Response of the two rare arable weed species *Lithospermum arvense* and *Scandix pecten-veneris* to climate change conditions

Kristian Peters · Bärbel Gerowitt

Abstract Rare weeds are currently under pressure due to intensifying arable management practices, and as a consequence of climate change, these practices will likely become even more intensive, together with a greater uniformity of land use. As a result, ecological stresses will increase for most species of rare weeds, in some cases leading to their further decline or even extinction. Moreover, climate change will alter the suitability of the environment for many plants, since average temperatures are predicted to increase and precipitation extremes to become more common. For most arable weed species it is unclear, whether the anticipated changes in environmental conditions are disadvantageous or beneficial. Little is known about specific biological responses of rare weeds to climate changes, and this study attempts to close some of these knowledge gaps. Here, the rare arable weed *Lithospermum arvense* and the endangered arable species *Scandix pecten-veneris* were investigated with regard to the effects of higher temperature and different crop densities on flowering time, shoot development, plant height, dry mass and seed production. Semi-field experiments were conducted with winter wheat crop for 3 years, involving 48 climate cages, in which every second was a variant of warmer temperature and contrasting crop density. We observed that *S. pecten-veneris* flowered earlier under warmer conditions and had fewer seeds and less biomass in the dense wheat crop compared to control conditions, while *L. arvense* grew taller, it produced fewer seeds in the high density crop. We suggest that such data concerning the biological responses of weeds can improve the precision of bioclimatic distribution models. Finally, we discuss strategies, such as relocation or nonintrusive management practices, for preventing further disappearances of rare arable weeds. Our results should be of considerable interest for the fields of plant ecology, biodiversity research and conservation.

Introduction

Several weeds that were previously common in arable lands became rare due to mechanisation and intensification of arable management practices. The first declines occurred about 150 years ago, when mineral fertiliser and mechanised management were introduced (Holzner and Immonen 1982), and additional declines in both abundance and diversity were initiated approximately 60 years ago with the adoption of

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widespread herbicide use (Küster 1995; Baessler and Klotz 2006). Climate change may represent a third threat for rare weeds, as increases in the use of mineral fertilisers, greater crop densities, as well as altered sowing dates and longer growing seasons as a result of higher temperatures are likely in the future (Maillet and Lopez-Garcia 2000; Howden et al. 2007; Neve et al. 2009). Furthermore, cereal development may be accelerated during winter and summer months, and warmer temperatures will favour the planting of climate-adapted cereal cultivars (Kenny et al. 1993; Wardlaw and Wrigley 1994; Batts et al. 1998). Rare arable weed species will most likely have disadvantages from these changed management practices and also from more uniform land use (Olesen and Bindi 2002; Cimalová and Lososová 2009), and this may lead to a further decline or even the extinction of rare species.

It is known that most rare weeds show specific trait syndromes, and these traits are often related to a short plant height, low competitive abilities, large seeds, poor seed dispersal, narrow germination timeframes, easy seed cleaning, late flowering, and thus also late seed ripening (Kazanis and Arianoutsou 2004; Storkey 2006; Lososová et al. 2008). Importantly, most of these traits became obsolete or even disadvantageous in the context of modern arable farming (Andreasen et al. 1996; Sutcliffe and Kay 2000; Baessler and Klotz 2006; Petit et al. 2011). The number and the extent of the rare trait syndromes reflect the low phenotypic plasticity of rare weeds in the context of changes in arable conditions (Ohlemüller et al. 2006; Lososová et al. 2008; Pompe et al. 2009). According to Baker (1965), a general-purpose genotype (the extent to which phenotypic plasticity is exhibited by a species) is one of the most important factors for the success of weeds growing on arable lands. As the suitability of the environment will be altered as a result of future climate change, the degree of phenotypic plasticity is likely an important determinant of the future distribution of arable weeds (Bradshaw and McNeilly 1991; Pautasso et al. 2010).

At present, little is known about the specific biological responses of rare arable weeds to climate changes. Nevertheless, it is likely that direct effects of climate change, such as rising temperatures and less precipitation during summer months, will increase ecological stresses for rare weeds and create environmental conditions that are less favourable for many rare weeds (Patterson 1995; Marshall et al. 2003). In contrast, by removing species from the species pool, extreme climate events or other ecological disturbances can result in less competition by other species, which can even be an opportunity for certain rare weeds (Hobbs and Huenneke 1992; Storkey et al. 2010; Sheppard et al. 2012). Currently, most rare weeds use the C_3 photosynthetic pathway. Despite the positive effects of rising levels of atmospheric CO_2, higher temperatures negate the effect of elevated CO_2 for most C_3 plants (Batts et al. 1998; Morison and Lawlor 1999).

