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Reintroduction of rare arable plants on agricultural fields

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SUMMARY

Since the emergence of agriculture in the Neolithic period, arable plants have adapted to the habitat conditions in arable fields and coexisted with crops. In Central Europe, the arable flora consists mainly of archaeophytes, which have been part of the cultural landscape for several thousand years. However, during the past decades, there have been major changes in agricultural land use that have markedly affected the arable flora. An immense decline in the diversity of arable vegetation was mainly caused by the intensification of agricultural production, but also by the abandonment of marginal land and other land-use changes. This decline has far-reaching consequences for associated organisms and functions in the agroecosystem. Beside highly competitive weed species, there are numerous arable plant species that cause insignificant yield losses. Land-sharing concepts may be the most suited strategy for the conservation of these species, since they offer the opportunity to reconcile the production of agricultural goods with objectives of nature conservation within the same field. So far, conservation efforts have been insufficient to counteract the impoverishment of the segetal flora. A major problem is the lack of spontaneous colonisation of suitable habitats, as both seed banks of most target species and effective dispersal strategies are missing. Therefore, the reintroduction of rare arable plant species is a necessary tool to promote agrobiodiversity. So far, however, restoration ecology has scarcely taken agricultural fields into account and there is still a great lack of knowledge about the factors which determine the establishment of threatened species.

The aim of this thesis is therefore to identify suitable seed provenances and management conditions that allow successful reintroduction of rare arable plants. For this purpose, the phenotypic differentiation of arable plant populations within Bavaria and their local adaptation to northern and southern regions of seed transfer zones was investigated. Furthermore, the effect of different crop types, crop sowing densities and types of soil tillage on establishment and the feasibility of reintroduction on practical farms were tested.

Topic of **Publication 1** is the significance of seed provenance for the establishment of five rare arable species (*Arnoseris minima*[1], *Consolida regalis, Cyanus segetum, Legousia speculum-veneris, Teesdalia nudicaulis*). For each species, seeds from 4–12 source populations distributed across four Bavarian seed zones were collected and cultivated for two generations in a greenhouse. The phenotype of F2 plants was used to investigate population differentiation with and without drought stress. Additionally, local adaptation to northern or southern regions within seed zones was tested with reciprocal transplant experiments. The populations hardly

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[1] Nomenclature follows the taxon list of vascular plants from Bavaria, Germany by Diewald and Ahlmer (2019).

differed in biomass production and phenology. However, drought stress led to species- and provenance-specific effects. The establishment and fitness of the species in the field were significantly influenced by the study year and the respective transplant site, but only to a minor degree by the seed provenance. The results indicate that seeds of these species used for reintroduction measures can be collected and mixed within the investigated seed zones. This seed-sourcing strategy may sustain a high degree of genetic diversity and provide future adaptation potential while, at the same time, reducing the risk of maladaptation.

Publication 2 investigates the impact of different management factors (crop sowing density, crop type, type of soil tillage) on the establishment of three winter annual species of limestone sites (*L. speculum-veneris, C. regalis, Lithospermum arvense*). The study design consisted of a replicated three-year field trial in the Munich plain. Sowing arable plants without crops had a particularly favourable effect and led to significantly higher establishment, not only in the first but also in the following study years. Depending on the crop type cultivated in the second year, the arable plants were able to reproduce either not at all (clover-grass), moderately (pea, triticale) or very well (spelt). However, in the following study year, plots were cultivated with rye and all species recovered again. The type of soil tillage (plough or cultivator) had different and mostly minor effects depending on the crop rotation and the target species. The results emphasize the importance of competition and disturbance (less the type but the timing) for the establishment of rare arable plants. Considering this, reintroduction can successfully be integrated in various crop rotations.

In **Publication 3**, the same three species were sown on four extensively managed arable fields located in the Munich plain with the aim to study their population development under practical farming conditions. Plant density, seed production, seed bank and seed dispersal were used as indicators for the success of reintroduction. Three years after sowing, the average establishment was highest in *L. speculum-veneris*, followed by *C. regalis*. In contrast, *L. arvense* established only poorly without building up a seed bank. The above-ground populations fluctuated during the study period depending on the agricultural management and differed greatly between the arable field sites. Seeds were dispersed up to 15 m out of the sowing plots, along the machining direction. The fluctuation of populations in the field and the importance of the seed bank must be considered in monitoring concepts.

The overall **discussion** summarises the findings of the three publications and addresses various abiotic and biotic factors that may influence the establishment success. Their significance and underlying mechanisms are discussed with reference to the literature. Practical recommendations for seed sourcing and sowing, as well as for management and monitoring, are derived. If the suggested workflow for the reintroduction of rare arable plants is implemented in cooperation between nature conservation and agriculture, as well as science and practice, this can be a useful tool for the restoration of species-rich arable fields and the promotion of rare arable plants.

ZUSAMMENFASSUNG

Seit Beginn des Ackerbaus in der Jungsteinzeit begleiten Ackerwildpflanzen den Anbau von landwirtschaftlichen Kulturen. In Mitteleuropa besteht die Segetalflora vor allem aus Archäophyten, die seit mehreren tausend Jahren Bestandteil der Kulturlandschaft sind. Während der letzten Jahrzehnte fanden jedoch starke Veränderungen in der Landwirtschaft statt, die sich deutlich auf die Segetalflora ausgewirkt haben. Vor allem die Intensivierung der landwirtschaftlichen Produktion, aber auch die Nutzungsänderung von Grenzertragsstandorten sowie weitere Landnutzungsänderungen führten zu einem immensen Rückgang der Agrophytodiversität. Dieser Rückgang hat weitreichende Konsequenzen für assoziierte Organismen und Funktionen im Agrarökosystem. Neben konkurrenzstarken Problemunkräutern und -gräsern gibt es zahlreiche Ackerwildpflanzen, die kaum Ertragseinbußen hervorrufen. Die Förderung dieser Arten lässt sich besonders gut in *land-sharing* Konzepten verwirklichen, indem die Produktion landwirtschaftlicher Güter mit der Umsetzung von Naturschutzzielen auf einer Fläche vereinbart wird. Die bisherigen Schutzbemühungen reichen jedoch nicht aus, um den Verlusten der Segetalflora entgegenzuwirken. Ein Hauptproblem stellt die mangelnde spontane Wiederbesiedlung geeigneter Habitate dar, denn es fehlen sowohl die Samenbankvorräte der meisten Zielarten als auch effektive Ausbreitungsstrategien. Die Wiederansiedlung seltener Segetalarten ist daher eine notwendige Maßnahme zur Förderung der Agro-Biodiversität. Äcker standen bisher kaum im Fokus der Renaturierungsökologie und es bestehen große Wissensdefizite, welche Faktoren die Etablierung von gefährdeten Arten beeinflussen.

Ziel der Dissertation ist es geeignete Samenherkünfte und Bewirtschaftungsbedingungen zu identifizieren, die eine erfolgreiche Wiederansiedlung seltener Ackerwildpflanzen ermöglichen. Hierfür wurden die phänotypische Differenzierung von Ackerwildpflanzen-Populationen innerhalb Bayerns und deren lokale Anpassung an nördliche und südliche Regionen von Saatgutzonen untersucht. Zudem wurde der Einfluss von unterschiedlichen Feldfrüchten, Saatstärken und Arten der Bodenbearbeitung auf die Etablierung getestet. Die Ansaat auf Praxisbetrieben soll zeigen, unter welchen Bedingungen die Wiederansiedlungsmaßnahmen in die landwirtschaftliche Praxis integriert werden können.

Thema von **Publikation 1** ist die Bedeutung der Samenherkunft für ein Spektrum von fünf Ackerwildkrautarten (*Arnoseris minima*[2], *Consolida regalis, Cyanus segetum, Legousia speculum-veneris, Teesdalia nudicaulis*). Je Art wurden Samen von 4–12 Spenderpopulationen verteilt über vier bayerische Saatgutzonen gesammelt und für zwei Generationen

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[2] Die Nomenklatur folgt der Taxonliste der Gefäßpflanzen in Bayern, Deutschland gemäß Diewald and Ahlmer (2019).

im Gewächshaus kultiviert. Anhand des Phänotyps der F2 Pflanzen wurde die Differenzierung der Populationen mit und ohne Trockenstress untersucht. Zusätzlich wurden reziproke Transplantationsversuche durchgeführt, um die lokale Anpassung an nördliche bzw. südliche Regionen innerhalb der Saatgutzonen zu testen. Die Populationen unterschieden sich in ihrer Biomasseproduktion und Phänologie kaum voneinander. Trockenstress führte jedoch zu art- und herkunftsspezifischen Effekten. Die Etablierung und Fitness der Arten im Freiland wurde maßgeblich vom Versuchsjahr und der jeweiligen Empfängerfläche, jedoch kaum von der Samenherkunft beeinflusst. Entsprechend sollten Samen dieser Arten für Wiederansiedlungsmaßnahmen innerhalb der untersuchten Saatgutzonen gesammelt und gemischt werden. So kann eine hohe genetische Vielfalt und Anpassungsfähigkeit erzielt werden bei gleichzeitig geringer Gefahr von Maladaptation.

Inhalt von **Publikation 2** ist der Einfluss verschiedener Bewirtschaftungsfaktoren (Saatstärke der Kultur, Kulturart, Art der Bodenbearbeitung) auf die Etablierung von drei winterannuellen Arten der Kalkäcker (*L. speculum-veneris*, *C. regalis, Lithospermum arvense*). Das Versuchsdesign bestand aus einem dreijährigen, replizierten Feldversuch in der Münchner Ebene. Besonders günstig wirkte sich eine Ansaat der Ackerwildpflanzen ohne Deckfrucht aus. Dies führte auch in den darauffolgenden Jahren zu signifikant höherer Etablierung. Je nach Kulturart im zweiten Jahr konnten sich die Ackerwildpflanzen entweder nicht (Kleegras), mittelmäßig (Erbse, Triticale) oder sehr gut (Dinkel) reproduzieren. Im darauffolgenden Roggen waren jedoch wieder alle Arten zu finden. Die Art der Bodenbearbeitung (Pflug oder Grubber) hatte je nach Fruchtfolge und Art unterschiedliche und meist geringe Effekte. Die Ergebnisse heben die Bedeutung von Konkurrenz und Störung (weniger die Art, sondern der Zeitpunkt) für die Etablierung von Ackerwildpflanzen hervor. Sofern dies berücksichtigt wird, kann die Wiederansiedlung in den Anbau unterschiedlicher Fruchtfolgen integriert werden.

In **Publikation 3** wurden dieselben drei Zielarten auf vier extensiv bewirtschafteten Ackerflächen der Münchner Ebene ausgesät, um deren Populationsentwicklung unter Praxisbedingungen zu beobachten. Die Pflanzendichte, Samenproduktion, Samenbank und Samenausbreitung dienten dabei als Indikatoren für den Wiederansiedlungserfolg. Drei Jahre nach der Aussaat war die Etablierung von *L. speculum-veneris* im Mittel am besten gelungen, gefolgt von *C. regalis*. Im Gegensatz dazu konnte sich *L. arvense* nur schlecht etablieren und keine Samenbank aufbauen. Die oberirdischen Populationen schwankten im Laufe des Versuchszeitraums je nach Kulturart und unterschieden sich stark zwischen den Ackerflächen. Entlang der Bearbeitungsachse kam es zu einer Verschleppung der Samen bis zu 15 m aus den Aussaatplots heraus. Die Fluktuation von Populationen im Feldbestand und die Bedeutung der Samenbank müssen bei Monitoringkonzepten berücksichtigt werden.

Die übergeordnete **Diskussion** fasst die Erkenntnisse der drei Publikationen zusammen und geht auf verschiedene abiotische und biotische Faktoren ein, die den Etablierungserfolg beeinflussen können. Deren Bedeutung und Wirkungsweise wird unter Einbeziehung der Literatur diskutiert. Es werden praktische Empfehlungen zur Samensammlung und -aussaat sowie zum Management und Monitoring abgeleitet. Wenn die einzelnen Arbeitsschritte einer Wiederansiedlung in Kooperation zwischen Naturschutz und Landwirtschaft sowie Wissenschaft und Praxis umgesetzt werden, kann dies ein erfolgversprechendes Instrument zur Renaturierung von Äckern und zur Förderung gefährdeter Ackerwildpflanzen sein.

INTRODUCTION

Development and change of the arable flora and vegetation

Origin and development of the arable flora and vegetation

Arable fields can host a species-rich vegetation of ***arable plants*** growing spontaneously beside the cultivated crop (see Box 1 for definition and classification). The arable flora goes back to the origins of agriculture about 13,000 years ago (Diamond, 2002). In the course of the Neolithic Revolution, humans began to settle down and changed their way of life from hunter-gatherers to farmers. The arable land created a new man-made ecosystem marked by regularly recurring management operations including soil tillage and crop cultivation. Worldwide there are several origins of agriculture with the earliest ones localized in parts of China and the Fertile Crescent belt in the Middle East (Diamond, 2002). There, the domestication of plants for farming purposes began, including cereals such as einkorn wheat (*Triticum monococcum*), legumes such as pea (*Pisum sativum*) and flax (*Linum usitatissimum*) (Weiss and Zohary, 2011). Many arable plant species are native to these geographic regions and were unintentionally transported to other parts of the world by expansion of humans and crops.

In Central Europe, the arable flora comprises mainly ***archaeophytes*** (see Box 1 for definition), which have been part of the cultural landscape for thousands of years. Additionally, some ***natives*** from open habitats, e.g. rocky dry grasslands, have colonized arable fields as secondary habitats (Schneider et al., 1994; Leuschner and Ellenberg, 2017). Arable plants have evolved under the selective pressures in agroecosystems (Vigueira et al., 2013). Most of them are r-strategists, that have a short life cycle (usually annual, some biennial) and produce lots of seeds (Lososová et al., 2006). Many arable plant species can form a large, long-lived seed bank and seeds may survive unfavourable conditions for several years or even decades (Schneider et al., 1994). The European arable flora contains about 400 plant species of which about 150 are ***obligate segetal species*** (Box 1; Meyer, 2020; Munoz et al., 2020). For Germany, Albrecht (2003), suggests a list of 118 ***characteristic arable plant species***, which have their main habitat in arable fields. ***Facultative arable plant species***, such as ruderals, perennials as well as noxious weeds were excluded from this list.

Until the 1950s, traditional low-intensity agriculture offered best conditions for a species-rich arable flora. Plant communities included a high proportion of specialists, reflecting geology, crop types and management regime (Hofmeister and Garve, 2006; Meyer et al., 2013). Overall, the pre-industrial cultural landscape was highly variable in time and space with a small-scaled mosaic of semi-natural and natural habitats providing a high level of biodiversity (Fuller et al., 2017).

Box 1: Definition and classification of arable plants

Arable plants are plants that grow spontaneously on regularly cultivated arable fields. They are also called ***segetal plants*** based on the Latin term *segetalis* which means "belonging to standing crops" (Meyer, 2013).

As some arable species can cause considerable disservices in the agroecosystem, e.g. yield losses, they are also referred to as arable ***weeds***. This term is translated with a negative prefix in many languages, e.g. French *mauvaise herbe* or German *Unkraut* (Godinho, 1984). However, besides pernicious arable weeds, there are many arable species with biodiversity value and intermediate or low competitive ability (Storkey and Westbury, 2007). The term *arable plant* (German *Ackerwild*- or *Segetalpflanze*) is a more neutral designation than *arable weed* and thus used throughout this thesis.

Arable plants "represent a melting pot of species with different biogeographic and ecological backgrounds" (Bourgeois et al., 2019). The definition of an arable plant species pool is contentious and was only recently suggested by Munoz et al. (2020) for temperate Europe. According to these authors, Meyer (2020), Metcalfe et al. (2019) and Albrecht (2003) the vegetation of arable fields includes:

a) ***Characteristic arable plant species*** that are specifically found in arable fields, also called messicoles, agrestal, resident or ***obligate segetal species***, and
b) ***Facultative arable plant species***, also called transient species, that are less specialized and also found in open non-arable habitats, e.g. species from ruderal or dry grassland communities.

Furthermore, arable plants can be classified regarding their origin and colonization time as:

a) ***Natives*** (indigenous),
b) ***Archaeophytes*** (introduced before the discovery of America in 1492), and
c) ***Neophytes*** (introduced after 1492) (Preston et al., 2004).

Several options are proposed for the classification of arable communities (Leuschner and Ellenberg, 2017). Management (e.g. summer vs. winter crops) and edaphic factors (e.g. base richness of soil) are the main factors used to classify arable communities. However, nowadays there are only fragments left of the arable communities (Meyer et al., 2015a).

Impoverishment of the arable flora

All over Europe, the segetal flora has changed markedly and suffered heavy losses, as large-scale meta-analyses by Storkey et al. (2012) and Richner et al. (2015) showed. In Germany, the mean cover of arable plants decreased from 30% to 3%, and the species number of archaeophytes declined from a median of ten to three species per sample between the 1950s/60s and 2009 (Meyer et al., 2013). Losses of arable plants were most pronounced for specialist species on limestone, on nutrient-poor sandy and on temporarily flooded sites (Lukács et al., 2013; Meyer et al., 2013; Albrecht et al., 2019). This has resulted in homogenized and impoverished arable plant communities with dominance of a few highly competitive arable weed species (Meyer et al., 2013). Today, extensively managed fields are among the most endangered biotope types in Germany (Red-List status 1 *acute threat of complete destruction*; Finck et al., 2017). Also genetic diversity of arable plants has suffered from decreasing population sizes and fragmentation (Brütting et al., 2012a; Brütting et al., 2012b). This can have negative effects on fitness, survival and the ability to adapt to a changing environment, caused for example by climate change (Booy et al., 2000).

