evolution. *Economic Botany* 39:191–199.

Laikre, L., M.K. Schwartz, R.S. Waples, N. Ryman, and The GeM Working Group. 2010. Compromising genetic diversity in the wild: unmonitored large-scale release of plants and animals. *Trends in Ecology & Evolution* 25:520–529.

Lambert, A.M., S.G. Baer, and D.J. Gibson. 2011. Intraspecific variation in ecophysiology of three dominant prairie grasses used in restoration: cultivar versus non-cultivar population sources. *Restoration Ecology* 19:43–52.

Langevin, S.A., K. Clay, and J.B. Grace. 1990. The incidence and effects of hybridization between cultivated Rice and its related weed Red Rice (*Oryza sativa* L). *Evolution* 44:1000–1008.

Levin, D.A. 2001. The recurrent origin of plant races and species. *Systematic Botany* 26:197–204.

Li, Q. 1989. Seed production in Birdsfoot trefoil (*Lotus corniculatus* L.). PhD-Thesis. Massey University. New Zealand.

Liu, G.X., and J.G. Han. 2008. Seedling establishment of wild and cultivated *Leymus chinensis* (Trin.) Tzvel. under different seeding depths. *Journal of Arid Environments* 72:279–284.

Lloyd, D.G. 1988. A general principle for the allocation of limited resources. *Evolutionary Ecology* 2:175–187.

Lumaret, R. 1990. Invasion of natural pastures by a cultivated grass (*Dactylis glomerata* L.) in Galicia, Spain: process and consequence on plant-cattle interactions. In: Di Castri, F. , A.J Hansen, and M. Debusche (eds.): Biological Invasions in Europe and the Mediterranean Basin. Kluwer Academic Publisher. Dordrecht

Lynch, M. 1991. The genetic interpretation of inbreeding depression and outbreeding depression. *Evolution* 45:622–629.

Maass, B.L. 2006. Changes in seed morphology, dormancy and germination from wild to cultivated hyacinth bean germplasm (*Lablab purpureus* : Papilionoideae). *Genetic Resources and Crop Evolution* 53:1127–1135.

Maass, B.L., and M.F. Usongo. 2007. Changes in seed characteristics during the domestication of the lablab bean (*Lablab purpureus* (L.) Sweet : Papilionoideae). *Aus-*

tralian Journal of Agricultural Research 58:9–19.

Magnussen, L.S., and T.P. Hauser. 2007. Hybrids between cultivated and wild carrots in natural populations in Denmark. *Heredity* 99:185–192.

Malaval, S., B. Lauga, C. Regnault-Roger, and G. Largier. 2010. Combined definition of seed transfer guidelines for ecological restoration in the French Pyrenees. *Applied Vegetation Science* 13:113–124.

Maxted, N., M. Scholten, R. Codd, and B. Ford-Lloyd. 2007. Creation and use of a national inventory of crop wild relatives. *Biological Conservation* 140:142–159.

McGrath, S., T.R. Hodkinson, T.M. Charles, D.G. Zen, and S. Barth. 2010. Variation in inflorescence characters and inflorescence development in ecotypes and cultivars of *Lolium perenne* L. *Grass and Forage Science* 65:398–409.

McKay, J.K., C.E. Christian, S. Harrison, and K.J. Rice. 2005. "How local is local?" - A review of practical and conceptual issues in the genetics of restoration. *Restoration Ecology* 13:432–440.

Mercer, K.L., D.A. Andow, D.L. Wyse, and R.G. Shaw. 2007. Stress and domestication traits increase the relative fitness of crop-wild hybrids in sunflower. *Ecology Letters* 10:383–393.

Mercer, K.L., R.G. Shaw, and D.L. Wyse. 2006. Increased germination of diverse crop-wild hybrid sunflower seeds. *Ecological Applications* 16:845–854.

Meyer, S.E., and S.G. Kitchen. 1994. Life-history variation in Blue Flax (*Linum perenne*, Linaceae) - Seed-germination phenology. *American Journal of Botany* 81:528–535.

Miller, S.A., A. Bartow, M. Gisler, K. Ward, A.S. Young, and T.N. Kaye. 2011. Can an ecoregion serve as a seed transfer zone? Evidence from a common garden study with five native species. *Restoration Ecology* 19:268–276.

Molder, F. 2000. Gefährdung und Möglichkeiten zur Erhaltung von Biodiversität bei landschaftsbaulichen und Biotopentwicklungsmaßnahmen. *Rasen-Turf-Gazon* 31:41–46.

Montalvo, A.M., and N.C. Ellstrand. 2000. Transplantation of the subshrub *Lotus scoparius*: Testing the home-site advantage hypothesis. *Conservation Biology* 14:1034–1045.