To date, only a few studies have analysed the effects of climate change on rare arable weeds (Morison and Lawlor 1999), so there is a lack of knowledge concerning their capacity to exhibit adaptive responses to changing climate conditions and the role of phenotypic plasticity. This study addresses these issues experimentally, using two rare weed species. The first species, *Lithospermum arvense* subsp. *arvense* L. (Syn. *Buglossoides arvensis* subsp. *arvensis* (L.) I. M. Johnst.) (Corn Gromwell, or Field Gromwell), is a white flowering weed of the family Boraginaceae. This species is mostly found in warm and exposed locations in Central Europe. It prefers sandy-clay soils, which are rich in nutrients, slightly basic and moderately calcareous (Moss et al. 2004). The second species, *Scandix pecten-veneris* L. (Venus' Comb, or Shepherd's Needle), is a short-statured weed of the family Apiaceae. This species prefers calcareous soils with low to moderate nitrogen levels and is typically found in warm exposed locations with moderate water availability (Moss et al. 2004; Chantre et al. 2009).

These two weed species have a different history of dispersal in Central Europe. While *L. arvense* originated in summer-warm continental regions in the far east, and seeds were found in Europe dating back to the Neolithic Era (approximately 5,000 years ago), *S. pecten-veneris* most likely originated in continental Eurosibiric or sub-Mediterranean regions and migrated to Central Europe along with cereal cultivation about 600–700 years ago (Tuexen 1950; Willerding 1986; Küster 1995). The two weeds were common in European fields until about 150 years ago (Schneider et al. 1994), when sophisticated seed-cleaning mechanisms were developed, mineral fertilisers were introduced and management methods became increasingly mechanised, all of which have

been proposed as reasons for their first decline (Holzner and Immonen 1982; Küster 1995). Both species started to experience a second decline about 60 years ago upon the introduction and widespread use of certain herbicides (Sala et al. 2000; Chapin et al. 2000; Baessler and Klotz 2006).

In present day Central Europe, both species are the relics of extensively managed fields, and they are often restricted to field boundaries (Chantre et al. 2009). Furthermore, while *L. arvense* is currently common only in parts of Poland and mountainous European regions, *S. pecten-veneris* is near extinction in most parts of Central Europe (Schneider et al. 1994). In recent decades in the UK, the use of herbicides, together with earlier harvesting of winter crops, had a strong negative effect on *S. pecten-veneris* (Rich and Woodruff 1995; Robinson and Sutherland 2002). In contrast, over the last few decades the abundance of *L. arvense* in Great Britain increased slightly (Potts et al. 2010), and it became a troublesome neophyte in winter crops in the semiarid regions of Southern Argentina and in the United States (Chantre et al. 2009). As is typical for species from the family Boraginaceae, *L. arvense* has silicate hairs that may cause a reduced uptake of water-bound herbicides into the plant. However, it should be noted that despite this characteristic, the most European populations of *L. arvense* are still susceptible to herbicides (Neururer and Herwisch 1976).

In this study, we aim at analysing the morphological responses of the two rare weeds to warmer conditions and high crop density in a semi-field experiment. We elucidate the influence of phenotypic plasticity and the role of certain rare weed trait syndromes with regard to warmer conditions and changes in the management practices.

Materials and methods

The seeds of *L. arvense* and *S. pecten-veneris* were collected near Göttingen, Germany in 2000. Wild plants originated from different field populations in that area. Both species were kept in ex situ cultivation in the experimental area of the University of Rostock, where the semi-field experiments were also conducted. Seeds were stored until the experiments were started. The experiment was initiated with a preliminary study in the season of 2009/2010. Five different densities of a

winter wheat crop (*Triticum aestivum* cultivar Dekan) were used for a preliminary study involving 250–450 plants/m^2, increasing in each treatment in increments of 50 plants/m^2. Crop densities of 200 and 400 plants/m^2 were used in the following two seasons (2010/2011 and 2011/2012) (Fig. 1).