Due to their sharp population declines many arable plant species are rare or even extinct in several European countries (Storkey et al., 2012). Their rarity is often expressed by their status in the Red Lists of threatened plants. However, this varies among countries due to different perceptions concerning the general conservation value of arable plants (Albrecht et al., 2016). Moreover, there are several common and sometimes problematic weeds, that have been less or not at all affected by the decline, for example *Cirsium arvense, Echinochloa crus-galli* and *Galium aparine*. Using a functional group approach, Storkey et al. (2010) defined a “rare weed syndrome of short stature, large seed, and late flowering” for species that have suffered the strongest decline over recent decades. Based on further trait analysis of rare arable plants, Pinke and Gunton (2014) identified annuals with short flowering period and preference for low nitrogen levels as well as specialists of stubble fields to be most affected by intensification.

Causes of the decline in arable plant species

In order to increase yields and to ease production processes including technical progress, numerous changes have taken place on field and landscape scale, especially since the middle of the 20th century (Tscharntke et al., 2005; Firbank et al., 2008; Storkey et al., 2012). These changes were promoted by the European Union's Common Agricultural and by the worldwide competition for maximum yields in order to produce cheap agricultural goods, mostly neglecting social and ecological sustainability (Anton et al., 2020). Storkey et al. (2012) showed for 29 European countries that increasing cereal yields positively correlated with increasing numbers of threatened or extinct arable plant species.

The main causes of the arable flora's impoverishment are summarized in several publications, e.g. Albrecht et al. (2016), Meyer et al. (2013) and Storkey et al. (2012). They include: (i) land consolidation, which led to the loss of landscape elements, small fields and field margins; (ii) increasing application of pesticides, most importantly herbicides with a direct negative impact on arable plants; (iii) high input of insecticides and plant growth regulators, that decimate pollinators and raise crop competition; (iv) increasing nitrogen concentration in the agricultural landscape, particularly caused by synthetic fertiliser and slurry application; (v) soil amelioration by liming or acidifying fertilisers; (vi) reduction of crop diversity with focus on few high-yield varieties with loss of traditional crops, e.g. flax; (vii) shortening of crop rotation cycles with tillage immediately after harvest, which negatively affects species requiring stubble for reproduction; and (viii) improved seed cleaning techniques, which prevent the reseeding and dispersal of arable plants with contaminated crop seeds.

Beside the agricultural intensification, however, the abandonment of marginal land, the conversion to grassland and the increasing loss of arable land through soil sealing contributed to the decline of arable plant habitats (Meyer, 2020).

Arable plants as essential elements of the agroecosystem

The role of arable plants for associated taxa

Beside the crops arable plants are the most important primary producers on arable land. They are therefore the basis for many associated animal species, not only for herbivores that use arable plants as food, shelter or reproductive habitat, but also for carnivores that forage in arable fields (Marshall et al., 2003; Fischer and Türke, 2016; Smith et al., 2020). For example, arable plants are of great importance for flower-visiting insects like honey bees and wild bees (Rollin et al., 2013; Bretagnolle and Gaba, 2015; Requier et al., 2015). While studies on this subject are mainly available for arable plants in general, there is a lack of knowledge regarding rare and threatened species. Nevertheless, there are examples for the importance of rare arable plant–insect visitor networks, e.g. hover flies (Syrphidae) visiting rare Asteraceae like *Glebionis segetum* (Rollin et al., 2016). Moreover, not only interspecific but also intraspecific diversity of plants must be considered in this context, since greater genetic diversity can also increase arthropod diversity (Bàrberi et al., 2010).

Ecosystem services supported by arable plants

Several studies demonstrated the importance of biodiversity for agroecosystem functioning, while knowledge about the specific role of functional groups in providing ecosystem services is scarce (Altieri, 1999; Moonen and Bàrberi, 2008). In their review, Blaix et al. (2018) report 129 articles that prove regulating, supporting and provisioning ecosystem services by arable plants. Pest control, through the arable plants' provision of habitat for natural enemies, was with 91 articles the most common ecosystem service. The most frequent underlying mechanism was the attraction of beneficial organisms as natural enemies of pests (Norris and Kogan, 2000; Blaix et al., 2018). A further regulating service, is the support of pollinators by arable plants, which in turn can increase the yield of insect-pollinated crops (Gibson et al., 2006). In the sense of supporting services, arable plants can increase the soil nutrient amount, e.g. by erosion control or active nitrogen fixation, and soil physical properties, e.g. water storage (Blaix et al., 2018). Provisioning services include the potential of arable plant species to be used as crop or medicinal plants. Above all, there is also an intrinsic and aesthetic value of species-rich arable fields (Swift et al., 2004).

Disservices provided by arable plants

Beside ecosystem services provided by arable plants, there are also disservices that must be considered. Arable plants are frequently named as one of the main causes of crop yield losses beside animal pests and pathogens (Oerke, 2006). Several species like *Alopecurus myosuroides* or *Cirsium arvense* are well known for their high competitive ability causing substantial crop yield losses (Zimdahl, 2004). The reduction of crop yields (quantity and quality) can be caused by competition for light, water and nutrients or by allelopathy (Weston and Duke, 2003). There are also species that impede the harvesting process or make it difficult to dry and clean the crop. Some arable plant species contain pyrrolizidine alkaloids and bear the risk of contaminating crop products (Nitzsche et al., 2018). Furthermore, it is possible that arable plants promote the occurrence of fungi or pests, e.g. by serving as intermediate hosts (Norris and Kogan, 2000).

However, there is also evidence that biodiversity on arable land is necessary to maintain agroecosystem functioning and the capacity to produce agricultural goods, especially in the long-term view (Tscharntke et al., 2012). In Central Europe, only a minor part of the arable plant species can be categorized as problematic weeds, while the majority are weak or intermediate competitors (Holzner and Glauninger, 2005; Hofmeister and Garve, 2006). The challenge is therefore to manage arable fields for biodiversity with reducing noxious and promoting rare arable plant species. In this sense, Storkey (2006) suggested to use functional groups of arable plants with low-competitive ability which at the same time provide biodiversity value.

Options for the conservation and restoration of species-rich arable fields

Land-sparing and *land-sharing* concepts

A great challenge for the implementation of conservation and restoration measures are conflicts in land use. On the one hand, land is increasingly required for food production, buildings and infrastructure (Fischer et al., 2014), on the other hand, it is urgently needed to counteract the dramatic biodiversity loss in agricultural landscapes (see above). Reconciling arable plant conservation and the production of agricultural goods can thus be implemented either by *land-sparing* or *land-sharing* concepts (Albrecht et al., 2016). In *land-sparing* concepts, conservation areas are separated from arable land by aiming on high-yield farming, while *land-sharing* combines nature conservation and agricultural production in the same area by aiming for multifunctional, low-intensity farming (Phalan et al., 2011). *Land-sharing* concepts, including organic, integrated and other forms of low-intensity farming, are particularly suitable for the conservation of arable plants as they are adapted to traditional farming practices with recurring disturbances (Albrecht et al., 2016). Nevertheless, field reserves and conservation measures at field margins are also possible tools to promote arable plant diversity and can rather be classified as *land-sparing* concepts.

Conservation options for arable plants

First initiatives for the conservation of arable plants and their habitats in Central Europe date back to the 1950s (Meyer, 2013). Since then, scientists, conservation authorities and NGOs have advocated the conservation of arable plants, which are often underrepresented in nature conservation. Although arable plant species are included in Red Lists of many countries, they are scarcely protected by law. Concepts and options for the conservation of arable plants were reviewed by Albrecht et al. (2016) and Meyer (2020):

(i) One option to preserve existing arable plant communities is the establishment of **field reserves or conservation fields** with securing appropriate management on the whole field. This concept was applied in the German project *100 Fields for Biodiversity* (Meyer and Leuschner, 2015). Though they have proven to be valuable tools for the long-term conservation of important species-rich fields, the number of these fields is not sufficient to maintain the segetal flora and associated ecosystem functions in the agricultural landscape.

(ii) Another option to enhance biodiversity on arable fields are **agri-environment schemes (AES)**, which have increasingly been implemented in the European Common Agricultural Policy since the 1980s (Henle et al., 2008). Depending on the country, AES include various biodiversity programs in which farmers can participate voluntarily and receive financial compensation. AES types targeted on arable plant conservation are either focused on uncropped or cropped field margins (i.e. annual fallows or conservation headlands) or on whole fields (Meyer et al., 2010). Evaluations of these measures show that they can be very effective in promoting the typical arable flora (Wietzke et al., 2020) and threatened species, especially if suitable sites without weed infestation are selected (Walker et al., 2007). Disadvantages include the often unattractive program design for farmers (complex rules, bureaucratic burden, low financial support) and the short duration of usually <5 years. Further AES types that are usually more attractive to farmers are annual and perennial flower strips. These flower strips are commonly sown in spring and contain highly competitive species with negative effects on the segetal flora.

(iii) Furthermore, there is the possibility of implementing arable plant conservation through **compensation measures**. These are environmental offset schemes that legally ensure environmental improvement of a site (Druckenbrod and Beckmann, 2018). In Germany, production-integrated compensation measures were introduced in the early 2000s and could be particularly promising for arable plant conservation. However, they are, so far, more focused on grassland and orchards than on extensively managed arable fields.

(iv) **Organic fields** are cultivated without herbicides and synthetically produced fertiliser. This management type basically offers good conditions for the preservation of threatened species and usually shows higher plant diversity than conventional fields (Hole et al., 2005; Albrecht et al., 2020; Stein-Bachinger et al., 2020). The area of organic farming amounted 7.5% of the EU agricultural land in 2018 and continues to increase in many countries (Eurostat, 2020), which represents an opportunity for extending arable plant conservation in the sense of a *land-sharing* concept.

(v) ***Ex-situ* conservation** like the cultivation of rare and highly endangered species in botanical gardens is a useful addition to *in-situ* conservation. However, for the conservation of populations, their genetic diversity and adaptability under field conditions is of primary importance (Albrecht et al., 2016).

Limits of natural restoration

The change from high to low intensive agriculture through one of the above mentioned *in-situ* conservation options might be sufficient to restore habitat conditions with spontaneous recovery of rare arable plant populations (Fig. 1). However, this requires that species are still present in the seed bank or that source populations for colonization are available in the surrounding landscape (Bischoff, 2005).

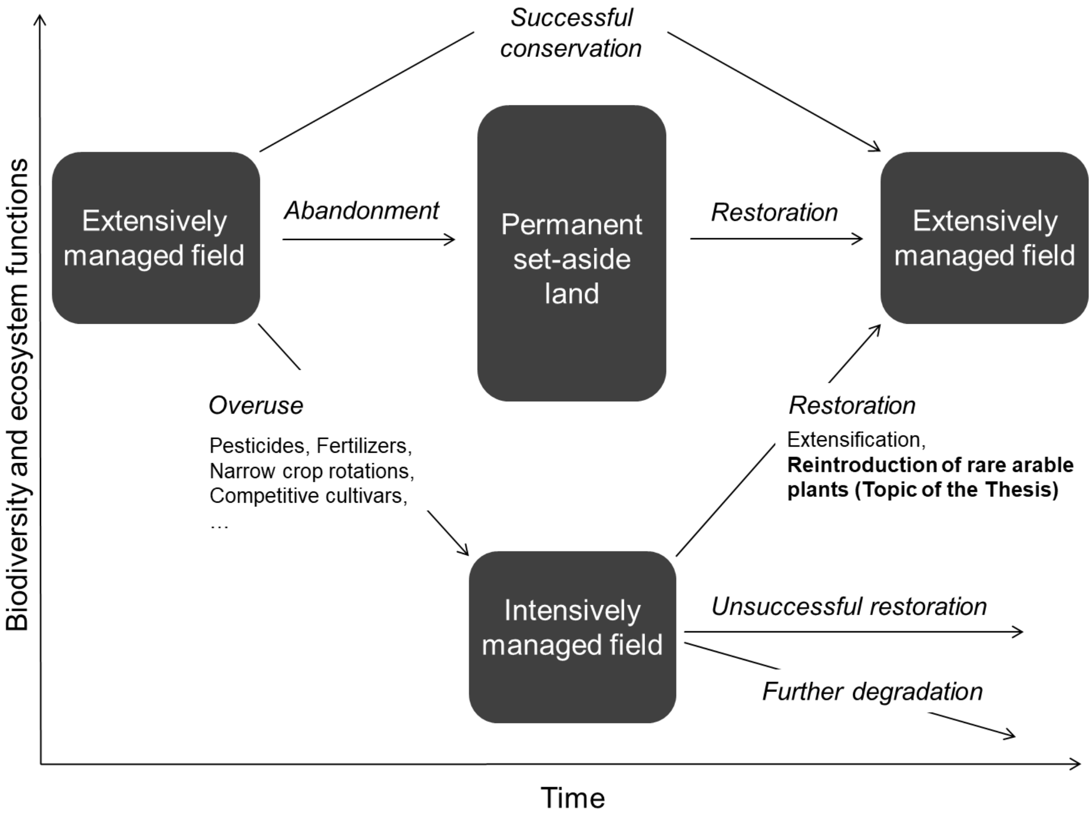


Fig. 1: Theoretical framework for the conservation and restoration of arable fields. Biodiversity and ecosystem functions of extensively managed fields can either be preserved through appropriate conservation or recovered through restoration measures, when they have been degraded or transformed by overuse or abandonment from their original state. While intensively managed fields are usually species-poor and provide hardly any ecosystem functions except food provision, permanent set-aside land (i.e. uncultivated fallows) can present alternative target states with varying value for nature conservation, depending on site, landscape context and state of succession. The restoration of species-rich arable fields includes the extensification of previously intensively managed fields or the resumption of farming of set-aside land. If natural recovery fails, active restoration with the reintroduction of target species is necessary. Figure modified after Zerbe and Wiegleb (2009).

As many arable plant species develop dense and long-lived seed banks, the chance of natural colonization is principally given, though it is strongly dependent on the previous management of the site (Albrecht, 2005; Wäldchen et al., 2005). In the case of set-aside land (in terms of uncultivated long-term fallows), it is possible that species have been preserved in the seed bank, especially when stored in deeper soil layers and tillage may be sufficient to reactivate the species' potential (Albrecht et al., 2016). This was demonstrated by Kohler et al. (2011) who found natural regeneration of at least some threatened arable species when ploughing fields in the Swiss Alps after 50 years of abandonment. Since set-aside land can develop valuable alternative habitats with high biodiversity and ecosystem functions (Tscharntke et al., 2011), it is necessary to weigh up the nature conservation goals. In contrast, after many years of intensive farming, seed banks are often depleted due to regular stimulation of germination and subsequent destruction (Bischoff and Mahn, 2000; Wietzke et al., 2020).

Additionally, the probability of spontaneous re-colonization from outside the field is low (Albrecht et al., 2000; Bischoff, 2005). Most arable species lack dispersal strategies, e.g. by wind or animals, instead, their seeds are shed just beneath the parent plant (seed dispersal by gravity, *barochory*; Benvenuti, 2007). However, there is the possibility that seeds are dispersed by seed trade and agricultural management operations (seed dispersal by humans, *anthropochory*, ibid.). While dispersal by uncleaned crop seeds was quite common in traditional land use, it became unlikely in modern agriculture with advanced seed cleaning methods (Poschlod and Bonn, 1998). Thus, the chances for long-distance dispersal are limited. On the field and farm scale, seeds can be dispersed directly by soil or biomass displacement or indirectly by adhesion to machinery (Benvenuti, 2007). However, these dispersal events are very rare and only short dispersal distances of few meters per year were documented for rare arable plant species (Bischoff and Mahn, 2000). Though, the assisted restoration including reintroduction of target species is a reasonable tool to overcome the limits of natural restoration in arable fields (Atkinson and Bonser, 2020) and is a necessary addition to the maintenance of remnant populations in arable plant conservation (Fig. 1).

Reintroduction of rare arable plants

Definition and aim of reintroduction

The ***translocation*** of rare or threatened plant species has gained importance and acceptance in nature conservation worldwide and several conventions, laws and practical guidelines have been published on this topic (Armstrong and Seddon, 2008; Godefroid et al., 2011; IUCN/SSC, 2013). Conservation translocations can be classified in several categories depending on the release area, the presence of conspecifics and the aim of the translocation (Box 2). The focus of this thesis is on the ***reintroduction*** of rare arable plant species, which means the transfer to an area that once had been part of its historic range but from which it has disappeared (Seddon, 2010). However, this does not mean reintroduction in the strict sense of a former population to be proven at the exact site of release, e.g. the area of an arable field (Godefroid et al., 2011). The aim of reintroductions is the establishment of populations that are able to reproduce, to persist in the long-term on their own and to adapt to changing environmental conditions (Godefroid et al., 2011).

Box 2: Classification of conservation translocations

Conservation ***translocation*** is the “intentional movement and release of a living organism” with the main goal to improve the conservation status of the translocated species and/or to restore ecosystems functions (IUCN/SSC, 2013). According to the IUCN Guidelines conservation translocations can be classified in:

1. *Population restoration*, when the release is performed within the historic range of the species. If conspecifics are present at the translocation site this activity is called *reinforcement*, otherwise ***reintroduction***.
2. *Conservation introduction*, when the release is performed outside the historic range of the species. If the aim of this translocation is to avoid population extinction this is called *assisted colonisation*, if the aim is to maintain ecological functions, this is called *ecological replacement*.

State of knowledge about the reintroduction of rare arable plants

The literature about conservation translocations had been very scarce until the 1990s, but has been growing for plant and animal species in the past decades, especially for key species (Armstrong and Seddon, 2008; Menges, 2008). The success of plant reintroductions and factors determining the success were reviewed by Godefroid et al. (2011) including 249 datasets worldwide. So far, arable plant species were rarely addressed in such investigations.