Neugebauer, A., and T. Tscharntke. 1997. Insektengesellschaften auf Gräsern unterschiedlicher Sorten. *Mitt. Dtsch. Ges. Allg. Angew. Ent.* 11:755–758.

Obeso, J.R. 2002. The costs of reproduction in plants. *New Phytologist* 155:321–348.

Oliveira, G., A. Nunes, and A.C.O. Clemente. 2012. Testing germination of species for hydroseeding degraded Mediterranean Areas. *Restoration Ecology* 20:623-630.

Ollerton, J., and A. Lack. 1998. Relationships between flowering phenology, plant size and reproductive success in *Lotus corniculatus* (Fabaceae). *Plant Ecology* 139:35–47.

Pertoldi, C., R. Bijlsma, and V. Loeschcke. 2007. Conservation genetics in a globally changing environment: present problems, paradoxes and future challenges. *Biodiversity and Conservation* 16:4147–4163.

Peter-Schmid, M.K.I., R. Kolliker, and B. Boller. 2008. Value of permanent grassland habitats as reservoirs of *Festuca pratensis* Huds. and *Lolium multiflorum* Lam. populations for breeding and conservation. *Euphytica* 164:239–253.

Pons, T.L. 1992. Seed germination of *Plantago major* ssp. *major* and *Plantago lanceolata*. In: Kuiper, P.J.C ,and M. Bos (eds.): Plantago: A Multidisciplinary Study. Springer. New York

Posselt, U.K. 2000. Genetische Diversität bei Wildformen und Zuchtsorten von *Lolium perenne* L. *Schriftenreihe für Vegetationskunde* 32:79–85.

Prasse, R., D. Kunzmann, and R. Schröder. 2010. Entwicklung und praktische Umsetzung naturschutzfachlicher Mindestanforderungen an einen Herkunftsnachweis für gebietseigenes Wildpflanzensaatgut krautiger Pflanzen. Unveröffentlichter Abschlussbericht DBU-Projekt (AZ: 23931). With assistance of W. Durka. LU Hannover, Institut für Umweltplanung.

Primack, R.B., and J. Antonovics. 1982. Experimental ecological genetics in *Plantago*. VII. Reproductive effort in populations of *P. lanceolata* L. *Evolution* 36:742–752.

R Development Core Team. 2012. R: a language and environment for statistical computing. Edited by R Foundation for Statistical Computing. Vienna, Austria. Available at: http://www.r-project.org.

Rafferty, N.E., and A.R. Ives. 2012. Pollinator effectiveness varies with experimental shifts in flowering time. *Ecology* 93:803–814.

Rees, M. 1994. Delayed germination of seeds - a look at the effects of adult longevity, the timing of reproduction, and population age/stage structure. *American Naturalist* 144:43–64.

Rees, M. 1996. Evolutionary ecology of seed dormancy and seed size. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* 351:1299–1308.

Rice, K.J., and N.C. Emery. 2003. Managing microevolution: restoration in the face of global change. *Frontiers in Ecology and the Environment* 1:469–478.

Rogers, D., and A. Montalvo. 2004. Genetically appropriate choices for plant materials to maintain biological diversity. California, University of. Lakewood, CO (Report to the USDA Forest Service, Rocky Mountain Region).

Rojas-Arechiga, M., A. Casas, and C. Vazquez-Yanes. 2001. Seed germination of wild and cultivated *Stenocereus stellatus* (Cactaceae) from the Tehuacan-Cuicatlan Valley, Central Mexico. *Journal of Arid Environments* 49:279–287.

Sagar, G.R., and J.L. Harper. 1964. *Plantago major* L, *P media* L and *P lanceolata* L. *Journal of Ecology* 52:189–221.

Saltonstall, K. 2002. Cryptic invasion by a non-native genotype of the common reed, *Phragmites australis*, into North America. *Proceedings of the National Academy of Sciences of the United States of America* 99:2445–2449.

Satterthwaite, W.H. 2010. Competition for space can drive the evolution of dormancy in a temporally invariant environment. *Plant Ecology* 208:167–185.

Schlaepfer, D.R., M. Glättli, M. Fischer, and M. van Kleunen. 2010. A multi-species experiment in their native range indicates pre-adaptation of invasive alien plant species. *New Phytologist* 185:1087–1099.

Schoen, D.J., and A.H.D. Brown. 2001. The conservation of wild plant species in seed banks. *Bioscience* 51:960–966.