For the semi-field experiments, 48 established barrels were used that were embedded in the ground since 1998, and so contained consolidated soil. They were cropped annually with cereals, oilseed rape or a grass crop. Each barrel had a diameter of 0.94 m and a depth of 1.50 m. The distance to the adjacent barrels was 2.06 m (Fig. 1). The barrels were arranged in 6 rows with 8 barrels per row. Plot size was 20 m by 26 m (Fig. 1). Winter wheat was sown in varying densities in the last week of September in the barrels (sowing period, Table 1). In the preliminary experiment, weed seeds were sown simultaneously in germination trays, and young plants were then planted in the barrels during the second week of March. In the following two seasons, a different approach was taken: manual broadcast sowing of weeds was carried out directly in the wheat crop in the sowing period. Each barrel was protected with a glass cover to prevent birds and mice from interfering with germination and growth during the first 4 weeks. No other actions were performed during the winter.

During the second week of March (early growth period, Table 1), seedlings were removed to ensure the same number of seedlings in each barrel. Every other barrel was surrounded with a metal frame (1.70 m in height) that was completely covered with transparent foil other than the top, which was made of transparent gauze with a mesh breadth of 0.5 mm, to allow necessary air exchange and to ensure a uniform temperature inside. These structures are referred here as cages with warmer conditions (barrels represented by a solid thick line in Fig. 1). In the season of 2011/2012 the remaining barrels were also equipped with metal frames that were covered with a white mesh (mesh breadth of 0.5 cm). The mesh was used to create comparable light conditions in both variants, since the transparent foil used with the warm cages absorbed a fraction of the radiation originating from the sun. The mesh was also useful to prevent birds from interfering. These are referred here as cages with control conditions (barrels with a dashed line in Fig. 1).

During the second week of May, young plants were counted; their height was measured, and the BBCH
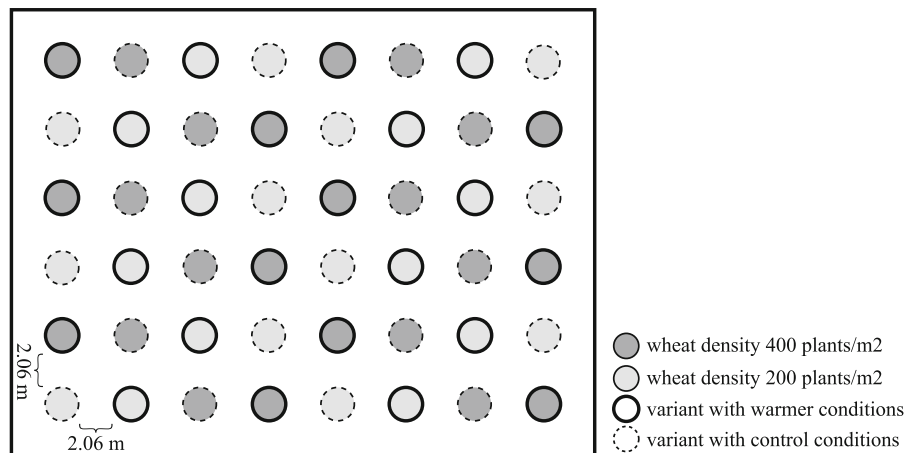
Fig. 1 Design of the experiment in the season 2011/2012. A schematic of the 48 barrels used in the semi-field is shown the experiment. Plot size was 20 m × 26 m

Table 1 Overview of the work performed

Period	Period	Work performed
Last week of September	Sowing period	Sowing of winter wheat in different densities in barrels
		Sowing of weeds in barrels
Second week of March	Early growth period	Removal of excessive weed seedlings
		Building the climate cages
		Setting up data loggers
Second week of May	Flowering period	Determining the BBCH stage
		Measuring the plant height
		Counting the number of shoots per plant
First week of August	Harvesting period	Harvesting weed plants in each barrel
		Harvesting wheat
		Counting seeds
		Determining dry mass

The field experiment was repeated three times. Wheat densities and climate change conditions varied between the experiments

stage was recorded according to Hess et al. (1997) (flowering period, Table 1). Both wheat and weeds were harvested during the first week of August (harvesting period, Table 1). The dry mass (without seeds or roots) was determined, and the seeds were counted for each plant. Interfering weeds were removed by hand during the season. Snails were controlled by molluscicides as required. Each barrel was fertilised with 75 g Compo Hakaphos® Blue

(equal to 112.5 kg N and 75 kg P ha^{-1}) before sowing in the last week of March.