Sowing uncleaned crop seeds was tested for the introduction of the highly threatened arable plant species *Bromus grossus* (Piqueray et al., 2018). This approach resulted in establishment success in the first year after sowing, while the species was not present anymore in the following year. However, the total number of arable species increased from 12 to 43 species. Accordingly, this transfer method can be successful for the restoration of species-rich arable fields, but it also bears the risk of undesired transfer of pernicious weed species. The same applies to top soil translocation, which has been tested by Piqueray et al. (2020).

In this thesis, sowing pure seeds of rare arable plant species was chosen as transfer method. This offers the advantages that regarding to the transplant site, selected species can be sown individually or in mixtures with a precise definition of sowing rates (Lang et al., 2016b). Furthermore, seed material can be stored temporarily and sowing time can be chosen according to the crop and arable plant species (Torra et al., 2020). Field experiments by Lang et al. (2016b) and Twerski et al. (2021) showed that sowing autochthonous seed material of low competitive rare arable plant species can be performed in managed fields without significant impact on crop yield; this was also proven in a greenhouse study by Epperlein et al. (2014). The effects of different agricultural management practices on the performance of sown arable plants were reviewed by Albrecht et al. (2016). Most relevant management factors were crop type, crop density, fertilization, cultivation of cover crops, herbicide application and sowing time of the crop.

However, there are several knowledge gaps about the reintroduction of rare arable plants to restore species-rich arable fields, which are addressed in the three publications of this thesis.

1. The role of appropriate seed material for restoration is intensively debated among researchers and conservation authorities (e.g. Broadhurst et al., 2008; Bucharova et al., 2019). In order to identify suitable seed material for restoration purposes, regional differentiation and local adapation of plants must be considered (Vander Mijnsbrugge et al., 2010). However, corresponding studies on rare arable plants are still missing.
2. A further prerequisite for restoration success is the provision of suitable habitat and management conditions targeted on the requirements of the introduced species (IUCN/SSC, 2013). The arable habitat is significantly shaped by agricultural management. The beneficial or negative effects of management measures on arable plant vegetation have already been addressed in several studies, but scarcely in the context of reintroduction measures with monitoring >1 year (Albrecht et al., 2016).
3. Previous studies on the seed translocation of rare arable plants were mostly performed under controlled experimental conditions (Albrecht et al., 2016). There is a lack of knowledge about the extent to which this can be implemented under practical farming

conditions. Population development including soil seed banks and dispersal has been hardly monitored so far.

Aim of Publication 1: Detecting regional differentiation and local adaptation

Plants can show high intraspecific variability, expressed for example by varying fitness or phenology among individuals or populations of a species (Vanandel, 1998). Phenotypic variation can either be due to phenotypic plasticity or genetic differences (Kawecki and Ebert, 2004). Genetic differences among populations might be caused by genetic drift, inbreeding or ***local adaptation***. The basis for local adaptation are divergent selection pressures, which emerge from different abiotic or biotic conditions, e.g. soil, climate or pollinators, experienced by different populations of the same species in their respective habitats (Kawecki and Ebert, 2004). Local adaptation will than lead to a higher relative fitness of the population in its local environment in comparison with populations originating from other environments (see Box 3 for more precise definitions and possible study approaches). A meta-analysis by Leimu and Fischer (2008) compared 1031 plant population pairs and found local adaptation in 71% of the studied cases, while ***local adaptation in the strict sense*** was detected only in 45%. Local adaptation was proven on very different spatial scales, reaching from few meters to several thousand kilometres (Leimu and Fischer, 2008). While the degree of local adaptation was independent of geographic scale, habitat heterogeneity and plant life history, it was most pronounced in large populations with >1000 individuals.

Box 3: Local adaptation in plants: Definitions and experimental approaches

The basic definition of ***local adaptation*** is that a local population has higher fitness at its local site than foreign populations that are introduced to that site (Blanquart et al., 2013). This *local vs. foreign* approach can be tested in a common garden experiment by growing plants from several source populations together at one site.

In the ***strict sense of local adaptation*** (Kawecki and Ebert, 2004) several sites have to be investigated and at each site the local population must perform better than the average of non-local ones. This requires reciprocal transplant experiments with at least two populations introduced in their respective local and non-local environment.

The latter approach can be used to compare the average fitness of populations in their local sites *sympatry* to those growing in other sites *allopatry*, which was applied in Publication 1 of this thesis following Bucharova et al. (2017).

For rare arable plants, there are hardly any genetic or phenotypic investigations which tested population differentiation and local adaptation (but see Bischoff et al., 2010; Brütting et al., 2012a; Meyer et al., 2015b). On the one hand, differentiation and local adaptation may be low due to the lack of divergent selection, e.g. caused by low environmental difference or high temporal variation, which favours generalist genotypes (Kawecki and Ebert, 2004). Additionally, persistent seed banks can act as buffer against selection processes (Tellier, 2019). Moreover, gene flow can hinder population differentiation, e.g. by frequent dispersal in former times (Poschlod and Bonn, 1998). On the other hand, local adaptation in arable species may be strong due to their short life cycle speeding up differentiation processes and due to habitat fragmentation with low dispersal and gene flow during the past decades (Vigueira et al., 2013). One factor, that can induce population differentiation in plants is adaptation to drought stress (Heschel et al., 2004). Such drought adaptation may be increasingly important in the course of climate change and especially for rare arable plants which have specific germination requirements (Rühl et al., 2016).

Profound knowledge on the regional differentiation and local adaptation of rare arable plants is needed to delineate regions, e.g. seed zones, where they can be transferred without consequences for population fitness. Germany has already implemented a regional seed concept for herbaceous plants including 22 seed transfer zones based on grouping natural units according to their geology, soil type and climate (Bucharova et al., 2019). Within these zones several source populations are harvested and either directly or after an intermediate propagation applied as mixture to the target site. The suitability of this approach for rare arable plant reintroduction is controversially perceived and, in contrast to common grassland species, has not been evaluated yet (Durka et al., 2017).

The aim of Publication 1 is to detect regional differentiation and local adaptation of rare arable plants to provide a basis for seed sourcing strategies in restoration projects.

Aim of Publication 2: Identifying favourable management practices

There are several field surveys reporting effects of environmental and management factors on species diversity and composition of spontaneous vegetation on arable fields (Fried et al., 2008; Pinke et al., 2012; Rotchés-Ribalta et al., 2015a). These can be used as a basis to define suitable restoration conditions for rare arable plants. Similarly, successful conservation instruments can provide guidance on how to design habitat and management conditions according to the target species' requirements. Further, the reintroduction guidelines by IUCN/SSC (2013) highlight that knowing the causes of decline helps to choose suitable management conditions.

How agricultural management practices affect the performance of arable plants was reviewed by Albrecht et al. (2016) for the particular case of sown study plants: The effect of different crop types was tested mainly for cereals and in comparison to uncropped conditions. Good results were obtained without crops, with crops sown in reduced densities and for low competitive cereals, e.g. spelt, which can be attributed to high light availability for the arable plants (Kleijn and Voort, 1997; Rotchés-Ribalta et al., 2016). Fertilization can enhance the performance of arable plants when growing without crop but in the presence of a crop the effect is usually inverse (Rotchés-Ribalta et al., 2016). Herbicides generally have a negative effect on arable plants, but with variation depending on respective compounds, e.g. graminicides can even favour establishment of herbaceous species by reducing competition of grasses (Albrecht et al., 2016). Fewer studies are available for the effects of soil tillage types and the cultivation of forage crops such as clover-grass mixtures on the performance of rare arable plant establishment (ibid.). Moreover, establishment success was mainly examined in the first year after sowing target plants, while long-term investigations including different crop rotations are missing.

The aim of Publication 2 is to determine the effects of crop density, crop type and soil tillage on the establishment of rare arable plants over three years.

Aim of Publication 3: Evaluating establishment under practical farming conditions

In terms of the *land-sharing* concept, low-intensity fields offer a good opportunity to increase the biodiversity of arable fields. In organic farming, diversity and abundance of arable plants are usually higher than in conventional farming (Hole et al., 2005). Waiving of pesticides and synthetic fertilisers as well as less dense and more diverse crop rotations essentially contribute to this effect. However, even under such favourable management conditions chances for spontaneous colonization are frequently low (see section ‘Limits of natural restoration’ in the introduction). A questionnaire by Wiesinger et al. (2010) demonstrated that numerous organic farmers in Germany would be generally open-minded for the sowing of low-competitive arable plants on their fields. However, the extent to which such reintroduction measures can be integrated into farming practice has hardly been scientifically documented and published to date. In organic farming, mechanical weeding like currying or hoeing or the cultivation of competitive crops, e.g. clover-grass mixtures, could prevent the establishment of arable plants.

In many studies, also the establishment of the target plants is poorly recorded and the criteria for the success of reintroductions are vaguely defined (Menges, 2008; Godefroid et al., 2011). The measurement of introduction success is particularly challenging for arable plants. The reasons therefore are temporal variable above-ground populations and seeds in the soil seed bank which frequently represent a considerable part of the total population (Bakker et al., 1996). Soil seed banks depend both on seed dormancy and seed persistence. Many arable species show cyclic dormancy, which increases the chance of germination under favourable conditions (Venable and Brown, 1988). Seed persistence varies greatly depending on the species and can range from <1 year to several decades (Schneider et al., 1994). The influencing factors include seed and germination traits as well as burial depth controlled by soil cultivation (Saatkamp et al., 2011; Gaba et al., 2017).

Beside soil seed banks, dispersal must be considered when measuring the establishment of a population. On the field scale, horizontal movement by cultivation operations plays a major role for dispersal and may influence the patches of sown species and their monitoring. Bischoff (2005) found dispersal rates of arable plants limited to several meters per year but species-specific knowledge, especially for rare arable plants, is poor.

The aim of Publication 3 is to evaluate whether sown rare arable plant species can develop viable populations under real-farm conditions. Furthermore, the relevance of soil seed bank and dispersal along the machining direction for monitoring the reintroduction success are figured out.

OBJECTIVES AND OUTLINE

The goals of this thesis are to investigate the reintroduction of rare arable plants on arable fields and to identify suitable seed provenances and agricultural management conditions. More specifically, the objectives are to:

1) Detect regional differentiation and local adaptation of rare arable plants;
2) Determine the effects of crop density, crop type and soil tillage on establishment; and
3) Evaluate whether the introduced species can develop viable populations under practical farming conditions.

The publication-based dissertation includes an introductory and methodology section, a summary of each publication (Publications 1–3), as well as a discussion and conclusion section across the different topics. The three publications use different study approaches covering a gradient from controlled to practical conditions to create a better understanding of intraspecific variation of rare arable plants and their performance under different management scenarios (Fig. 2).

Publication 1 (Lang et al., 2021a) analyses the effect of seed provenance on the establishment (plant density) and performance (biomass, phenology) of rare arable plants. Regional differentiation and local adaptation of five target species are tested under greenhouse conditions and in field experiments to provide a basis for seed sourcing strategies in restoration projects.

In **Publication 2** (Lang et al., 2021b) autochthonous seeds of the three winter annual species *Legousia speculum-veneris*, *Consolida regalis* and *Lithospermum arvense* are sown in a field trial to investigate the effects of management measures (crop density, crop type and soil tillage) on their establishment and seed production. Population growth rates in relation to competition (i.e. crop and weed cover) and different soil tillage types allow a comprehensive understanding of the development of rare arable plants during the course of different three-year crop rotations.

Publication 3 (Lang et al., 2018) tests the applicability of these achieved results under practical conditions on four organic farms. Seed production, soil seed banks and dispersal from sown plots are monitored over three years to get an impression of long-term establishment and suitable monitoring indicators under real-farm conditions.

The discussion summarizes the main findings of the three publications and places them into the context of current literature to evaluate factors that determine the reintroduction of rare arable plants on extensively managed fields. Based on the scientific findings, seed sourcing and sowing strategies as well as management and monitoring recommendations are proposed. Finally, perspectives on long-term persistence of introduced rare arable plant populations and options for practical implementation of reintroductions are discussed.

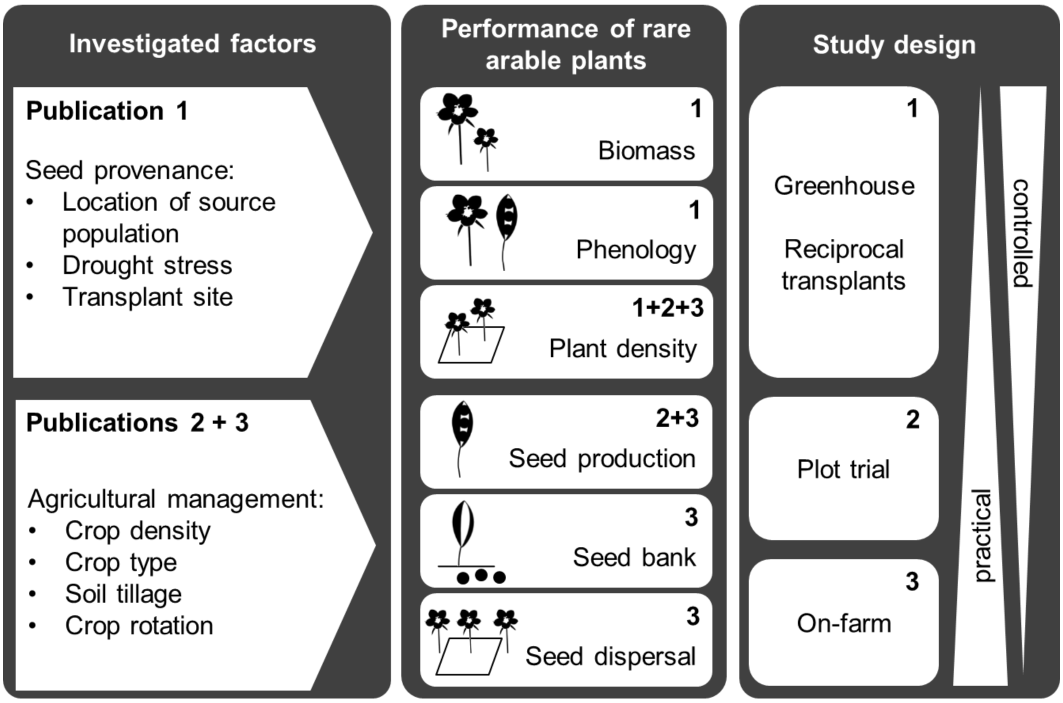


Fig. 2: Graphical overview of the thesis with Publications 1–3 on factors controlling the performance and establishment of introduced rare arable plants in different greenhouse and field experiments covering a gradient from controlled to practical conditions.

MATERIAL AND METHODS

Study area and experimental sites

The data for the three publications of this thesis were sampled in Bavaria, South Germany in four seed transfer zones (Bucharova et al., 2019), which are in this area equivalent to the major natural units *Main-Franconian Plates* (*Mainfränkische Platten,* zone 11 in Fig. 3), *Franconian Keuper-Lias Land* (*Fränkisches Keuper-Lias-Land*, 12), *Franconian Jura* (*Fränkische Alb*, 14) and *Lower Bavarian Hills and Isar-Inn Gravel Beds* (*Unterbayerisches Hügelland und Isar-Inn-Schotterplatten*, 16; Ssymank, 1994).

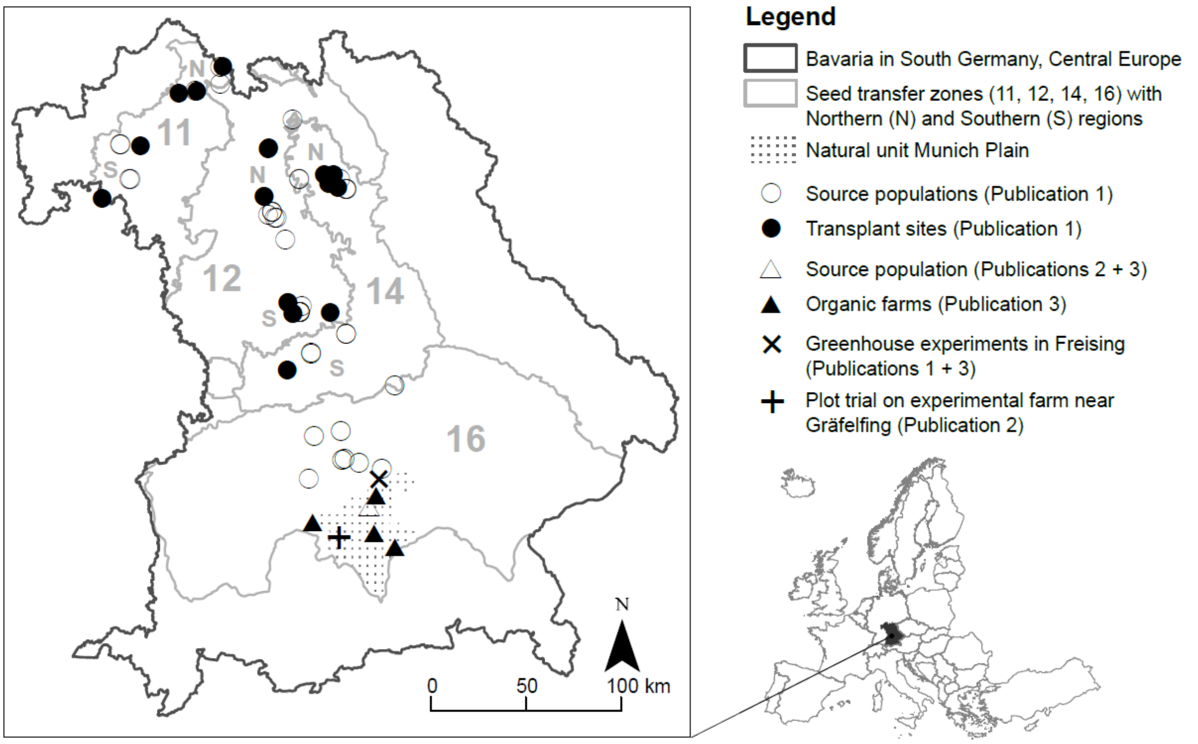


Fig. 3: Map of the study area showing the location of experimental sites in Bavaria, South Germany, Central Europe.
The study area comprises four seed transfer zones (11 = *Main-Franconian Plates*, 12 = *Franconian Keuper-Lias-Land*, 14 = *Franconian Jura*, 16 = *Lower Bavarian Hills and Isar-Inn Gravel Beds*). Regional differentiation of rare arable plants was tested within and among these zones and local adaptation was determined by reciprocal transplant experiments to the northern and southern regions within zones (Publication 1). The effect of agricultural management on establishment of rare arable plants was investigated in the *Munich Plain* (Publications 2, 3). Source populations (open symbols) and transplant sites (full symbols), location of the Greenhouse Laboratory Center Dürnast in Freising and of the plot trial on an experimental farm near Gräfelfing are shown.