Schröder, R., M. Graf, J. Jochum, G. Rode, J. Schemmel, and I. Thimm in press. Testing the effects of a regionalized seed production on the germination behavior of wild plant species. *Ecological Restoration.*

Schröder, R., and R. Prasse. 2013. Cultivation and hybridization alter the germination behavior of native plants used in revegetation and restoration. *Restoration Ecology* DOI: 10.1111/rec.12018.

Sheley, R. L., and M. L. Half. 2006. Enhancing native forb establishment and persistence using a rich seed mixture. *Restoration Ecology* 14:627–635.

Sheridan, P.M., and D.N. Karowe. 2000. Inbreeding, outbreeding, and heterosis in the yellow pitcher plant, *Sarracenia flava* (Sarraceniaceae), in Virginia. *American Journal of Botany* 87:1628–1633.

Slatkin, M. 1974. Hedging ones evolutionary bets. *Nature* 250:704–705.

Smith, S.L., A.A. Sher, and T.A. Grant. 2007. Genetic diversity in restoration materials and the impacts of seed collection in Colorado's restoration plant production industry. *Restoration Ecology* 15:369–374.

Snow, A.A., P. Moran-Palma, L.H. Rieseberg, A. Wszelaki, and G.J. Seiler. 1998. Fecundity, phenology, and seed dormancy of F-1 wild-crop hybrids in sunflower (*Helianthus annuus*, Asteraceae). *American Journal of Botany* 85:794–801.

Society for Ecological Restoration International Science & Policy Working Group. 2004. The SER International Primer on Ecological Restoration. Edited by Society for Ecological Restoration International. www.ser.org & Tucson.

Stevens, J.M., and J.S. Fehmi. 2011. Early establishment of a native grass reduces the competitive effect of a non-native grass. *Restoration Ecology* 19:399–406.

Stiny, J. 1908. Die Berasung und Bebuschung des Ödlandes im Gebirge als wichtige Ergänzung getroffener technischer Maßnahmen und für sich betrachtet. Reprint. Kessinger Publishings. USA

Therneau, T. 2010. Survival: Survival analysis, including penalised likelihood. original Splus->R port by Thomas Lumley. Available at: http://cran.r-project.org/package=survival.

Thiele, J., R.B. Jorgensen, and T.P. Hauser. 2009. Flowering does not decrease vegetative competitiveness of *Lolium perenne. Basic and Applied Ecology* 10:340–348.

van Assche, J.A., K.L.A. Debucquoy, and W.A.F. Rommens. 2003. Seasonal cycles in the germination capacity of buried seeds of some Leguminosae (Fabaceae). *New Phytologist* 158:315–323.

van Gaal, T.M., S.M. Galatowitsch, and M.S. Strefeler. 1998. Ecological consequences of hybridization between a wild species (*Echinacea purpurea*) and related cultivar (E-purpurea 'White Swan'). *Scientia Horticulturae* 76:73–88.

van Groenendael, J.M. 1985a. Differences in life histories between two ecotypes of *Plantago lanceolata* L. In: J. White (ed.): Studies on plant demography: a "Festschrift" for John L. Harper. Academic Press. London

van Groenendael, J.M. 1985b. Selection for different life histories in *Plantago lanceolata* L. Ph.D. Thesis. University of Nijmwegen.

van Treuren, R. 2008. AFLP fingerprinting of Kentucky bluegrass (*Poa pratensis* L.) from undisturbed Dutch grasslands: implications for conservation. *Plant Genetic Resources Newsletter* 153:1–8.

van Treuren, R., N. Bas, P.J. Goossens, J. Jansen, and L.J.M. van Soest. 2005. Genetic diversity in perennial ryegrass and white clover among old Dutch grasslands as compared to cultivars and nature reserves. *Molecular Ecology* 14:39–52.

Vanden Broeck, A., V. Storme, J.E. Cottrell, W. Boerjan, E. van Bockstaele, P. Quataert, and J. van Slycken. 2004. Gene flow between cultivated poplars and native black poplar (*Populus nigra* L.): a case study along the river Meuse on the Dutch-Belgian border. *Forest Ecology and Management* 197:307–310.

Vander Mijnsbrugge, K., A. Bischoff, and B. Smith. 2010. A question of origin: Where and how to collect seed for ecological restoration. *Basic and Applied Ecology* 11:300–311.

Venable, D.L., and J.S. Brown. 1988. The selective interactions of dispersal, dormancy, and seed size as adaptations for reducing risk in variable environments. *American Naturalist* 131:360–384.

Walker, K.J., K.H. Hodder, J.R. Bullock, and R.F. Pywell. 2004a. A review of the potential effects of seed sowing for habitat recreation on the conservation of intraspecific biodiversity. Centre for Ecology and Hydrology. Monks Wood.