Data loggers were needed to assess the difference in the conditions of the cages with control conditions from the cages with warmer conditions. At an interval of 30 min, weather conditions (temperature and air moisture) were recorded with data loggers at a point 5 cm above the ground, one for each climate variant. The recorded weather data were used to calculate the growing degree days using the daily minimum and maximum air temperatures for the time in which the measurements were performed at the flowering and harvesting period. The following base temperatures were used: 3.8 °C for *L. arvense* and 8.0 °C for *S. pecten-veneris* (Chantre et al. 2009).

Statistical analysis was carried out using the R software package (Ihaka and Gentleman 1996), together with the additional packages MASS, lme4, languageR, gplots, coin and agricolae. To compare the different biological parameters, generalised linear models (GLM) were applied, using climate and wheat density as fixed factors. For the main experiments in 2010/2011 and 2011/2012, the year was chosen as an additional fixed factor. BBCH stages were compared using the Wilcoxon–Mann–Whitney test (function wilcox_test in R). Data were transformed before statistical analysis, if the conditions of normality were not met, to improve homogeneity of variances (see Tables 2, 3). The distribution and homogeneity of variances were visually checked with the help of histograms and diagnostic plots, performed by the glm and glm.nb functions in R, respectively (Zuur et al.

Results

Measured conditions in the cages

A comparison of the cages with warmer conditions and those with control conditions revealed that the difference in the temperatures between the two varied with weather conditions. The average temperature was 0.9 °C higher in the cages with warmer conditions, ranging from a difference of 3.2 °C in sunlight during the day and a mean of 0.5 °C at night. Wind decreased the temperature inside the cages. At the flowering time, there was a difference of 16 growing degree days between the cages with control conditions and the cages with warmer conditions. At the harvesting time, the difference was 59 growing degree days between the two climate variants. As a result of the higher base temperature, *S. pecten-veneris* had approx. 2/3 fewer growing degree days available when compared to *L.*

Table 2 Preliminary experiment: Plant properties measured in the flowering period (flowering plant height) and in the harvesting period (plant height, seeds per plant and dry mass)

Weed species	Factor	Flowering plant height (cm)	Harvesting plant height (cm)	Seeds per plant	Dry mass (g)
L. arvense	Statistical test	glm	glm	glm.nb	glm.nb
	Transformation	Square	sqrt	–	–
	Distribution	Poisson	Gaussian	neg.bin	neg.bin
	P_{wd}	**0.001**	0.564	0.848	0.366
	P_c	**0.001**	0.646	0.918	0.647
S. pecten-veneris	Statistical test	glm	glm	glm	glm.nb
	Transformation	Square	–	sqrt	–
	Distribution	Poisson	Gaussian	Gaussian	neg.bin
	P_{wd}	**0.002**	0.301	0.059	0.408
	P_c	**0.001**	0.911	**0.042**	0.430

Data were square, square root (sqrt) or not transformed according to their distribution (Gaussian, Poisson or negative binomial). *P* values are given. Wheat density (wd) and climate (c) were used as fixed factors. Significant results are marked in bold letters. $n = 240$ for both species (data shown in Figs. 2, 3)

Table 3 Plant properties measured in the flowering period (plant height, shoots per plant and BBCH stage) and in the harvesting period (seeds per plant and dry mass)

Weed species	Factor	Plant height (cm)	Shoots per plant	BBCH stage	Seeds per plant	Dry mass (g)
L. arvense	Statistical test	glm	glm.nb	Wilcox test	glm.nb	glm.nb
	Transformation	–	–	–	sqrt	sqrt
	Distribution	Gaussian	neg.bin	–	neg.bin	neg.bin
	P_{wd}	**0.001**	**0.001**	0.076	**0.016**	**0.001**
	P_c	**0.020**	0.077	0.537	0.962	0.624
S. pecten-veneris	Statistical test	glm	glm.nb	Wilcox test	glm	glm
	Transformation	–	–	–	Fourth root	Fourth root
	Distribution	Gaussian	neg.bin	–	Gaussian	Gaussian
	P_{wd}	**0.035**	**0.031**	**0.011**	**0.001**	**0.001**
	P_c	**0.040**	**0.001**	**0.001**	0.135	**0.001**