The experiments on regional differentiation and local adaptation of rare arable plants (Publication 1) were performed in the Greenhouse Laboratory Center Dürnast (TUM, Freising) and on 16 transplant sites (latitude: 48.92–50.35 °N, longitude: 9.67–11.39 °E, altitude: 241–554 m) based on seed collections from 38 source populations. The effect of agricultural management was investigated in a plot trial within an experimental farm near Gräfelfing (Publication 2) and on four organic farms (Publication 3) in the *Munich Plain* (*Münchner Ebene*, 48.09–48.33 °N, 11.23–11.81 °E, 459–553 m). For this purpose, seeds were collected from source populations in the field reserve *Kastner Grube* (Fig. 3).

The study area is characterised by different geology and increasing humidity from northern to southern Bavaria. The northernmost seed transfer zone 11 includes shell limestone and Keuper with soil types based on clay and loam. The climate is dry and continental with mean annual precipitation (MAP, period 1981–2010) of 666–745 mm and temperature (MAT) of 8.3–9.7 °C, measured at the experimental sites (DWD Climate Data Center). Zone 12 is shaped by sandstones of Keuper and sandy river deposits with permeable, nutrient-poor soils (MAP 679–768 mm, MAT 8.9–9.2 °C). The limestone and dolomite bedrock of the Jurassic period in zone 14 formed shallow layers of base rich clay with a low water holding capacity. The climate corresponds to a dry low mountain range type (MAP 748–952 mm, MAT 7.9–8.9 °C). The southernmost zone 16 included, on the one hand, loamy soil types based on tertiary sediments and alluvial deposits, some of them with sand overflows (Publication 1), and on the other hand, mainly nutrient-poor soils on calcareous gravel in the natural unit *Munich Plain* (Publications 2, 3). The climate in zone 16 is humid (MAP 746–963 mm, MAT 8.3–8.9 °C).

The agricultural landscape of Bavaria is relatively small-structured (mean arable field size of 1.84 ha; Zenger and Friebe, 2015) with a proportion of 12% organic farming (Bundesanstalt für Landwirtschaft und Ernährung, 2020) and a decreasing gradient from south to north in terms of crop yield potential (Bayerische Vermessungsverwaltung, 2020). Several decades ago, the arable fields of the whole study area were marked by a species-rich arable flora, especially at yield-poor sites. In the period 1950–1980, Albrecht (1989) documented a sharp decline of arable plant species in Bavaria and nearly one third of them are now on the Red List of threatened plants (Metzing et al., 2018).

Study species

In total, this thesis covers six annual study species which are typical representatives of the endangered segetal flora in Central Europe: *Arnoseris minima* (L.) Schweigg. & Koerte, *Consolida regalis* Gray, *Cyanus segetum* Hill (syn. *Centaurea cyanus* L.), *Legousia speculum-veneris* (L.) Chaix, *Lithospermum arvense* L. (syn. *Buglossoides arvensis* (L.) I.M.Johnst.) and *Teesdalia nudicaulis* (L.) R. Br. (Fig. 4). Five of them were investigated in Publication 1, and three in Publications 2 and 3 (Table 1). Their nomenclature follows the taxon list of vascular plants from Bavaria, Germany by Diewald and Ahlmer (2019); common synonyms are given in brackets according to The Plant List (2013). All of them are r-strategists and characteristic segetal species (see Box 1) predominantly occurring in cereal fields. They belong to five families and cover a gradient from near threatened *C. segetum* to endangered *A. minima* (Metzing et al., 2018; Table 1). While *L. speculum-veneris* and *C. regalis* are considered archaeophytes in Central Europe, both by Kästner et al. (2013) and Schneider et al. (1994), the authors do not agree on the floristic status of the other species. According to them, *Arnoseris minima*, *C. segetum*, *L. arvense* and *T. nudicaulis* may also be native on open sandy or stony dry grasslands in their European ranges. The study species' distribution range is sub-atlantic for *A. minima* and *T. nudicaulis*, eurasian for *C. regalis* and sub-mediterranean to mediterranean for *C. segetum*, *L. speculum-veneris* and *L. arvense*. As character species of different plant communities they grow either on siliceous and/or calcareous soils (Table 1). All species are weak competitors with a mean plant height <50 cm and low impact on crop yields, except *C. segetum* which can develop higher biomass and an intermediate competitive ability (Table 1).

In the study area of the thesis all investigated species germinate in autumn but spring germination is also possible, especially in *C. segetum* and *L. speculum-veneris*. Depending on species, germination period and environmental variables, flowering starts April–June and ends May–October (Table 1). Pollination is provided by bees, bumble bees, wasps, bomblides or syrphids, while self-pollination is possible in *L. speculum-veneris* and *T. nudicaulis*, and prevailing in *A. minima* and *L. arvense*. Hundreds of small seeds (1000 seed weight <6 g) are usually produced per plant (Table 1) and can become part of a large soil seed bank. However, there are contrasting and for some species not enough results on the persistence of seeds in soil, with values varying species-specific between few and >10 years (Schneider et al., 1994; Kästner et al., 2013).

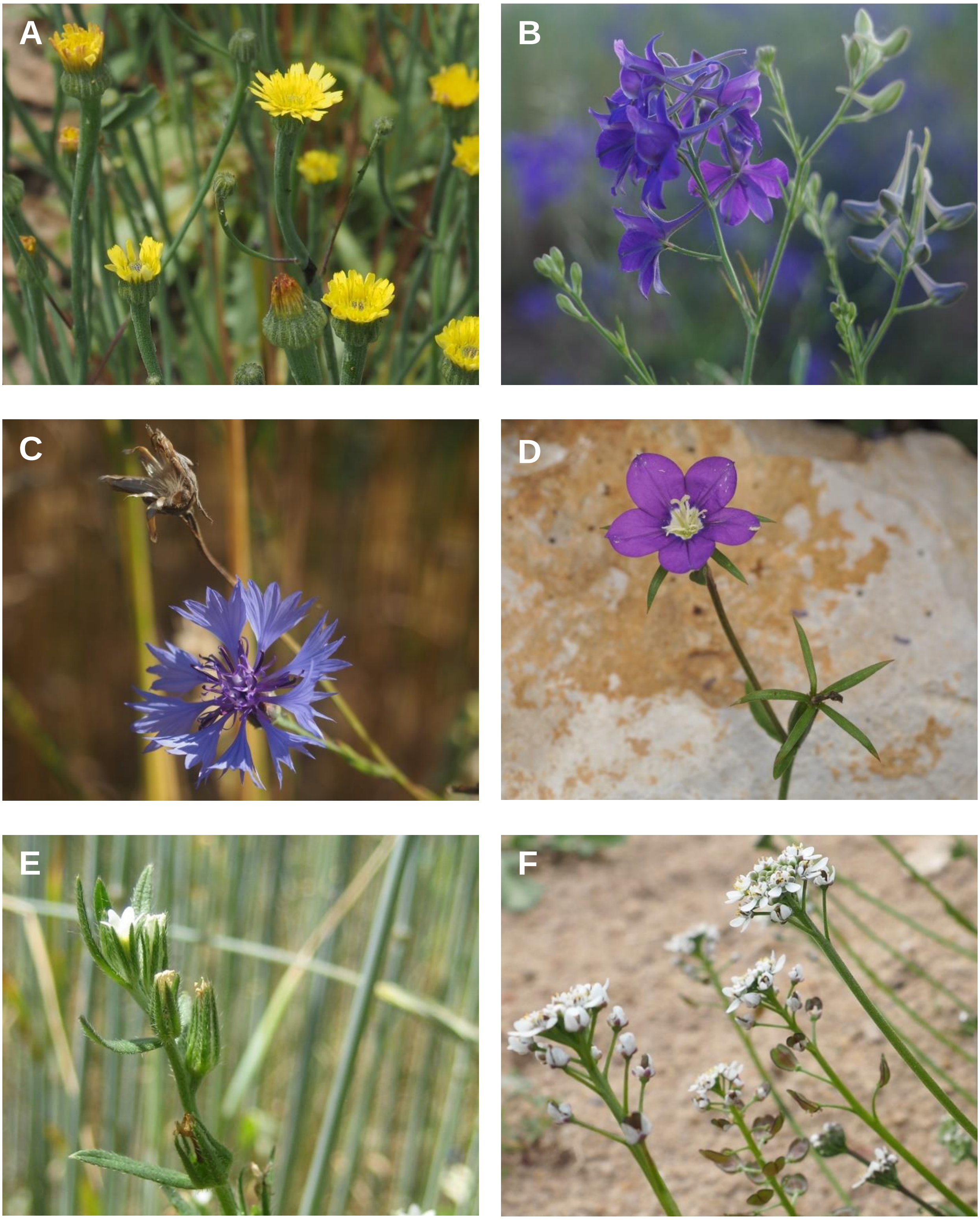


Fig. 4: Flower stands of the six investigated rare arable plant species.
(A) *Arnoseris minima*, (B) *Consolida regalis*, (C) *Cyanus segetum*, (D) *Legousia speculum-veneris*, (E) *Lithospermum arvense* and (F) *Teesdalia nudicaulis*.

Table 1: Biological and ecological characteristics of the six study species.
Red List status in Germany (RL D; Metzing et al., 2018) and Bavaria (RL BY; Scheuerer and Ahlmer, 2003) with the categories: Least concern (*, no current risk of loss), near threatened (V), vulnerable (3), endangered (2). Plant community according to Hofmeister and Garve (2006). Soil indicator values by Ellenberg et al. (1991) for moisture (range from 1 very dry to 9 wet), reaction (range from 1 strongly acidic to 9 alkaline and calcareous conditions) and nitrogen (range from 1 poorest to 9 excessively rich nitrogen concentration). Competitive capacity according to Holzner and Glauninger (2005) (range from 1 very low to 5 strongly competitive species; NA = no data available). Flowering months of the year and pollen vectors (Klotz et al., 2002). Values for germination period, plant height, 1000 seed weight and number of seeds per plant are based on own records within the study area.

Publication	**Species**	**Family**	**RL D**	**RL BY**	**Plant community**	**Indicator (Moisture, Reaction, Nitrogen)**	**Germination period**	**Height in cm, mean (min – max)**	**Competitive capacity**	**Flowering month**	**Pollen vector (abundance)**	**1000 seed weight in g, mean ± SE**	**Seeds per plant, mean**
1	*Arnoseris minima* (L.) Schweigg. & Koerte	Asteraceae	2	2	Teesdalio–Arnoseridetum minimae	4, 3, 3	autumn	33 (27 – 42)	NA	6 – 9	Selfing (the rule), insects (rare)	0.34 ± 0.01	758
1, 2, 3	*Consolida regalis* Gray	Ranunculaceae	3	3	Caucalidion platycarpi	4, 8, 5	autumn (and spring)	43 (21 – 71)	1 – 2	5 – 8	Insects (the rule)	1.20 ± 0.04	397
1	*Cyanus segetum* Hill	Asteraceae	V	V	Aperion spicae-venti	indifferent	autumn and spring	64 (41 – 84)	3	6 – 10	Insects (the rule)	3.33 ± 0.16	55
1, 2, 3	*Legousia speculum-veneris* (L.) Chaix	Campanulaceae	2	3	Violenea arvensis	4, 8, 3	autumn and spring	34 (23 – 50)	2	6 – 8	Insects (the rule), selfing (at failure of outcrossing)	0.19 ± 0.01	483
2, 3	*Lithospermum arvense* L.	Boraginaceae	V	3	Violenea arvensis	indifferent, 7, 5	autumn	43 (26 – 64)	2	4 – 7	Selfing (the rule), insects (possible)	5.30 ± 0.12	180
1	*Teesdalia nudicaulis* (L.) R. Br.	Brassicaceae	*	3	Teesdalio-Arnoseridetum minimae	3, 1, 1	autumn	27 (23 – 31)	NA	4 – 5	Insects (the rule), selfing (at failure of outcrossing)	0.28 ± 0.01	1541

Seed material

Seeds of rare arable plants were collected from low-intensity fields, e.g. organic farms, contract-based conservation fields and field reserves (collection sites are displayed in Fig. 3). Seeds were harvested by hand from populations with >100 individuals from at least 50 plants per site to achieve genetic variability of the seed material. For experiments in Publications 2 and 3, huge amounts of seeds were required. Therefore, some of the originally collected seeds were further propagated by a local seed producer (Johann Krimmer, Pulling, Germany). Seeds were cleaned and stored dry, cool and dark before sowing.

Regional differentiation and local adaptation of rare arable plants was tested on F2 generations of the study species to reduce maternal effects (Bischoff and Müller-Schärer, 2010). Therefore, seeds were sown in the greenhouse, and the F1 generations were grown under standard conditions before harvesting their seeds, which were subsequently used in the experiments (details are given in Publication 1). Establishment in response to agricultural management was tested on F1 generations of the study species (Publications 2, 3). For this purpose, the three study species *L. speculum-veneris*, *C. regalis* and *L. arvense* were sown in a mixture of 10:4:3 at 850 seeds m^{-2} in total. In all experiments, seeds were sown per hand and pressed on the soil surface to enable good conditions for the mainly light-dependent germinators.

Study design

Publication 1: Greenhouse study on regional differentiation

Regional differentiation was examined for five study species (Table 1), each with seeds originating from 4–12 source populations from the whole study area (Fig. 3). 15 plants (F2) per species and source population were grown in separate, randomly arranged pots under standard conditions in the greenhouse (Fig. 5A). To test the effect of drought stress on intraspecific phenotypic variation, half of the plants were exposed to reduced water supply (details in Publication 1).

Publication 1: Reciprocal transplant experiments

A subset of three species (*A. minima, C. regalis* and *T. nudicaulis*) was used to investigate local adaptation of rare arable plants to the northern or southern regions of seed transfer zones. Therefore, reciprocal transplant experiments were set up on arable fields within three seed zones (Fig. 3). For each species suitable transplant sites were selected on which 25-m² plots were established at the field margin. There, 100 seeds per source population were sown in parallel, separate rows (Fig. 5B). The fields were cultivated with autumn-sown cereals in reduced (50–75% of the normal) density, without weed control and fertilization. Source populations included sympatric provenances from the same region as the transplant site (i.e. *local*) and allopatric ones from the opposite region (i.e. *non-local*). The experiment was repeated in two subsequent years.

Publication 2: Plot trial experiment in Gräfelfing

The establishment of rare arable plants depending on different management factors (crop density, crop type, soil tillage) was tested for *L. speculum-veneris*, *C. regalis* and *L. arvense* in a three-year plot trial experiment located on an experimental farm. In total, 70 plots with 14 different management combinations, each replicated five times, were arranged in a completely randomized block design (Fig. 5C). Crops were cultivated on 48-m² plots with arable plants sown in year 1 in the central part of 24 m². To test the effect of crop sowing density on establishment of the study species, three treatments were applied in year 1: No crop (0%), spelt in reduced (40 husked seeds m^{-2}) or in normal sowing density (160 seeds m^{-2}). In the following two years, rye was grown on the plots. To test the effect of crop type, rye was cultivated in year 1, followed by four different crop types: autumn-sown spelt, spring-sown triticale, spring-sown pea or clover-grass that was sown directly after harvest. Rye was cultivated on all plots in year 3. The effect of soil tillage was tested in two different crop rotations: ‘rye–clover-grass–rye’ and ‘without-crop–rye–rye’. Between years 1 and 2, soil was tilled either with a mouldboard plough (cultivation depth approximately 15 cm, inversion tillage) or with a rotary cultivator (5–10 cm, non-inversion tillage).

Publication 3: On-farm studies in the Munich Plain

Reintroduction under practical conditions was investigated on four organic farms in the Munich Plain (Fig. 3). One field per farm was chosen to provide basically suitable site conditions for the study species, i.e. relatively nutrient-poor calcareous soils without major weed infestation. Inside each field four 25-m² plots were arranged at least 15 m away from the field margin and with a distance of 7.5 m between each other, parallel to the machining direction. Arable plants were sown in year 1 and their establishment was monitored during the three-year study period. In years 1 and 2 all farmers cultivated autumn-sown cereals (rye, spelt or wheat) in reduced density. Neither mechanical weed control nor fertilization were applied in order to provide suitable conditions for the study species. In year 3, farmers were free to choose their specific crop and management. Thus, either wheat without weed control, curried spelt, curried oat or curried and hoed soybean were cultivated.