Walker, K.J., P.A. Stevens, D.P. Stevens, J.O. Mountford, S.J. Manchester, and R.F. Pywell. 2004b. The restoration and re-creation of species-rich lowland grassland on land formerly managed for intensive agriculture in the UK. *Biological Conservation* 119:1–18.

Warren, J.M., A.F. Raybould, T. Ball, A.J. Gray, and M.D. Hayward. 1998. Genetic structure in the perennial grasses *Lolium perenne* and *Agrostis curtisii*. *Heredity* 81:556–562.

Warren, J., F. Wilson, and A. Diaz. 2002. Competitive relationships in a fertile grassland community - does size matter? *Oecologia* 132:125–130.

Waser, N.M., and M. Price. 1994. Crossing-distance effects in *Delphinium nelsonii* - outbreeding and inbreeding depression in progeny fitness. *Evolution* 48:842–852.

Waters, C.M. (2001) Guiding the delimitation of local provenance for Australian native grasses. In: Second National Conference of the Native Grasses Association. Stipa Native Grasses Association Inc., NSW. Available at: http://www.regional.org.au/au/stipa/papers/stipa2001-09.htm (Accessed: July 2010)

Weiner, J. 1990. Asymmetric competition in plant-populations. *Trends in Ecology & Evolution* 5:360–364.

Wesserling, J., and T. Tscharntke. 1993. Insektengesellschaften an Knaulgras (*Dactylis glomerata*): Der Einfluß von Saatgut-Herkunft und Habitattyp. *Verhandlungen der Gesellschaft für Ökologie* 22:351–354.

Williams, S.L. 2001. Reduced genetic diversity in eelgrass transplantations affects both population growth and individual fitness. *Ecological Applications* 11:1472–1488.

Wilson, S.B., and L.K. Mecca. 2003. Seed production and germination of eight cultivars and the wild type of *Ruellia tweediana*: A potentially invasive ornamental. *Journal of Environmental Horticulture* 21:137–143.

Zuur, A.F., E.N. Ieno, N.J. Walker, A.A. Saveliev, and G.M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer. New York

Acknowledgments

Eidesstattliche Erklärung

Eidesstattliche Erklärung

Hiermit versichere ich, die vorliegende Dissertation selbständig angefertigt und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt zu haben. Die Arbeit wurde noch nicht als Dissertation oder als Prüfungsarbeit vorgelegt. Teile der Dissertation wurden mit Zustimmung des Betreuers Prof. Dr. Rüdiger Prasse in folgenden Beiträgen vorab veröffentlicht:

Schröder, R. and R. Prasse (2013): Cultivation and hybridization alter the germination behavior of native plants used in re-vegetation and restoration. *Restoration Ecology* 21: 793-800
doi: 10.1111/rec.12018

Schröder, R. and R. Prasse (2013): From nursery into nature: A study on performance of cultivated varieties of native plants used in re-vegetation, their wild relatives and evolving wild x cultivar hybrids. *Ecological Engineering* 60: 428-437
doi: 10.1016/j.ecoleng.2013.09.036

Schröder, R. and R. Prasse (2013): Do cultivated varieties of native plants have the ability to outperform their wild relatives? *PLoS ONE* 8: e71066
doi: 10.1371/journal.pone.0071066

Schröder, R., Graf, M., Jochum, J., Rode, G., Schemmel, J. and I. Thimm (2013): Testing the effects of a regionalized seed production on the germination behavior of wild plant species. *Ecological Restoration* 31: 295-301
doi: 10.3368/er.31.3.295

Hannover, den 10.12.2013
Roland Schröder

Curriculum vitae

Curriculum vitae

Roland Schröder

Geburtsdatum: 03.02.1978
Geburtsort: Emsdetten
Staatsangehörigkeit: deutsch

Schulausbildung

1984-1988   Ludgerus Grundschule, Wettringen

1988-1997   Arnold Janssen-Gymnasium, Neuenkirchen/St. Arnold

Hochschulausbildung

1998-2005   Studium der Landschaftsökologie,
                 Westfälische Wilhelms-Universität Münster
                 Abschluss: Diplom-Landschaftsökologe

Arbeitsverhältnisse

2005-2006   Wissenschaftliche Hilfskraft, Institut für Evolution und Biodiversität,
                 Abteilung Limnologie, WWU Münster

2005-2007   Wissenschaftliche Hilfskraft, Institut für Didaktik der Geographie,
                 WWU Münster

2007   Angestellter, EFTAS Fernerkundung Technologietransfer GmbH,
                 Münster

seit Nov. 2007 Wissenschaftlicher Mitarbeiter, Institut für Umweltplanung,
                 Leibniz Universität Hannover