Data were square, square root (sqrt), fourth root or not transformed according to their distribution (Gaussian, Poisson or negative binomial). *P* values are given. Wheat density (wd) and climate (c) were used as fixed factors. Significant results are marked in bold letters. $n = 1,409$ for both species (data shown in Figs. 4, 5)
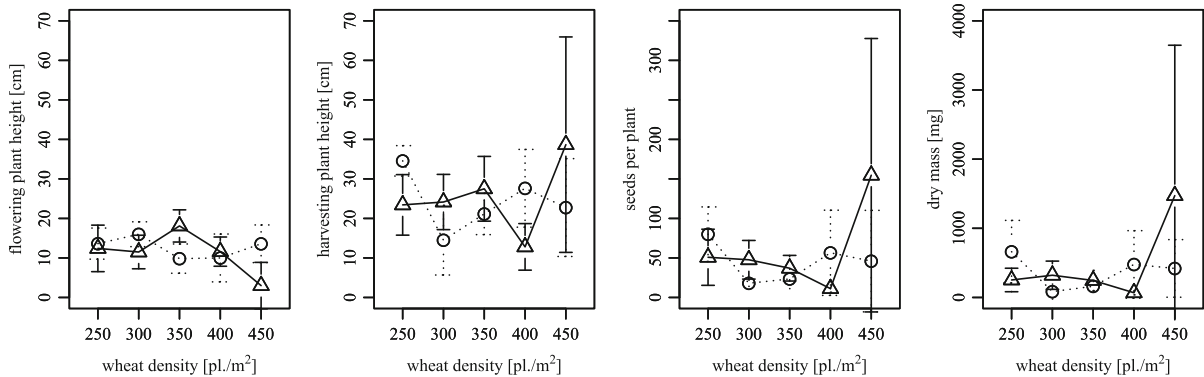
Fig. 2 Preliminary experiment: Plant height measured in the flowering period, and plant height, seeds per plant and dry mass measured in the harvesting period for *Lithospermum arvense*. *Circles* represent medians under control conditions, whereas *triangles* represent medians under warmer conditions. *Lines* are drawn to differentiate the five contrasting wheat densities in the climate cages under control conditions (*dotted line*) from the cages with warmer conditions (*solid line*). n = 240 for both species

arvense. Relative humidity was about 79 % in the cages with control conditions and 1.5 % higher in the cages with warmer climate in the first and second season, and 1.1 % lower in the third season.

Results of the preliminary experiment

Lithospermum arvense plants in the flowering period grown under control conditions were the tallest in the wheat crop grown at a density of 300 plants/m². However, the tallest plants were found in the crop with a density of 350 plants/m² grown under warmer conditions (Fig. 2). In the harvesting period, *L. arvense* grown under control conditions were the

tallest in the crop with the lowest density; this relationship was reversed in the cages with warmer conditions (Fig. 2). Similar results were found for the seed production per plant and plant dry mass, although the significant differences were apparent only for the plant height (Table 2). In the flowering period, most *S. pecten-veneris* plants were taller under warmer conditions (Fig. 3; Table 2), and this relationship was reversed at the time of harvesting. *S. pecten-veneris* plants were smaller and produced significantly fewer seeds under warmer conditions than under control conditions (Fig. 3; Table 2); upon reaching the harvesting period, no plants survived in the highest wheat density under warmer conditions (Fig. 3).
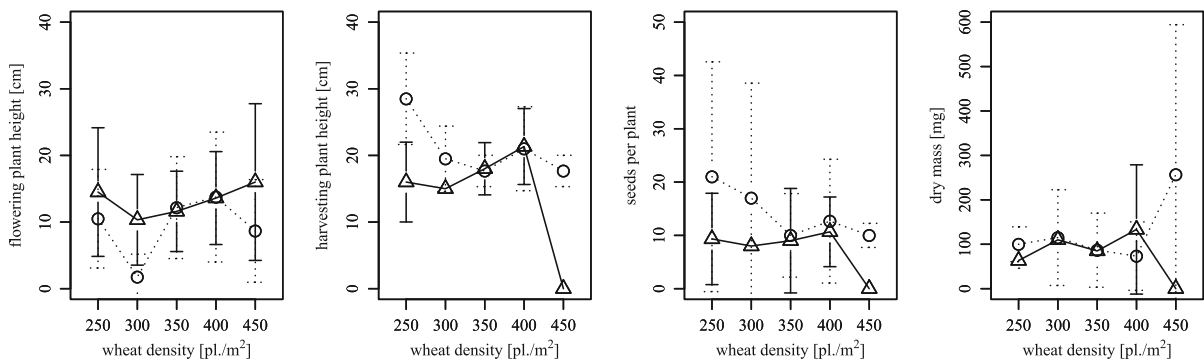