Data sampling

Plant performance and phenology

Performance of arable plants was measured as biomass (all publications) and seed production per individual (Publications 2, 3). Biomass was determined by cutting the sampling plants at the end of the growing season above-ground (Fig. 5D) and drying them at 65 °C for 48 h before weighing. In Publication 2 and 3, seed production was determined for a subset of five plants per plot and species by counting fruits per plant and seeds per fruit. Since seed production was significantly correlated with biomass, seed production of further plants was calculated based on the species-specific mean seed number per biomass. Furthermore, phenological development was measured in the greenhouse experiment on regional differentiation (Publication 1). For this purpose, a phenological index was calculated based on the proportion of reproductive units (flower buds, closed, open, immature and mature fruits) present on a plant.

Establishment of rare arable plants

To evaluate establishment of rare arable plants in the field experiments of this thesis, plant densities, seed production per area and soil seed banks were measured. Plant densities were sampled by counting all plants per sown row (transplant experiment in Publication 1) or per 1-m^2 sample unit randomly placed four times within sown plots (Publications 2, 3; Fig. 5E). Seed production per area was calculated by multiplying the number of reproductive plants with seed production per individual (see above). Seed production per area divided by the initially sown seeds per area was further used to calculate overall population growth rates of the rare arable plants at the end of the plot trial study period. Soil seed banks were sampled on all plots of the on-farm experiment three years after sowing the study species (Publication 3). Soil cores were used to collect 2.5 kg soil per plot up to the depth of the plough layer. The fresh soil was immediately transferred to the greenhouse where each sample was distributed among six fleeced trays (30 cm × 40 cm). Over the next 14 months, emerging seedlings of the target species were recorded and seedlings of all species were removed on a regular basis (Fig. 5F). The seed bank density of target species was calculated as number of germinated seedlings per species and tray divided by fresh soil mass (kg) * dry weight content (%) * bulk density (g/cm^3) * ploughing depth (cm) * 0.1.

Seed dispersal

Seed dispersal along the main direction of agricultural management was determined in the on-farm experiments (Publication 3). Sampling took place in autumn of year 3 after winter cereals (spelt or rye) were sown on all study fields. Seedlings of the study species were counted on 1-

m² sample units placed every 2 m along the machining direction up to 16 m adjacent to the sown plots.

Recording crop and weed cover

In addition to the study species' establishment, crop and weed cover were recorded in each sampling unit of the plot trial experiment (Publication 2). This was done by visual estimation in autumn, spring and summer of each year. Mean values were used for further analysis.

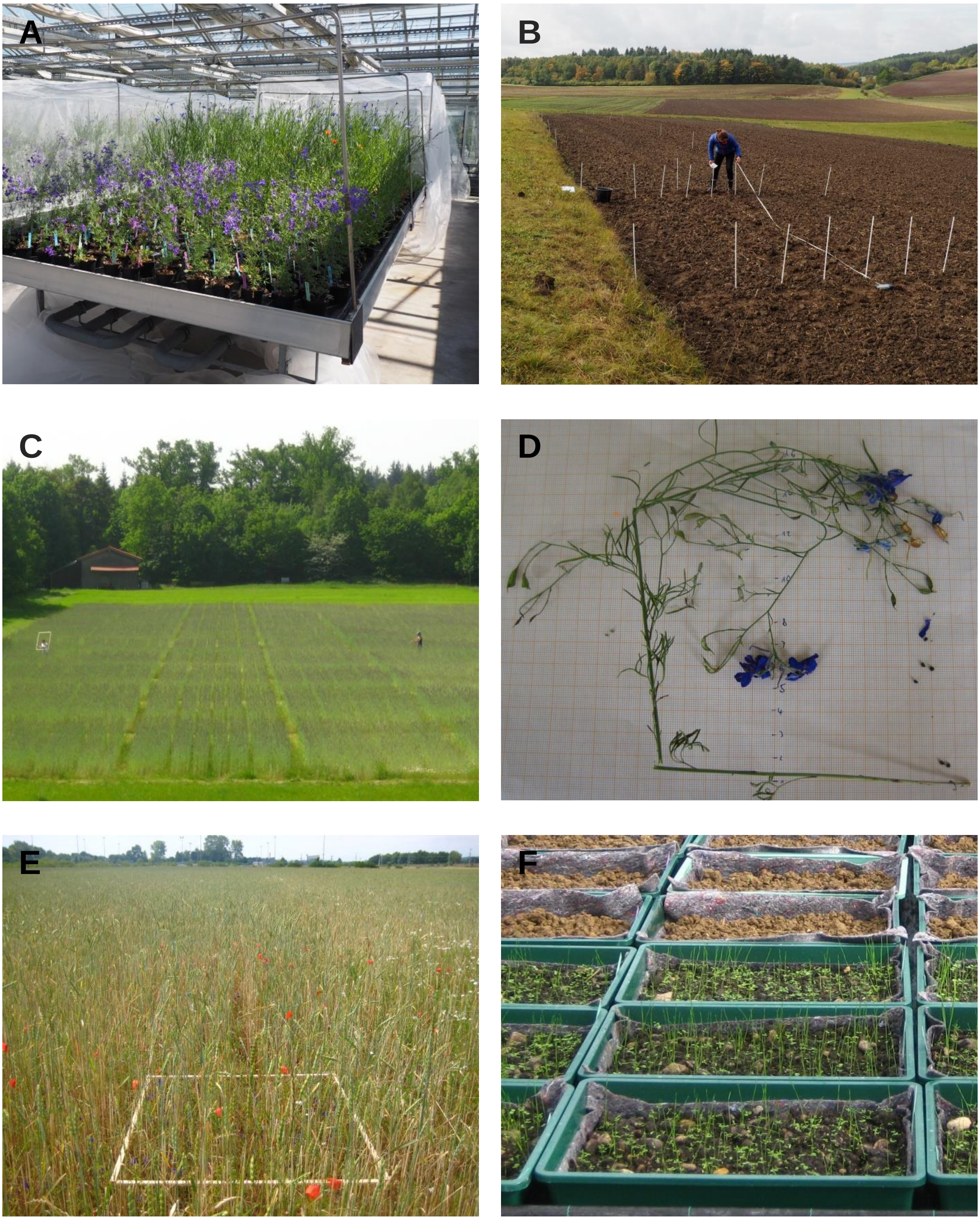


Fig. 5: Field and greenhouse experiments with data sampling.
Publication 1: (A) Greenhouse study on regional differentiation and (B) sowing seeds on a transplant site in the field. Publication 2: (C) Plot trials on the experimental farm in Gräfelfing and (D) harvesting biomass of *Consolida regalis*. Publication 3: (E) Monitoring of plant density on 1-m² plots and (F) soil seed bank samples in the greenhouse.

Statistical analyses

For conduction of the statistical analyses, R Versions 3.0.2 and 3.5.1. were used (R Core Team, 2018). Depending on the data, analyses of variance (ANOVA) or linear mixed effects models were used (Pinheiro and Bates, 2000). Response variables were establishment (seed production), performance (biomass or phenology) or population growth rates of the rare arable plants. Explanatory variables included fixed factors (e.g. source population and drought stress), interactions between these factors and random factors (e.g. replicate). In several cases, data were transformed (log10 or square-root), different variance structures were used or some outliers were removed to achieve normal distribution and avoid heteroscedasticity (Zuur et al., 2009). Full models were simplified using an automatic backward stepwise selection procedure by AIC (Akaike's Information Criterion; Venables and Ripley, 2002). For comparison between test groups post-hoc tests, e.g. the Kruskal-Wallis test, were used at the 0.05 level of significance.

SUMMARY OF PUBLICATIONS

Publication 1: Low levels of regional differentiation and little evidence for local adaptation in rare arable plants

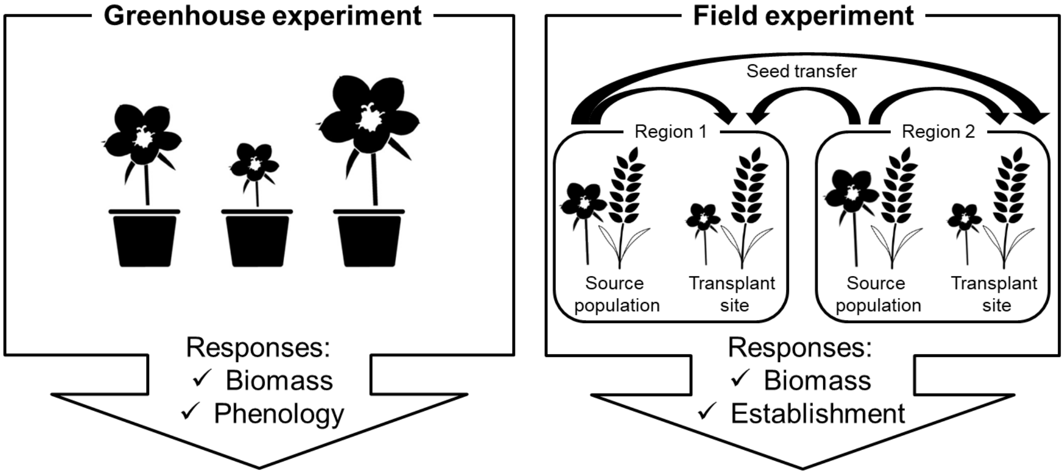
Publication

Lang, M., Albrecht, H., Rudolph, M., & Kollmann, J. (2021) Low levels of regional differentiation and little evidence for local adaptation in rare arable plants. *Basic and Applied Ecology* 54: 52–63.

Author contributions

Harald Albrecht (HA) and Johannes Kollmann (JK) initiated the research project; Marion Lang **(ML)** designed the experiments, supervised by HA and JK; **ML** collected and analysed the data; **ML** wrote and all co-authors contributed to the manuscript.

Graphical abstract



- **Low regional differentiation** within the study area
- Provenance-specific responses to **drought stress** in *Legousia speculum-veneris* and *Arnoseris minima*

- **Little evidence for local adaptation** to northern and southern regions within seed zones
- High **phenotypic plasticity** in response to study year and transplant site

Fig. 6: Graphical abstract of Publication 1 showing regional differentiation and local adaptation of rare arable plants in South Germany.
Regional differentiation was measured with or without drought stress in greenhouse experiments with different seed provenances of five study species. Local adaptation to the northern or southern regions within seed zones was tested in reciprocal transplant experiments in the field for three study species.

Summary

The selection of seed material is an essential part of restoration measures and requires understanding of regional differentiation and local adaptation of target species. So far, mainly grassland and tree species have been investigated in genetic studies and reciprocal transplant experiments. Seed transfer zones and official sourcing strategies are available for those species but not for rare arable plants, which play an essential role in restoration of arable fields. Active restoration, including translocation measures, are necessary to avoid the loss of these species and their respective ecosystem functions. Intensified droughts in the course of climate change might become another problem, at least for some populations and species. Publication 1 combines greenhouse and field experiments to test intraspecific phenotypic variation and local adaptation of rare arable plants in South Germany (Fig. 6).

Seeds from five representative species of the threatened segetal flora were collected from 4–12 source populations spread across four seed transfer zones. In the first year of the greenhouse experiment, F1 generations of all study species were grown under standard conditions to reduce maternal effects. In the second year, F2 generations were tested for genetically-based differentiation in biomass production and phenology either with or without drought stress. Differences among source populations varied among species and were overall low. Drought stress reduced the biomass of *Consolida regalis* and *Cyanus segetum*, whereas provenance-specific responses were found for biomass of *Legousia speculum-veneris* and phenology of *Arnoseris minima.* While those fitness differences may be affected by genetic drift or inbreeding, reciprocal transplant experiments can provide more reliable results on local adaptation.

Corresponding field experiments were set up for three species, i.e. *A. minima, C. regalis* and *Teesdalia nudicaulis*, and repeated for two years. Thus, local adaptation to the northern or southern regions of three seed transfer zones was tested for the establishment and biomass production of plants grown in *sympatry* (i.e. *local*) or *allopatry* (i.e. *non-local*). There was no significant difference between seed provenances in 76% of the cases consisting of three species, two years and 19 transplant sites. However, in 14% of the cases local adaptation and in 10% maladaptation were found. Furthermore, there were significant differences in plant performance among transplant sites and study years indicating high phenotypic variability.

Based on these results a *regional admixture provenancing* seed-sourcing strategy within seed zones is suggested for the reintroduction of the investigated study species and regions. This provides both high genetic diversity which is needed to face environmental change and a low risk of maladaptation. Further research is needed to find optimal seed-sourcing strategies for other regions and arable plant species, especially in the case of very specialized, highly endangered species.

Publication 2: Reintroduction of rare arable plants in extensively managed fields: Effects of crop type, sowing density and soil tillage

Publication

Lang, M., Kollmann, J., Prestele, J., Wiesinger, K., & Albrecht, H. (2021) Reintroduction of rare arable plants in extensively managed fields: effects of crop type, sowing density, and soil tillage. *Agriculture, Ecosystems & Environment* 306: 107–187.

Author contributions

Harald Albrecht (HA), Johannes Kollmann (JK), Julia Prestele (JP) and Klaus Wiesinger (KW) designed the research; Marion Lang **(ML)**, JP performed the experiments; **ML** analysed the data and wrote the manuscript; HA and JK corrected the manuscript.

Graphical abstract

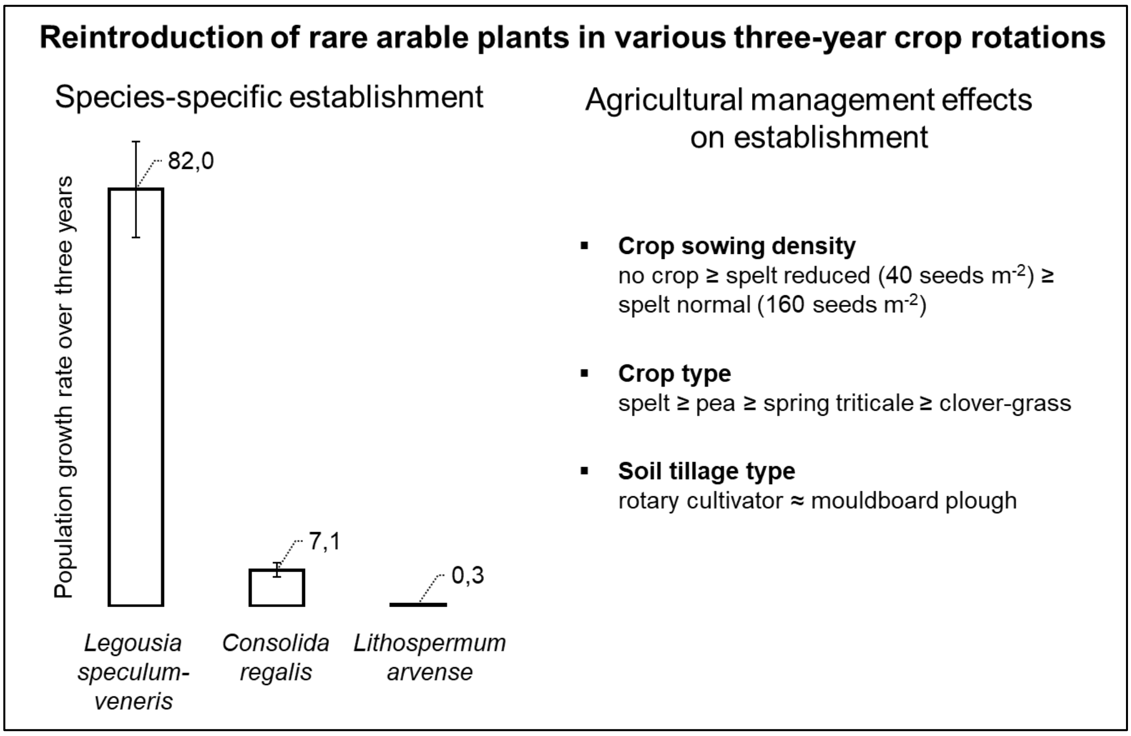


Fig. 7: Graphical abstract of Publication 2 showing results for the reintroduction of rare arable plants in various three-year crop rotations.
Results were obtained in a plot trial containing different crop densities, crop types and soil tillage types. Population growth rates were calculated as seed production per area at the end of the study period divided by the initially sown seeds per area.

Summary

In addition to preserving remnant populations, the introduction of autochthonous seeds in extensively managed fields is a promising measure to promote rare arable plants and to restore agroecosystems. However, knowledge about suitable establishment conditions and agricultural management for sown species is scarce. Publication 2 investigates the establishment of three winter annuals (*Legousia speculum-veneris*, *Consolida regalis*, *Lithospermum arvense*) in various three-year crop rotation systems (Fig. 7).

A completely randomized block design with 14 management treatments, each replicated five times, was established on an organic farm near Munich, Germany. Arable plants were sown in a mixture of 850 seeds m^{-2}. Three experimental blocks were set up to study the arable plants' seed production depending on (i) crop sowing density in year 1 (no crop, spelt in reduced or normal sowing density), (ii) crop type in year 2 (autumn-sown spelt, spring-sown triticale, pea, clover-grass) and (iii) soil tillage before year 2 (rotary cultivator, mouldboard plough). To ensure comparability, rye was cultivated on all plots in year 3. At the end of the study period population growth rates of the study species were calculated by dividing their seed production per area by the initially sown seeds per area.