Fig. 3 Preliminary experiment: Plant height measured in the flowering period, and plant height, seeds per plant and dry mass measured in the harvesting period for *Scandix pecten-veneris*. *Circles* represent medians under control conditions, whereas *triangles* represent medians under warmer conditions. *Lines* are drawn to differentiate the five contrasting wheat densities in the climate cages under control conditions (*dotted line*) from the cages with warmer conditions (*solid line*). n = 240 for both species
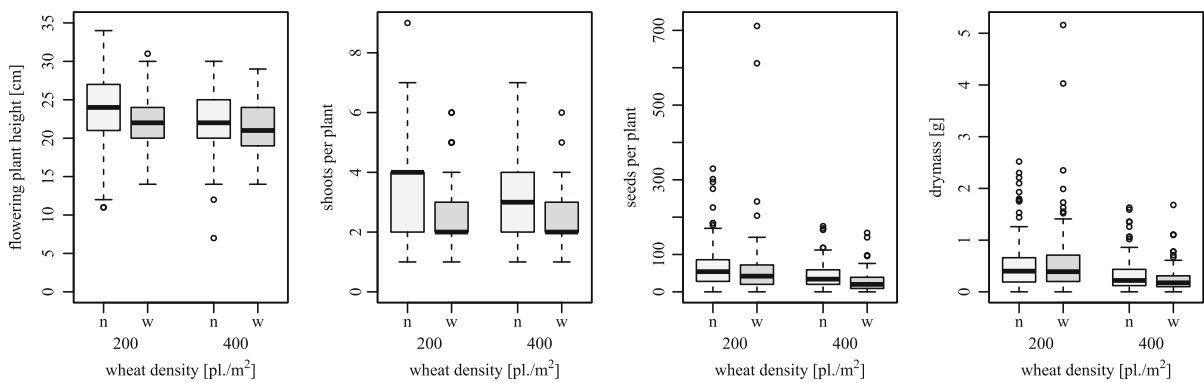
Measurements at flowering period

Under control conditions, *L. arvense* grew taller in the wheat crop with low density than with high density, while under warmer conditions plant heights were significantly greater in the dense wheat crop than in the low density crop (Fig. 4; Table 3). Under control conditions, *L. arvense* produced significantly more shoots in the crop with low density compared to the dense wheat crop (Fig. 4). Finally, the onset time and duration of flowering (the BBCH stages measured) did not differ significantly between the treatments (Table 3). *S. pecten-veneris* plants were smaller under warmer conditions than under control conditions, and

plants were smaller in the dense wheat crop than in the low density crop (Fig. 5; Table 3). *S. pecten-veneris* produced significantly fewer shoots under warmer conditions than under control conditions (Table 3) and had fewer shoots in the high density wheat crop than the low density crop (Fig. 5). Generally, a lower phenotypic plasticity, and thus less variation in plant height and plant stature, was observed for *S. pecten-veneris* compared to *L. arvense*. Plants of *S. pecten-veneris* flowered earlier and are also shorter when grown under warmer conditions (Table 3). Thus, BBCH stages were higher under warmer conditions (Table 3). The species also showed an earlier onset of flowering in the dense wheat crop (Table 3).
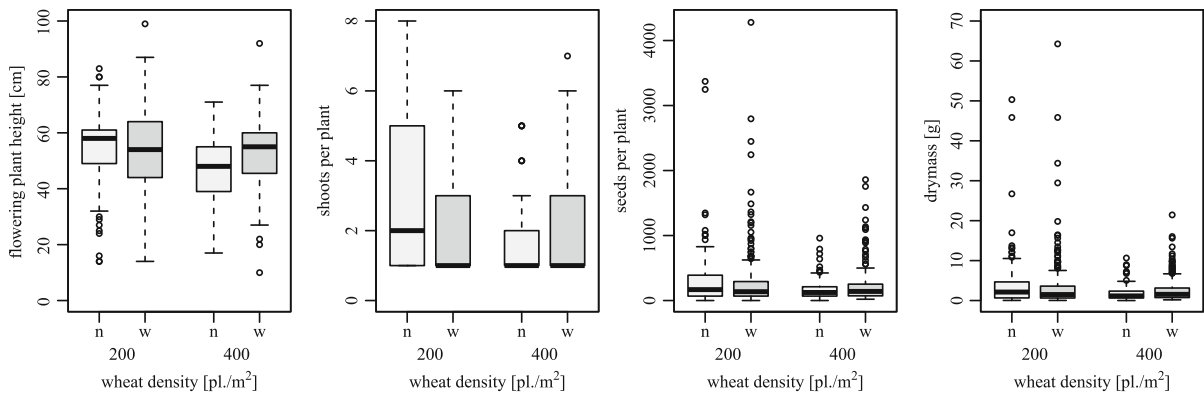
Fig. 4 Characteristics measured in the flowering period (plant height and shoots per plant) and in the harvesting period (seeds per plant and dry mass) for *L. arvense* in two different wheat densities (200 and 400) in climate cages under control conditions (*n*) and warm climate cages (w). *n* = 1,409 for both species