Across all treatments, the populations of *L. speculum-veneris* and *C. regalis* increased strongly, whereas *L. arvense* decreased. High cover of crops and weeds negatively affected population growth, while no effect of soil tillage was observed. Focusing on the single management effects revealed a significant effect of initial crop sowing densities on first-year establishment of the study species (no crop ≥ spelt reduced ≥ spelt normal sowing density). In case of *L. speculum-veneris* and *C. regalis*, this effect persisted up to year 2 and 3, respectively. Moreover, establishment of the study species was significantly affected by the crop type in year 2. All species failed to establish in clover-grass and achieved highest reproduction in spelt. Responses to pea and spring triticale were species-specific. However, establishment was overall high in year 3 when all plots were cultivated with rye. The type of soil tillage had no effect within the crop rotation ‘rye–clover-grass–rye’, while rotary cultivation in ‘without-crop–rye–rye’ was positive for the establishment of *L. speculum-veneris* and *L. arvense*.

The results indicate that reintroduction of rare arable plants can be successful under various crop rotations with best results for fields with low crop competition, which should be maintained especially in the sowing year.

Publication 3: Reintroduction of rare arable plants: seed production, soil seed banks and dispersal 3 years after sowing

Publication

Lang, M., Prestele, J., Wiesinger, K., Kollmann, J., & Albrecht, H. (2018) Reintroduction of rare arable plants: seed production, soil seed banks, and dispersal 3 years after sowing. *Restoration Ecology* 26: 170–178.

Author contributions

Harald Albrecht (HA), Johannes Kollmann (JK), Julia Prestele (JP) and Klaus Wiesinger (KW) designed the research; Marion Lang **(ML)**, JP and HA performed the experiments; **ML** analysed the data; **ML** wrote the manuscript; all authors edited the manuscript.

Graphical abstract

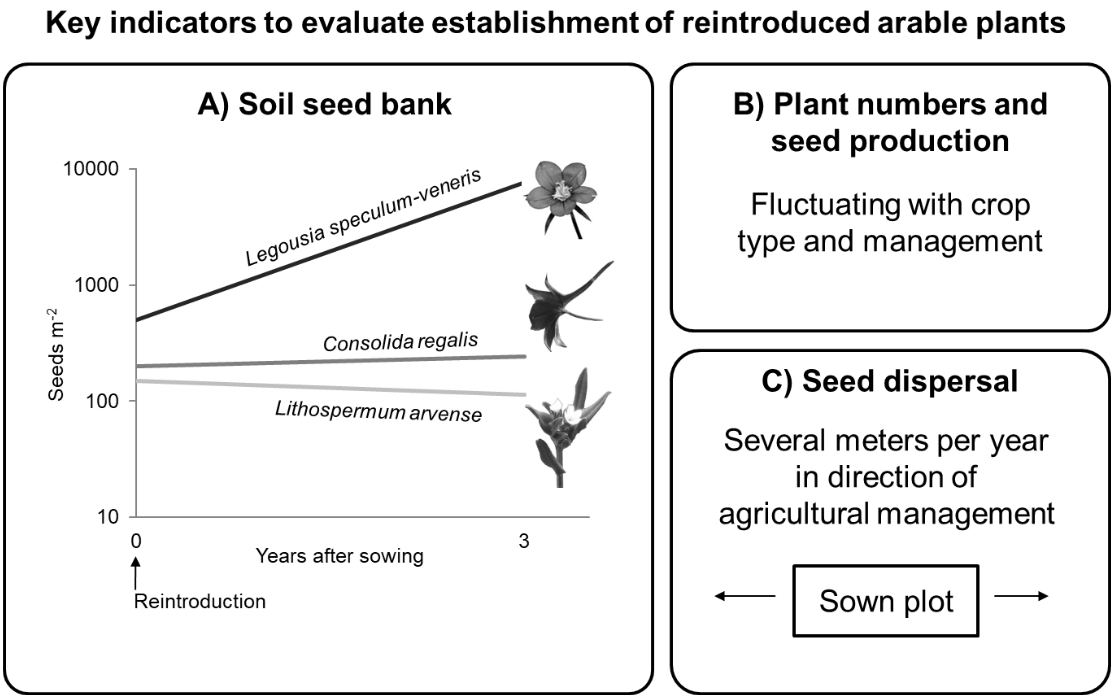


Fig. 8: Graphical abstract of Publication 3 showing key indicators to monitor and evaluate establishment of sown rare arable plant species.
Results for the establishment of three target species under practical farm conditions are shown for a study period of three years by reporting their soil seed banks (A), plant numbers and seed production (B), as well as seed dispersal along the machining direction (C).

Summary

Publication 3 tests the reintroduction of rare arable plants under real-farm conditions (Fig. 8). The same species as in Publication 2 (*Legousia speculum-veneris, Consolida regalis, Lithospermum arvense*) were sown at 850 seeds m^{-2} on four organic farms near Munich, Germany. Establishment of the study species was determined by their seed production and soil seed bank on four 25 m²-plots within each field and monitored over three years. In addition, seed dispersal caused by arable management was evaluated along the main machining direction. Farmers applied standard management practices, but were obligated to cultivate winter cereals without mechanical weed control and fertilization in the first two years.

This enabled the study species to emerge at all sites with a seed production mostly exceeding the initial sowing rates. In the following crop rotations, plant numbers and seed production were overall high in autumn-sown cereals, low in spring-sown oat (except *L. speculum-veneris*) and almost zero in soybean. Best results were obtained without mechanical weed control. Three years after sowing, establishment varied among species and farms with highest seed production (mean ± SE) in *L. speculum-veneris* (7,048 ± 840 seeds m^{-2}), followed by *C. regalis* (840 ± 174 seeds m^{-2}) and *L. arvense* (178 ± 36 seeds m^{-2}). While *L. speculum-veneris* became very common in the seed bank on all farms, *C. regalis* was less abundant and *L. arvense* hardly developed soil seed banks. Seedlings of *L. speculum-veneris* and *L. arvense* were found up to 15 m and seedlings of *C. regalis* up to 13 m away from the sown plots along the machining direction. The proportion of plants outside to inside the initially sown plots was approximately one third.

Publication 3 highlights the practicability of successfully reintroducing rare arable plants on extensively managed organic farms. Species lacking a long-term seed bank depend on suitable crop rotations that allow regular seed production each year. Since above-ground populations can fluctuate according to agricultural management, the evaluation of seed banks provides important additional information for monitoring restoration success. As seed dispersal by management is only a few meters per year, seeds should be sown on larger parts of the reintroduction field. For the monitoring of population sizes also the area adjacent to the sown plots must be considered.

DISCUSSION

Factors that determine the establishment of rare arable plants

In plant reintroductions a complex interaction of abiotic and biotic factors determines the establishment of target species (Godefroid et al., 2011; van Wieren, 2012). It is often difficult to disentangle the effects of single factors which requires appropriate study approaches. The controlled greenhouse and field experiments in Publication 1 allowed to identify the effect of seed provenance on performance and establishment of rare arable plants. Further, Publication 2 analysed agricultural management effects, with varying results for crop type, crop density and soil tillage type. In Publication 3, which was performed at different agricultural field sites, some of these results were confirmed and new insights were gathered. Additional factors in terms of seed material, sowing techniques, agricultural management and site conditions, that may influence the establishment, are reviewed based on the available literature and their relevance is discussed with respect to the three publications of this thesis (Fig. 9). Moreover, the transferability of results to other target species is evaluated.

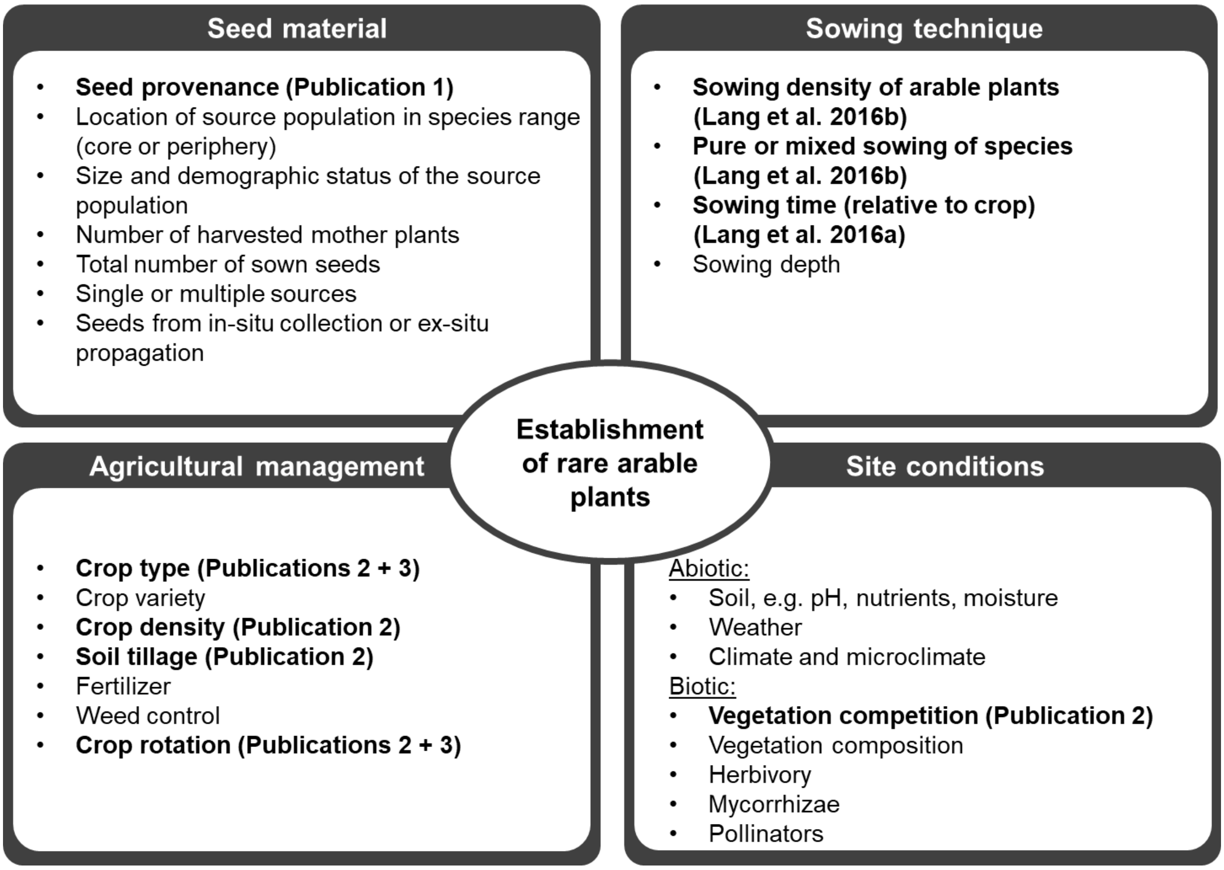


Fig. 9: Factors that influence the establishment of sown rare arable plants: Seed material, sowing technique, agricultural management and site conditions.
Factors addressed in Publications 1–3 and further publications by the author of this thesis are highlighted in bold letters.

Seed material

Seed provenance is considered as a main factor determining establishment of introduced plant species (Bischoff et al., 2006; Vander Mijnsbrugge et al., 2010; Godefroid et al., 2011). This is mainly based on the fact that plant populations are usually differentiated and locally adapted, although it is often unclear at which spatial scale (Leimu and Fischer, 2008). Publication 1 gathered important basic knowledge by examining the regional differentiation and local adaptation of five rare arable plant species in South Germany. Overall, there was low genetically-based differentiation measured in biomass and phenology among the different source populations within the study area. Reciprocal transplant experiments in the field revealed low local adaptation to the northern or southern regions within the seed zones (Publication 1). In contrast, establishment and performance of rare arable plants varied significantly among transplant sites and study years.

Possible explanations for these results are (i) a lack of divergent selection between source sites, e.g. due to small environmental and geographic distances within the study area, (ii) high gene flow between populations, e.g. due to frequent seed dispersal by traditional farming systems in the past (Poschlod and Bonn, 1998; Kawecki and Ebert, 2004) and (iii) soil seed banks acting as buffer (Tellier, 2019). This is in line with Meyer et al. (2015b) who found low levels of genetic structure for *Adonis aestivalis* and *Consolida regalis* in several regions throughout Central Germany. Additionally, variation between transplant sites and study years can mainly be attributed to high phenotypic plasticity (Baker, 1965; Galloway and Fenster, 2000).

Furthermore, Publication 1 discovered an overall negative effect of drought stress on the fitness of rare arable plants. This enhanced population differentiation in *Legousia speculum-veneris* biomass and *A. minima* phenology. Such adaptation to drought stress of specific populations may be attributed to climate or soil conditions at their source sites. Climate change, including enhanced drought periods and more frequent heat waves, is predicted to play an increasingly important role for rare arable plants (Peters and Gerowitt, 2014; Rühl et al., 2016). This may change the importance of seed provenances in future reintroductions. Besides, the length of time that arable plant populations are isolated (due to habitat fragmentation as well as lack of seed and pollen exchange) is increasing and could reinforce local adaptation in future (Kawecki and Ebert, 2004). However, in very small, genetically impoverished populations, adaptability might also be reduced, which in the worst case can lead to extinction.

In general, genetic and phenotypic differentiation can vary among species (e.g. depending on breeding system or current and historic distribution; McKay et al., 2005), among landscapes (e.g. degree of fragmentation; Meyer et al., 2015b) and at various spatial scales (e.g. few meters or thousands of kilometers; Linhart and Grant, 1996). For example, Brütting et al.

(2012b) demonstrated that genetic differentiation of arable plants is related to their Red List status. Thus, further studies, especially on highly endangered species, are necessary to evaluate the effect of seed provenance on establishment.

Beside seed provenance, there are further aspects of seed material that can affect the establishment of introduced plants (Fig. 9). All of them influence the genetic diversity of founder populations and thus reintroduction success. One aspect is the location of a source population at the core or periphery of the species' geographical range (Eckert et al., 2008). Other aspects are the size and demographic status of the source population. In this context, small and declining populations are at risk of inbreeding and genetic impoverishment (Brütting et al., 2012b). Seeds for the experiments of this thesis were harvested from populations with at least 100 individuals. For estimation of the actual population size, it must be considered that only 1–10% of the seed bank density is reflected by seedling emergence (Roberts and Ricketts, 1979; Albrecht and Pilgram, 1997). Moreover, above-ground populations of arable plants are fluctuating and total population sizes are difficult to assess from one-year observations. Thus, different population sizes may have contributed to population differences in Publication 1. Moreover, the genetic diversity of seed material, e.g. by harvesting seeds from various numbers of mother plants, can affect establishment and fitness-related traits (Bischoff et al., 2010). Usually, the reintroduction success of a species increases in correlation to the initial number of sown seeds, due to reduced genetic bottlenecks and enhanced adaptive potential (Leimu et al., 2006; Armstrong and Seddon, 2008; Albrecht and Maschinski, 2012).

In their review, Godefroid et al. (2011) identified the mixing of diverse populations as the most important factor explaining variation in reintroduction success. This is in line with the *regional admixture provenancing* strategy, suggested by Bucharova et al. (2019). However, there are also studies that have proven negative hybridization effects when mixing source populations (Hufford and Mazer, 2003). For example, a negative outbreeding effect in fitness was found when mixing several European populations of the arable plant species *Papaver rhoeas* and *Agrostemma githago* (Keller et al., 2000). A further aspect that can affect establishment, is the origin of seed material either from *ex-situ* cultivations or from *in-situ* collections. *Ex-situ* cultivations bear the risk of selection effects and the loss of adaptations to *in-situ* conditions, especially in case of subsequent cultivation of several generations (Brütting et al., 2013; Nagel et al., 2019). All the above-mentioned factors concerning seed material were mainly studied in reference to species that are commonly used for restoration activities, e.g. seed mixtures for mesophilic grassland. Respectively, basic knowledge on the restoration of species-rich arable fields is missing.

Sowing technique

The establishment of sown arable plant species can also be determined by the sowing technique (Fig. 9). Experiments on the effect of sowing rate of *L. speculum-veneris*, *C. regalis* and *L. arvense* were performed by Lang et al. (2016b) at the same study site as Publication 2. Best results were achieved at sowing rates of 50–100 seeds m^{-2} per species. Lower sowing rates led to poor establishment, while higher sowing rates caused negative density effects due to intraspecific competition. Accordingly, the total sowing rate of 850 seeds m^{-2} in Publications 2 and 3 was relatively high. Sowing the three study species individually or in mixture did not affect their establishment (Lang et al., 2016b). However, this might become more relevant when far more than three species are sown with very similar niches (Young et al., 2005; Schöb et al., 2017). Moreover, sowing time can be decisive for the ability of rare arable plants to germinate and to establish (Wilson, 1990). Relative sowing time between arable plants and autumn-sown rye was tested in a study by Lang et al. (2016a) for five different sowing dates of the three study species mentioned above. With increasing time between sowing arable plants relative to the crop, establishment decreased significantly, which indicates priority effects.

In the field experiments of Publications 1–3, this time span was kept as short as possible by sowing arable plants maximal one week later than the crop. A further aspect that was controlled in this thesis was the sowing depth of the arable plants, as this can also influence reintroduction success. However, the effect of sowing depth depends on the specific germination requirements of each target species. As the majority of arable plant species are light germinators, seeds were placed on the soil surface for all experiments in this thesis. Nevertheless, there are some species that germinate better in darkness as demonstrated by Torra et al. (2016) for three Papaveraceae species.

Agricultural management

On arable land, agricultural management is probably the most important variable affecting arable plant establishment and long-term persistence (Walker et al., 2007). The main mechanisms that shape the effect of different management factors are competition, e.g. through cover or allelopathy, and disturbance regimes, e.g. the timing of soil tillage, seed bed preparation, sowing and harvest of the crop.