Fig. 5 Properties measured in the flowering period (plant height and shoots per plant) and in the harvesting period (seeds per plant and dry mass) for *S. pecten-veneris* in two different wheat densities (200 and 400) in climate cages under control conditions (*n*) and warm climate cages (w). *n* = 1,409 for both species

Measurements at harvesting period

On average, *L. arvense* plants produced 132 seeds/plant in the dense wheat crop and 152 seeds/plant in the low density crop. Occasionally, single plants produced up to 4,000 seeds (Fig. 4). Such outliers were only observed in the low density wheat crop. *L. arvense* plants had significantly less dry mass when grown in the dense wheat crop than in the low density crop (Fig. 4). However, the two climate conditions had no significant effect on seed production and dry mass of *L. arvense* in wheat crops of both densities (Table 3). On average, *S. pecten-veneris* produced 44 seeds/plant under control conditions and 32 seeds/plant under warmer conditions (Fig. 5). Seed production was likewise significantly reduced in the dense wheat crop compared to the low density crop (Table 3), and similarly, a significant reduction was observed for *S. pecten-veneris* dry mass (Table 3).

Discussion

In this experiment, both species responded differently to the experimentally warmer climate changes and also to crop density.

The warmer conditions had a stronger negative impact on the generative reproduction of *S. pecten-veneris* than on *L. arvense*. Concerning warmer conditions, *S. pecten-veneris* exhibited low phenotypic plasticity mostly regarding life history traits, which likely affect negatively the persistence in the long term of the weed (Storkey et al. 2010). One example is dispersal capacity, which is strongly associated with morphological traits such as seed production, seed size and the number of shoots (Gaudet and Keddy 1988). *S. pecten-veneris* grows very large seeds, which is an unusual trait for weeds growing on arable lands. The large size is an adaptation that can be advantageous if nutrients are limiting (Storkey et al. 2010); however, the ability to retain nutrients provides no advantages under current agricultural management methods, where the nutrients are typically not a limiting factor (Reich et al. 1992; Aerts 1999). On the other hand, *L. arvense* germinates in a narrow timeframe in autumn and spring (Svensson and Wigren 1986a). If future crop sowing occurs outside of this window, fewer *L. arvense* plants may emerge (Chantre et al. 2009).

The disadvantage of large seeds, fewer shoots and lower seed production under warmer conditions of *S. pecten-veneris* is more limiting and less likely to be changed by adaptation or compensated by variation than the narrow germination period of *L. arvense*. Thus, the mentioned rare weed syndromes for *S. pecten-veneris* have likely more negative impact on the generative reproduction rather than those of *L. arvense* (Fried et al. 2010). Under warmer conditions, *L. arvense* will, therefore, probably be able, to some degree, to migrate to a favourable climate gradient as the seeds are also distributed more easily due to their small size (Fahrig and Merriam 2002). However, *L. arvense* abundance may decrease in Central Europe if climate change occurs too rapidly and future agricultural management becomes more intensive. The lower generative reproduction of *S. pecten-veneris* under warmer conditions will likely increase the risk of extinction for *S. pecten-veneris* (Wilson 2006).

In this experiment, the seed output of the two species was lower in the dense crop at the time of harvesting. Both species responded negatively to increasing wheat crop densities, probably as a result of the increased shading caused by the high crop density (Korsmo 1930; Svensson and Wigren 1986b). However, our results showed that some *L. arvense* plants grew very tall and produced an unusually high number of seeds under warmer conditions in the dense wheat crop (Fig. 4). If these differences were caused by genetic diversity, this could lead to biotypes of *L. arvense* that are better adapted to the future climate conditions. Thus, this species may even show an increase in abundance in high density crops under warmer conditions. Similar selection patterns may explain the high competitive abilities of the invasive populations in Argentina and the United States, although the climatic selection of *L. arvense* has not been studied to date (Chantre et al. 2009). We note that such suggestions about the significance of selective effects are still speculative, and further research is needed to assess the importance of regional biotypes of *L. arvense*.

Warmer and dryer conditions can also have an accelerating effect on the flowering time of plants (Ballaré and Casal 2000). Due to climate change, the flowering period of winter wheat will most likely be shorter and harvesting may occur earlier (Kenny et al. 1993). Conversely, accelerated flowering may be advantageous for some weeds grown on arable

lands as they are expected to produce more ripe seeds in a shorter time before harvesting (Baker 1965; Kenny et al. 1993; Ballaré and Casal 2000). *S. pecten-veneris* flowered earlier and for a shorter time under warmer conditions, which resulted in significantly fewer seeds at the harvesting time. For *S. pecten-veneris*, this strategy ensures fertile and fully ripened seeds before harvesting, but is only advantageous on nutrient-poor soils and not under current management practices (Morison and Lawlor 1999; Storkey et al. 2010). Thus, due to low phenotypic plasticity, this weed species is also less buffered against the changes in other agronomic practices, such as sowing time or harvesting time, which affect the flowering period of the weed. This has previously been suggested as a reason for the general decline of rare weed species (Wilson and Wright 1990; Robinson and Sutherland 2002).

Clustering weed communities from arable lands by phytosociological characteristics have a long tradition in Central Europe (Tuexen 1950; Hüppe and Hofmeister 1990). *L. arvense* and *S. pecten-veneris* belong to the phytosociological class Secalinetea Br.-Bl. 1936 (Tuexen 1950; Küster 1995). They are typically found in communities such as Caucalidion platycarpi R. Tx. ex von Rochow 1951 (Tuexen 1950; Hüppe and Hofmeister 1990). Both species are competitive only under relatively nutrient-poor, calcareous soils and in crop conditions with low densities (Fried et al. 2010). Modern agricultural management practices encourage species of the phytosociological class Chenopodietea that are most competitive in nutrient-rich arable ecosystems (Otte 1990). Weed communities will be altered due to the climate change because 'old' species with obsolete traits are being replaced by 'new' species with opportunistic traits (Storkey et al. 2010). Species niches will change, and weed communities will have a different composition (Silvertown 2004; Broennimann et al. 2006; Cimalová and Lososová 2009). Thus, rare weed species may have to adapt to competition from different species in altered plant communities, in which they may not be able to effectively compete. While *S. pecten-veneris* is restricted to the aforementioned communities, the phenotypic plasticity of *L. arvense* allows the species to also appear in half-ruderal grassland (Convolvulo-Agropyrion repentis Görst 1966). This may allow *L. arvense* to sustain populations in alternative plant associations.

Finally, some of our results regarding *S. pecten-veneris* suggest a contradiction with recent bioclimatic modelling of the future species' distribution in the UK (Berry et al. 2007). This is most likely due to the spatial approach of the most current models, which only include species distribution data and bioclimatic or agronomic parameters (Morin and Thuiller 2009). Moreover, the comparative study of Morin and Thuiller (2009) indicates the need to connect spatial modelling with biological and ecological data, and future research should incorporate these factors to improve model precision (Summers et al. 2012; Kubisch et al. 2013). Since conservation measures often rely on accurate prediction of bioclimatic distribution models, additional biological and ecological data are vital for conservation strategies to succeed under future conditions (Loss et al. 2011; Bernazzani et al. 2012). Our results provide a first step towards such integration under certain climate change scenarios.

Conclusions

We found that changes in the crop density had a stronger negative effect than warmer temperature alone. Thus, the influence of climate-mediated changes on the intensification of management practices can outweigh the sole effect of direct climate changes on rare weeds. We suggest that conservation biologists should promote extensive and non-intrusive management for the two rare weed species under warmer climate conditions (Brooke 2008). Effective conservation also requires the maintenance of the communities in which both species typically occur. This will mainly mean the promotion of extensive agriculture on calcareous or nutrient-poor soils (Swetnam et al. 1999). However, it is also possible that different species-specific responses to warmer climate conditions will result in entirely novel communities (Williams et al. 2007). Conservation efforts could attempt to anticipate changes by translocating rare weed species in communities that would occur under warmer conditions (Harris et al. 2006). This concept is also known as managed relocation (Richardson et al. 2009) or assisted colonisation (Loss et al. 2011). Knowledge of biological responses of rare weeds and their responses within communities is vital if relocation measures are to succeed. Further studies of the

responses of rare weeds to community changes are needed to successfully incorporate the findings into adaptation strategies to future climate scenarios (Brooke 2008).

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