In the field plot trial of Publication 2, agricultural management in the sowing year significantly affected the establishment of rare arable plants, which was still observable in the following years. Best results were obtained by sowing the species without crop or at reduced sowing density of spelt. Positive effects of low crop sowing densities were also shown in other studies, which can be explained by increased light availability (e.g. Kleijn and Voort, 1997). However, arable plants can even be facilitated by the presence of a crop, e.g. through provision of a suitable microhabitat (Brooker et al., 2017) or through suppression of competitive weeds (Epperlein et al., 2014).

One of the most important factors that affects the vegetation on arable fields is the crop type (Lüscher et al., 2014; Rotchés-Ribalta et al., 2015a). This is in accordance with a high impact of crop type on above-ground populations of the target species observed in Publications 2 and 3. The different effects of crop types can be caused by coverage (e.g. gap detection mechanism; Thompson et al., 1977) or most importantly by the timing of the last soil cultivation (Leuschner and Ellenberg, 2017). Consequently, the winter annual study species benefited most from autumn-sown cereals, which provided good germination as well as suitable growth conditions. Moreover, Publications 2 and 3 demonstrated that unfavourable crops can be survived to some extent in the soil seed bank. While *L. speculum-veneris* and *C. regalis* were able to establish a seed bank in the on-farm experiment of Publication 3, this was not the case for *L. arvense*. The density of soil seed banks depends on various factors, e.g. soil properties, land-use system and species-specific traits (Albrecht and Forster, 1996; Leuschner and Ellenberg, 2017). In general, large seed banks are crucial for the survival of arable plants in agricultural fields with fluctuating habitat conditions. Unsuitable field conditions can be especially problematic for species without persistent seed banks, e.g. *Agrostemma githago* (Saatkamp et al., 2009).

In contrast to crop type and density, the type of soil cultivation was less important for the reintroduction success (Publication 2). There was no effect within the crop rotation 'rye–clover-grass–rye', while rotary cultivation in 'without-crop–rye–rye' was positive for the establishment of *L. speculum-veneris* and *L. arvense* in comparison to ploughing. The effect of soil cultivation depends on the burial depth of arable plant seeds, which determines their survival and emergence. The burial depth can vary depending on the machine, its working depth, soil structure and the seed traits of species. In general, regular soil cultivation is essential for rare arable plants in comparison to no-till treatments, as demonstrated for the emergence of 30 rare arable plant species in a field study by Torra et al. (2018).

In this thesis, the effects of agricultural management on establishment of rare arable plants were obtained for three threatened winter annuals. A large proportion of threatened arable plants are winter annuals of cereal fields, thus, results of Publications 2 and 3 could be representative for other species of conservation interest, too. However, there are rare arable species which germinate mainly in spring and would show different results to the management factors tested in this thesis. Moreover, there are some species that require special management, e.g. late flowering species of stubble fields like *Stachys annua*.

Further factors of agricultural management that can influence the performance of rare arable plants which were not covered by the thesis are crop variety (Brooker et al., 2017), fertilisation (Rotchés-Ribalta et al., 2016) and weed control, e.g. through mechanical disturbance or herbicides (Rotchés-Ribalta et al., 2015b) (reviewed in Albrecht et al., 2016; Fig. 9).

Site conditions

The strong variability of establishment and biomass production among study sites and years of Publication 1 and study sites of Publication 3 demonstrated that site conditions including abiotic and biotic factors are important for the establishment of rare arable plants. However, the study design of these experiments did not allow to disentangle the effects of single factors (Fig. 9). The importance of environmental variables compared to management variables on the composition of arable plant vegetation was studied by Pinke et al. (2012). They found that "temperature, crop type, precipitation, soil texture, altitude, soil pH, sodium and potassium content of the soil" explained most of the species composition on Hungarian arable fields. Albrecht and Auerswald (2003) investigated the soil seed bank of arable fields and its relationship to edaphic factors at different spatial scales in Bavaria. At the transregional scale, seed bank composition showed a close relationship to soil chemical factors. However, this might have been enhanced by differences in management, e.g. crop rotation, which is usually adapted to site conditions. Nevertheless, soil physics such as grain size can hardly be homogenised by management and therefore affect the arable vegetation, especially on a small scale (Albrecht and Auerswald, 2003). However, there is a lack of knowledge on how important abiotic site factors are for rare arable plant reintroductions. Generally, climate, microclimate, safe sites and year effects, such as seasonality of rain fall, can affect the establishment of plants (Young et al., 2005).

Among biotic site effects, vegetation competition obviously plays a major role for reintroduction success. Publication 2 showed that increasing competition by crops and weeds significantly reduced population growth rates of the study species in various three-year crop rotations. Competition by crops is mainly based on crop type, variety and density (see section 'Agricultural management' in the discussion). Competition by weeds is strongly field-specific and varies with vegetation density and composition (Bäumler, 2019). For example, Armengot et al. (2017) showed that grass infestations hamper the reintroduction success of *Agrostemma githago* and *Vaccaria hispanica* in wheat fields. Sauter (2019) investigated the impact of competition and soil parameters on the performance of *Arnoseris minima.* He found that on less productive sites resource limitation plays an important role, while competition can severely reduce the target species fitness on highly productive sites. Further, he discovered that the importance of root competition compared to shoot competition increases with rising site productivity. Introduction sites of Publication 1, 2 and 3 were rather poor soils, mainly without (grass) weed infestation problems which contributed to the overall high establishment. Further biotic effects can enhance or limit arable plant population development, but were not addressed in this thesis, e.g. herbivory/seed predation (Fischer and Türke, 2016) or interactions with mycorrhizae (Rinaudo et al., 2010) or pollinators (Gibson et al., 2006).

Practical recommendations

Workflow for the reintroduction of rare arable plants

The practical implementation of reintroduction measures requires several working steps (Fig. 10), which are in the following specified for arable plants based on Kaye (2008) and the guidelines by IUCN/SSC (2013).

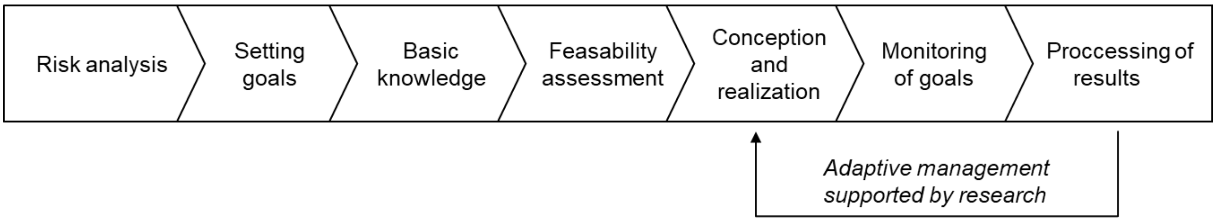


Fig. 10: Conceptional workflow for the practical implementation of plant reintroductions. Figure modified after IUCN/SSC (2013).

Prior to carrying out reintroductions, its benefits should be weighed against its costs and possible ***risks***. Risks may be the impairment of source populations by seed collection, invasive spread at the introduction site, effects on other species and on ecosystem functions or hybridization between introduced and resident individuals with potential outbreeding depression. These risks can be minimized by harvesting <20% of the total mature seeds available from arable plant populations (European Native Seed Conservation network, 2009) and selecting low-competitive species with native or archaeophytic status. The risk of outbreeding depression is still poorly understood (Keller et al., 2000; Vander Mijnsbrugge et al., 2010; Frankham et al., 2011). It can be avoided by transferring arable plants only to sites without resident populations, which requires preceding vegetation or soil sampling (Kurtz and Heinken, 2011). Further, negative hybridization effects can be reduced by using autochthonous seed material (Frankham et al., 2011).

Above all, the clear definition of restoration ***goals*** is required. This may be the long-term establishment of one or several viable populations. It may also be the provision of spatial and temporal specific ecosystem services, such as the aesthetic enhancement of rural areas or the promotion of pollination.

Furthermore, ***basic knowledge*** about the biology of the target species (e.g. breeding system, germination time), causes of its threat, and its habitat and climate requirements (e.g. specialisation on soil pH or moisture) need to be gathered.

The ***feasibility assessment*** includes the search for appropriate source populations and introduction sites with testing their availability. In terms of social feasibility, the compatibility with human interests and existing conservation plans or activities must be reviewed. For the reintroduction of rare arable plants this means for example the agreement with farmers and the exclusion of high-competitive species that could significantly reduce crop yields. Permissions, such as soil tillage of long-term fallows as well as the collection and release of threatened species are also relevant. Furthermore, financing and long-term maintenance of the restoration measure should be ensured (Kollmann et al., 2019).

There are several factors that need to be considered for the ***conception and realization*** of a reintroduction measure. First, the selection of target species depending on the goals is crucial. For Germany, a list of characteristic arable plant species is given by Albrecht (2003) and can be used as a basis for the species selection. Furthermore, a checklist for the segetal flora is currently developed, including the category “target species for reintroduction” (S. Meyer, personal communication, December 20, 2020). Source populations should be selected under consideration of genetic aspects (see recommendations further down based on results of Publication 1). Another factor is the translocation method, which should be chosen context dependent and may vary with the availability of source sites, restoration targets, time and costs of a project (Vander Mijnsbrugge et al., 2010; Kollmann et al., 2019). Moreover, the introduction must be performed in an adequate season and into an appropriately prepared site that meets biotic and abiotic requirements of the target species. In this context, rare arable plants must be sown in a seed bed of bare soil. Suitable sowing time depends on the target species, autumn should be preferred since most rare arable plants are winter annuals (Lang et al., 2016a; Torra et al., 2020). A further important factor for the reintroduction conception is the management, which requires particular attention for rare arable plants, as it must be integrated into agricultural processes (see recommendations further down based on results of Publication 2).

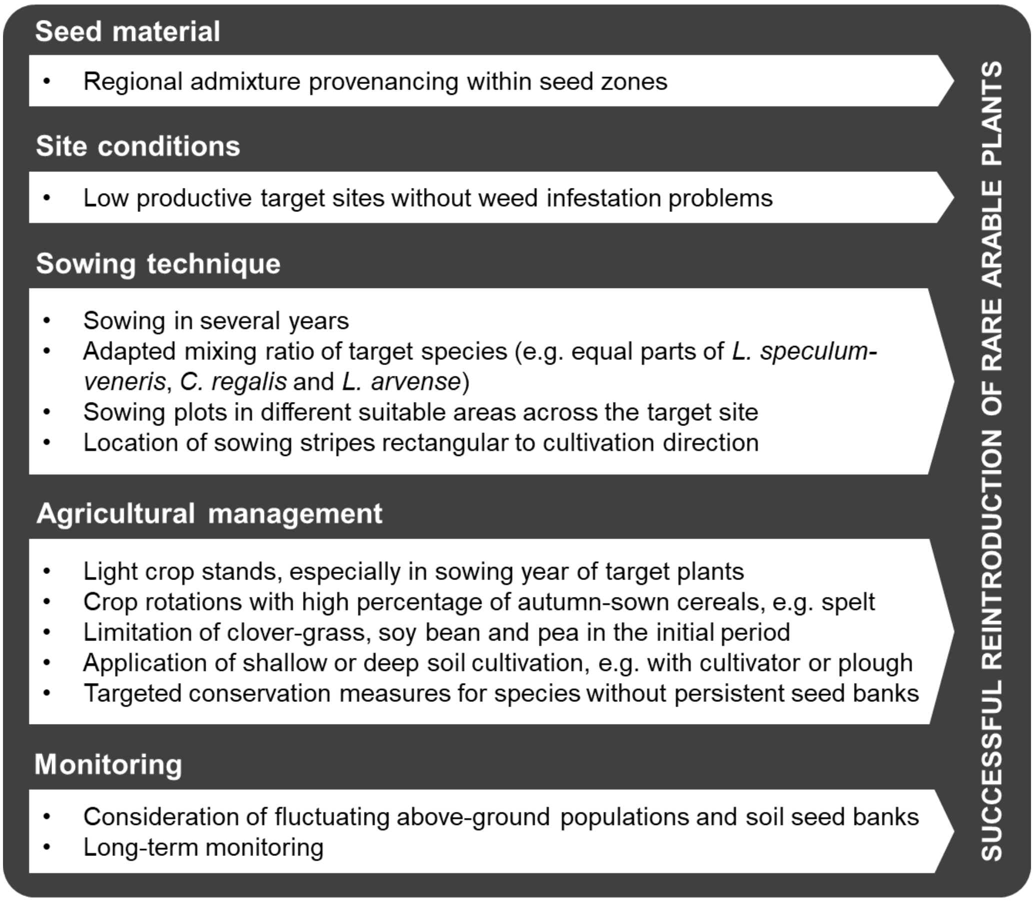
After the realization of the reintroduction, appropriate ***monitoring*** is necessary to assess the achievement of objectives, e.g. by recording demographic or ecological parameters (see recommendations further down based on results of Publication 3). Also, social and economic impact, such as the perception of the farmer and local community should be evaluated. Cooperation with farmers is particularly important in the conservation of arable plants.

Finally, the assessed ***results*** need to be documented, interpreted and communicated via research or practical platforms, regardless of success or failure. Translating research results into practice recommendations is of special importance.

Adaptive management is desired and allows to adjust agricultural management or to repeat reintroduction, ideally factoring in new research findings. Since arable fields are often highly degraded and unexpected environmental changes may occur in future, Hermann and Kollmann (2015) recommend *adaptive restoration*. In this approach, different management and restoration methods are systematically tested to subsequently optimise the development of an ecosystem. The optimum would be an ongoing cooperation between scientists, restoration practitioners and farmers.

Recommendations on selection of seed material, site conditions, sowing techniques and agricultural management

Recommendations on seed material, site conditions, sowing techniques, agricultural management and monitoring are given based on the main results of Publications 1–3 (Fig. 11).



Seed material

- Regional admixture provenancing within seed zones

Site conditions

- Low productive target sites without weed infestation problems

Sowing technique

- Sowing in several years
- Adapted mixing ratio of target species (e.g. equal parts of *L. speculum-veneris*, *C. regalis* and *L. arvense*)
- Sowing plots in different suitable areas across the target site
- Location of sowing stripes rectangular to cultivation direction

Agricultural management

- Light crop stands, especially in sowing year of target plants
- Crop rotations with high percentage of autumn-sown cereals, e.g. spelt
- Limitation of clover-grass, soy bean and pea in the initial period
- Application of shallow or deep soil cultivation, e.g. with cultivator or plough
- Targeted conservation measures for species without persistent seed banks

Monitoring

- Consideration of fluctuating above-ground populations and soil seed banks
- Long-term monitoring

SUCCESSFUL REINTRODUCTION OF RARE ARABLE PLANTS

Fig. 11: Practical recommendations on seed material, site conditions, sowing technique, agricultural management and monitoring for the successful reintroduction of rare arable plants based on the main results of Publications 1–3.

Publication 1 revealed low population differentiation but provenance-specific responses to drought. Thus, the *regional admixture provenancing* strategy proposed by Bucharova et al. (2019) seems to be the best suited seed-sourcing strategy to be applied in the study area. This involves collecting and mixing multiple source populations in a given region to provide a high level of genetic diversity and adaptive potential while at the same time considering local adaptation and evolutionary fit (Bucharova et al., 2019). However, further studies, especially on highly endangered species, are necessary to state profound recommendations on seed sourcing for other species and regions.

High variability of establishment among sites in Publications 1 and 3 demonstrated the importance of appropriate site conditions for the reintroduction success. Site conditions should be optimised under consideration of species-specific requirements. Usually arable fields with low yield potential, e.g. measurable by the field fertility index, are most suitable for the reintroduction of rare arable plants. The vegetation including the degree of weed infestation should be assessed before the reintroduction.

Since establishment was strongly species-specific in Publications 2 and 3, with very high values for *L. speculum-veneris* and low values for *L. arvense*, sowing density should be adapted. Instead of sowing a 10:4:3 mixture of *L. speculum-veneris*, *C. regalis* and *L. arvense,* equal amounts of each species, e.g. 200 seeds m^{-2}, are conceivable. In general, it must be ensured that a sufficient total number of seeds is sown to avoid undesirable founder effects (Albrecht and Maschinski, 2012). If seed availability is limited in a reintroduction project, it is recommended to spread the risk of losses and to distribute the sowing over several fields and dates. Furthermore, seeds should be applied to multiple suitable areas within an introduction field, preferable rectangular to the machining direction. This enhances the chance of matching appropriate microsites and increases dispersal processes within the field (Publication 3).

Regarding management, it is advisable to create optimal conditions at the beginning of a reintroduction project to maximise population growth and to build up a viable seed bank (Publication 2). Best results were obtained in Publication 2 by sowing rare arable plants without crop or with cereals in reduced sowing density. However, sowing without crop is only recommended on sites with low nutrient availability, as otherwise competition by weeds could become too strong. Reduced crop density can either be realized by sowing around 50% of the normal sowing rate or by wider crop row spacing, e.g. double or threefold spacing. The crop type had a major effect on establishment in Publications 2 and 3. Crop rotations should contain a high percentage of suitable crops, in the case of rare winter annuals this means autumn-sown cereals like spelt or rye. However, it is important to create a diverse crop rotation to avoid weed infestation and to promote arable plant with different germination requirements. Thus, crop rotations should also contain spring-sown or root crops. Unsuitable crops like clover-grass, soy bean and pea can be survived at least to some degree in the soil seed bank. They should not be cultivated directly after sowing the target species and be limited within the crop rotation, e.g. <25%. While disturbance by soil cultivation is essential for the persistence of rare arable plants, the type of soil cultivation was not decisive in Publication 2. Depending on soil structure and crop type, deep inversion tillage or shallow tillage may be more suitable. Deep ploughing usually reduces the seed density close to the soil surface and might prevent investation with noxious weeds. Moreover, Publication 3 demonstrated that not all study species were able to develop a seed bank within the study period of three years. Such species (without persistent seed bank) require annual reproduction and targeted conservation measures, e.g. continuous provision of favourable conditions in uncropped field margins.

Evaluation of reintroduction success and monitoring

The evaluation of reintroduction success is an important step in restoration projects. Most experimental studies use survival, flowering and fruiting rates as success criteria (Godefroid et al., 2011). However, measuring survival and plant densities are only weak indicators for reintroduction success, as the completion of a life cycle is crucial for the population. In case of arable plants, early crop harvest can prevent reproduction success, especially in late flowering and fruiting species (Pinke and Gunton, 2014). This is particularly relevant for crops with early harvest date like fodder crops or whole plant silage used for biogas. Apart from that, plant numbers alone are not meaningful, since arable plants show high phenotypic plasticity. Biomass and seed production per plant may contribute a significant part to population development. If the initial number of sown seeds is known, population growth rates can be calculated from total seed production, which is a valuable indicator for reintroduction success (Publications 2, 3). However, seed production is seldom recorded in reintroduction projects, as it involves greater effort (Godefroid et al., 2011). Practical studies usually require more simple approaches to measure reintroduction success. Vegetation surveys, transect records or the counting of target plants on representative sample plots could be useful here. To fully capture the species spectrum, two surveys per vegetation period may be helpful.

Nevertheless, for fully capturing population sizes at introduction sites the soil seed bank must be considered. Publication 3 demonstrated the importance of the soil seed bank as indicator for establishment, as it can be recorded independently of seasonal fluctuations and current management. Where possible, seed banks should be included in monitoring programmes. However, this might be unrealistic in many projects, since seed bank analyses are very resource-intensive (Kurtz and Heinken, 2011). For example, a huge number of samples would be necessary to detect very rare species with low population densities.

Another process that needs to be considered when evaluating reintroduction success is seed dispersal from the sown plots. Although seed dispersal in Publication 3 was only a few metres per year along the machining direction, it needs to be considered in monitoring programmes so that population sizes are not underestimated (Fig. 11). Generally, long-term monitoring programmes are necessary to capture arable plant populations due to their fluctuating above-ground plant numbers. If surveys are not feasible each year, they should be carried out at least once within the crop rotation, preferably when a cereal crop is cultivated.

Perspectives on long-term persistence and practical implementation

Perspectives on long-term persistence

Population growth rates of *Legousia speculum-veneris* and *Consolida regalis* far higher than one indicated that on-farm populations may persist in the longer term (Publications 2, 3). In contrast, it was uncertain whether *Lithospermum arvense* can maintain viable populations beyond the study period of three years. Further monitoring would be necessary to judge the long-term persistence of the study species. Usually, three years are too short to evaluate long-term success as establishment often decreases with time. This was demonstrated by Godefroid et al. (2011) who examined 249 plant species reintroductions and found only 6% flowering plants after four years. The authors further point out that reintroduction success is in most studies based on short-term results which leads to a bias towards positive results. Thus, ex-post monitoring should be applied to evaluate success, e.g. every five years after project end. This method is increasingly implemented, e.g. for the evaluation of agri-environmental schemes (Finn et al., 2009).

Overall, there is a lack of studies on the long-term persistence of reintroduced rare arable plant species (Albrecht et al., 2016). A long-term experiment on the reintroduction of five threatened species was set up by Mayer et al. (2019) on two fields located in the Franconian Jura. So far, they documented increasing plant densities and cover for all target species during six years of organic management. A major challenge for the long-term development of conservation and restoration fields is the prevention of weed infestations. Richner et al. (2015) reviewed the change in the arable flora of Europe and showed that “species preferring nutrient-rich sites, neophytes and monocotyledons generally increased since 1980”. These often highly competitive species can limit the diversity of arable plants and the reintroduction success (Armengot et al., 2017). Fields that are managed too extensively, e.g. applying hardly any soil tillage or missing a diverse crop rotation, are often prone to weed infestations.

In general, there is a risk that arable plant populations are quickly erased, e.g. by effective weed control or seed predation (Publication 3). On the long-term, also natural or human-induced ecosystem change may threat reintroduced populations (van Wieren, 2012). One major cause is global climate change which leads for example to “shifts in species distributions, changes in the timing of life-history events or phenology, decoupling of coevolved interactions such as plant-pollinator relationships, increased populations of species that are direct competitors of focal species for conservation efforts, and increased spread of invasive species” (Mawdsley et al., 2009). Another change that might become increasingly relevant for rare arable plants is the change in communities and competitive interactions in agroecosystems. For example, competitive species that are increasingly spread via flowering or bioenergy crop mixtures can pose a risk, especially if they turn invasive (Ende et al., 2021). Also, the increasing number of herbicide resistant weed species, currently 262 species worldwide, can be problematic for low competitive target plants (Heap, 2020). To face all these potential changes in future, genetic diversity of reintroduced populations and adaptive potential are of great importance.

Status quo and perspectives on practical implementation

The restoration of semi-natural grasslands, including species introduction, is frequently realized in Central Europe (Kiehl et al., 2010; Kollmann et al., 2019). However, such approaches are largely missing for the restoration of species-rich arable fields, although several options are conceivable for the reintroduction of rare arable plants. One option is the translocation in the sense of special species conservation measures, mostly targeted on single, highly endangered species. Such programmes, usually financed by public authorities, exist mainly for species that are protected by law but not for threatened arable plants. However, some species are cultivated in Botanical Gardens, which are responsible for reintroductions as well (Maschinski and Albrecht, 2017). An advantage of this option, is the professional handling with thorough documentation. Disadvantages are negative *ex-situ* cultivation effects on the genetic diversity of arable plants (Brütting et al., 2013) and mostly small-scale reintroduction measures involving only few seeds or plants.

Recently, several initiatives and projects have been launched aimed at collecting, propagating and introducing rare arable plants on suitable sites (Albrecht et al., 2016). For example, in France this is implemented in a national action plan to favour typical arable plants under the label *Vraies Messicoles*. In Germany, four federal states are currently pursuing the propagation and reintroduction of rare arable plants within natural units (Muchow and Fortmann, 2019).

A further option for practical implementation, is the extensification and species enrichment of arable fields in the course of compensation measures (Meyer, 2020). In Germany, such environmental offset schemes include *production-integrated compensation* which integrate conservation measures in agricultural production (Druckenbrod and Beckmann, 2018). They offer the possibility that species, seed provenances and sites have to be approved by nature authorities. Long-term financing is assured by the investor and management carried out by a farmer, ideally under supervision of a biologist with agronomic expertise (Druckenbrod and Beckmann, 2018).

Moreover, the promotion of arable plants by seed transfer could be implemented in agri-environmental schemes, which would be particularly effective in agricultural landscapes of low complexity (Tscharntke et al., 2005). Vegetation surveys of respective fields by Wietzke et al. (2020) indicated highly impoverished soil seed banks. The authors conclude that seed mixtures with rare arable plant species would be suitable to promote biodiversity in intensive farmland. However, up to date, regional seed material of arable plants and rules for their use on agricultural land are largely missing. An exception is *Cyanus segetum*, which is commonly used in flower mixtures, but often by means of non-regional seed material (Le Corre et al., 2014). The same applies to more common species, e.g. *Papaver rhoeas*. If the seed transfer within seed zones can be assured, it would also be conceivable to integrate arable plants in annual flower mixtures in order to enhance the value of theses mixtures for insects (Bretagnolle and Gaba, 2015; Warzecha et al., 2018). However, this should not be targeted on highly threatened segetal species, but rather on species that provide certain ecosystem functions, e.g. attractiveness for pollinators.

In conclusion, a new comprehensive nature conservation strategy is needed, including aims, guidelines and rules for the reintroduction of rare arable plants, based on scientific evidence. Beside species-specific seed-sourcing strategies, priority areas for either passive or active restoration should be figured out. Such novel approaches are necessary to stop the loss of genetic and species diversity in the arable flora.

CONCLUSION

The reintroduction of rare arable plants to suitable habitats is an important complement to the conservation of existing populations. This active restoration measure is necessary to stop further impoverishment of the segetal flora and loss of related ecosystem functions. The focus of this thesis was to investigate the conditions under which reintroductions of rare arable plants can be successful. The aim was to identify suitable seed provenances and agricultural management methods for the establishment of self-sustaining populations. The results show that rare arable plants can be established in extensively managed fields, albeit with varying success depending on species, site and management.

Different seed provenances within seed zones resulted in minor differences in fitness and establishment of the study species. Thus, the probability that a reintroduction fails because seeds are not sourced from the immediate vicinity of the target site is low. However, adaptation to drought of some species and provenances might play an increasingly important role in the context of climate change. Moreover, the effect of different seed provenances on resident populations, plant communities and biotic interactions must be further addressed. Above all, it must be considered that arable plants have always been dependent on dispersal by humans, both during their immigration to Central Europe and in traditional farming systems.

The arable habitat is characterised by a high temporal variability and frequently recurring disturbances. Arable plants are closely adapted to this habitat but are also very vulnerable to unfavourable management. In the plot field trial and on-farm experiments of this thesis, arable plants benefited most from low competition by crops and accompanying weeds. Unfavourable crops like clover-grass could at least partially be survived in the soil seed bank. Two of the three study species showed increasing population growth over the three-year study period. This is a good sign for the beginning of a viable, self-sustaining population. However, long-term feasibility and the respective effects of seed provenance and agricultural management must be investigated in further studies that include several environmental and human-induced change scenarios. Monitoring needs to involve soil seed banks and the great intraspecific variability of arable plants.

In conclusion, the integration of low-competitive arable plants on extensively managed fields is a suitable *land-sharing* option for their conservation. The reintroduction of rare species should be one important element of an improved strategy to increase species diversity on arable fields. In order to halt the overall loss of biodiversity in Central Europe, it is vital to focus on agricultural landscapes. The restoration of species-rich arable fields could become a new best practice example on how agriculture and nature conservation can be reconciled. Current evidence indicates that both sides will benefit from a more sustainable agriculture with an increased functionality of the agroecosystem.

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APPENDIX

A1 Curriculum Vitae

A2 Publication List

A1 Curriculum Vitae

Persönliche Angaben

Name	Marion Lang
E-Mail	Marion.Lang@tum.de
Geburtsdatum und -ort	5. Mai 1988, München

Berufserfahrung

Seit 09/2020	Stellvertretende Geschäftsführerin und Projektleiterin an der Bayerischen KulturLandStiftung, München
01/2016 – 08/2020	Projektbearbeiterin an der Bayerischen KulturLandStiftung, München • Projekt „Ackerwildkräuter für Bayerns Kulturlandschaft“
05/2015 – 04/2016	Fachberaterin für Naturschutz bei Bioland Beratung GmbH und biolog e.V., Augsburg • Projektbearbeitung „Wiederansiedlung von Ackerwildkräutern auf Biobetrieben“ • Biotopkartierung im Projekt „Firmen fördern Vielfalt“ der Universität Hannover
03/2014 – 12/2015	Wissenschaftliche Mitarbeiterin am Lehrstuhl für Renaturierungsökologie der Technischen Universität München und an der Bayerischen Landesanstalt für Landwirtschaft, Freising • Projektbearbeitung „Naturschutzleistungen des Ökologischen Landbaus: Wiederansiedlung seltener und gefährdeter Ackerwildpflanzen naturräumlicher Herkünfte auf Ökobetrieben“ • Mitarbeit im Projekt “LAND - Ecological effects of expanding nitrogen-fixing species in vulnerable ecosystems”
10/2012 – 11/2012	Freie Mitarbeit am Institut für Umweltplanung und Raumentwicklung, München
02/2011 – 04/2011	Praktikum an der Bayerischen Akademie für Naturschutz und Landschaftspflege, Laufen

Studium

01/2016 – 06/2021	Promotion am Lehrstuhl für Renaturierungsökologie der Technischen Universität München, Freising
10/2011 – 03/2014	Master of Science Umweltplanung und Ingenieurökologie, Technische Universität München
10/2008 – 08/2011	Bachelor of Science Biologie, Julius-Maximilians-Universität Würzburg

Schulbildung

09/1998 – 06/2007	Abitur, Karolinen-Gymnasium Rosenheim

Auslandserfahrung

11/2012 – 02/2013	Fachübergreifende Projektarbeit in Porto Alegre, Brasilien
01/2008 – 08/2008	Work and Travel in Australien

A2 Publication List

Peer reviewed journal publications

Lang, M., Albrecht, H., Rudolph, M. & Kollmann, J. (2021) Low levels of regional differentiation and little evidence for local adaptation in rare arable plants. Basic Appl. Ecol. 54, 52–63. https://doi.org/10.1016/j.baae.2021.03.015.

Sauter, F., Kollmann, J., Albrecht, H. & **Lang, M.** (2021) Competition components along productivity gradients – revisiting a classic dispute in ecology. Oikos. https://doi.org/10.1111/oik.07706.

Lang, M., Kollmann, J., Prestele, J., Wiesinger, K. & Albrecht, H. (2021) Reintroduction of rare arable plants in extensively managed fields: Effects of crop type, sowing density and soil tillage. Agric., Ecosyst. & Environ. 306, 107187. https://doi.org/10.1016/j.agee.2020.107187.

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Lang, M., Hanslin, H. M., Kollmann, J. & Wagner, T. (2017) Suppression of an invasive legume by a native grass – High impact of priority effects. Basic Appl. Ecol. 22, 20–27. https://doi.org/10.1016/j.baae.2017.06.005.

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Hermann, J. M., **Lang, M.**, Gonçalves, J. & Hasenack, H. (2016) Forest–grassland biodiversity hotspot under siege: land conversion counteracts nature conservation. Ecosyst. Health Sustainability 2 (6), e01224. https://doi.org/10.1002/ehs2.1224.

Other publications

Lang, M. (2019) Mut zur Farbe. Garten und Landschaft, 8, 20–22.

Wiesinger, K., **Lang, M.**, van Elsen, T., Albrecht, H., Prestele, J. & Kollmann, J. (2015) Wiederansiedlung seltener und gefährdeter Ackerwildkräuter im Biobetrieb. Online available: URL: http://www.lfl.bayern.de/mam/cms07/schwerpunkte/dateien/praxisbrosch%C3%BCre_ackerwildkraut.pdf.

Lang, M., Truffel, C., Prestele, J., Wiesinger, K., Kollmann, J. & Albrecht, H. (2015) Einfluss von Deckfrucht und Fruchtfolge auf die Wiederansiedlung gefährdeter Ackerwildpflanzen. In: Häring et. al. (Hrsg.): Beiträge zur Wissenschaftstagung Ökologischer Landbau, 17.–20.03.2015, Eberswalde, Deutschland. S. 231–235. Verlag Dr. Köster, Berlin.

Talks at international conferences

Lang, M., Kollmann, J. & Albrecht, H. (2019) Effects of farming practice on the establishment of rare arable plant species in different three-year crop rotations. 49th Annual Meeting of the Ecological Society of Germany, Austria and Switzerland, 09.–13.09.2019, Münster, Germany.

Lang, M., Kollmann, J., Prestele J., Wiesinger, K. & Albrecht, H. (2019) Impact of crop density, crop type and soil tillage on reintroduction of rare arable plants in three-year crop rotations. 7th meeting of the EWRS working group 'Weeds and biodiversity', 17.–19.06.2019, Stuttgart, Germany.

Lang, M., Albrecht, H., Himmler, D. & Kollmann, J. (2017) Re-introduction of rare arable plants by seed transfer. International Conference: Seed Quality of Native Species – Ecology, Production & Policy, 25.–29.09.17, London, UK.

Lang, M., Kollmann, J., Prestele, J., Wiesinger, K. & Albrecht, H. (2016) Re-introduction of rare arable plants on organic farms: Establishment and impact on crop yield. 10th European Conference on Ecological Restoration, 22.–26.08.2016, Freising, Germany.

Lang, M., Kollmann, J., Prestele, J., Wiesinger, K. & Albrecht, H. (2015) The challenge of re-introducing rare arable plants: Coping with crop density and rotation. 6th World Conference on Ecological Restoration, 23.–27.08.2015, Manchester, UK.

Lang, M., Kollmann, J., Prestele, J., Wiesinger, K. & Albrecht, H. (2015) Density-dependent effects during re-establishment of rare arable plants. 17th European Weed Research Society Symposium, 23.–26.06.2015, Montpellier, France.

Kollmann, J., **Lang, M.** & Albrecht, H. (2014) Re-introduction of rare arable weeds: Density effects, competition with other weeds and effects on crop yield. 9th European Conference on Ecological Restoration, 03.–08.08.2014, Oulu, Finnland.

Poster contributions to international conferences

Lang, M., Kollmann, J., Himmler, D. & Albrecht, H. (2019) Förderung von gefährdeten Ackerwildkrautarten durch Wiederansiedlung auf extensiv bewirtschafteten Ackerflächen. 49th Annual Meeting of the Ecological Society of Germany, Austria and Switzerland (GfÖ), 09.–13.09.2019, Münster, Germany.

Lang, M., Schmidt, C., Kollmann, J., Albrecht, H. & Himmler, D. (2016) Promotion of rare arable plant species by seed transfer – a benefit for cultural landscapes in Bavaria. 10th European Conference on Ecological Restoration, 22.–26.08.2016, Freising, Germany.

Albrecht, H., **Lang, M.**, Truffel, C., Prestele, J., Wiesinger, K. & Kollmann, J. (2015) Impact of cover crops and crop rotations on the re-establishment of threatened arable plants**.** 17th European Weed Research Society Symposium, 23.–26.06.2015, Montpellier, France.

Lang, M., Albrecht, H. & Kollmann, J. (2014) Density-dependent effects during re-establishment of rare arable weeds. 27th Conference of the Plant Population Biology, 29.–31.05.2014, Konstanz, Germany.