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Impact of temperature and germination time on the success of a C4 weed in a C3 crop: *Amaranthus retroflexus* and spring barley

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Elevation in temperatures due to climate change could promote the invasion by C4 weed species of arable fields in the boreal region, which are dominated by C_3 crops. The success of *Amaranthus retroflexus* L. (a C_4 weed) in spring barley (a C_3 crop) was studied at current and elevated temperatures (3 °C difference) in a greenhouse experiment in southern Finland. The competition treatments included no competition and four levels of competition with barley, differing in terms of germination time. The success of *A. retroflexus* was measured as growth (height and biomass) and seed production (number and biomass). Elevation in temperature enhanced seed production of *A. retroflexus*, but the impact on growth was minor (only difference in plant height in one treatment). The growth and seed production of *A. retroflexus* in competition with barley was minimal although the growth of barley decreased with the rise in temperature. The results indicate that climate change could improve growth of a C_4 weed such as *A. retroflexus*, but it is unlikely to succeed in spring barley.

Key-words: arable weed, climate change, seed production, species invasion

Introduction

Climate change has been predicted to broaden the distribution areas of arable weed species (Patterson 1995). A successful range expansion of arable weeds requires not only adaptation to the climatic conditions of a new region but also colonisation of cultivated fields. Therefore, crop-weed interactions must be considered in connection with range expansion of arable weeds as a consequence of global warming.

The key issue to understanding crop-weed interactions with respect to climate change lies in the

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different responses of C_3 and C_4 species to elevation in temperature and CO_2 concentration (Patterson and Flint 1980, Ziska 2001, 2003). C_3 plants benefit from the elevated CO_2 levels, whereas C_4 plants benefit from the elevated temperature (Pearcy et al. 1981, Sage and Kubien 2007). As a result climate change will affect crop-weed interactions disproportionately depending on the photosynthetic pathway of the crop and weed species (Ziska 2001, 2003). C_3 and C_4 species occupy a temporal niche in natural vegetation that is determined by temperature (see Sage and Pearcy 2000). This is also evident in arable weed communities since C_4 weeds usually occur in C_4 crops (e.g. Schroeder et al. 1993, Bunce and Ziska 2000), which are alike with respect to temperature requirements for germination and growth. Since the majority of the "world's worst weeds" are C_4 plants (Holm et al. 1977) and most crops are C_3 plants (Patterson 1995), global warming can be assumed to strengthen the competition from these weeds in the future (Ziska 2003, Tungate et al. 2007). Regarding range expansion, the pressure on C_4 weeds to invade northern regions, where they are currently rare, can be assumed to increase (Holm et al. 1997). This will require, however, the colonisation of C_3 crops by C_4 weeds.

One of the most widely distributed C_4 weeds in the world is *Amaranthus retroflexus* L., which is found in 60 crops in 70 countries (Holm et al. 1997, Costea et al. 2004). The main distribution area of *A. retroflexus* in Europe is in southern and central Europe, the northern border of the distribution area being in the Nordic and Baltic countries. At the margins of the distribution area, including Finland and Estonia, *A. retroflexus* is regularly found as a casual alien (Hämet-Ahti et al. 1998, Kukk and Kull 2005), i.e. a species that cannot establish permanent populations and is dependent on the regular supply of new seeds (Richardson et al. 2000). Based on its current distribution, *A. retroflexus* can be regarded as one of the most probable C_4 weed species to extend its distribution into the boreal region as a consequence of climate change. Previous studies showed that elevation in temperature increases growth of *A. retroflexus* (Guo and Al-Khatib 2003) but decreases seed production (Weaver 1984), indicating opposing responses regarding success as a consequence of climate change. Seed production is lowered in competition with a crop (McLachlan et al. 1995). The success of *A. retroflexus* as a competitor with C_3 cereals has not been established experimentally, but field observations suggest it is poorer than with C_4 crops (Costea et al. 2004).

The aim of the present study was to explore the growth response and the seed production of *A. retroflexus* at an elevated temperature with and without competition from a C_3 crop (spring barley). The study was conducted in Finland, where the dominant C_3 crop species is spring barley and which represents the northern distribution limit of *A. retroflexus*. Since the timing of germination is a critical factor affecting crop-weed competition (Knezevic et al. 1997) and the optimum germination temperature for *A. retroflexus* is high compared with that for barley (Ghorbani et al. 1999, Guo and Al-Khatib 2003), which indicates later germination and emergence times, several germination dates for *A. retroflexus* were included in the study. I expected the elevation in temperature to enhance growth but decrease seed production of *A. retroflexus*.

Material and Methods

Plant material

The seeds of *Amaranthus retroflexus* were collected from southern Sweden (55°45´ N; 13°19´ E) in September 2004. In summer 2008, the seeds were sown in pots and grown both outdoors and in a greenhouse in Jokioinen, southern Finland (60°49' N; 23°29' E) in order to produce seeds for the experiment. The seeds were stored at +4 °C but kept at -18 °C for two days in October 2008. The seeds of spring barley, *Hordeum vulgare* L., cultivar Rolfi, were obtained from a local agricultural market.

The plants for each treatment (see below) were grown in 3.5 l pots (diameter 18 cm) in a commercial peat-sand mixture ('Kylvöseos' by Kekkilä Oyj, Mellilä, Finland; pH 6.0, N: 70 mg l^{-1}, P:

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21 mg l^{-1}, K: 140 mg l^{-1}) and fine sand (grain size 0.2-1 mm) at a ratio of 2:1. The pots were watered regularly and fertilised (a mixture of 2.5 kg fertilization [N-P-K content 14-5-21 %, respectively] with 25 litres water mixed with irrigation water in a proportion of 1:50) 7 times during the experiment (total amount of fertiliser-water mixture per pot was 2.7 l).

The sowing density of barley was 12 seeds per pot sown in two rows (row width 7 cm), the same sowing density as in field cropping, and one seed or seedling of *A. retroflexus* placed in the middle of the pot. The seeds of *A. retroflexus* were either sown in the pot (treatments 1 and 2) or planted as 1–2 cm long seedlings (treatments 3–5). The seedlings were germinated on Petri dishes in a growth chamber at a temperature regime of 35/10 °C (16/8 h) with full light. If a seedling of *A. retroflexus* died within two weeks after the sowing date it was replaced by a new seedling of the same age grown in the same greenhouse. Seventy-seven (32.1% of all plants in the experiment) such replacements were made during the experiment. At the end of the experiment, 12 *A. retroflexus* individuals were dead of which 9 were replacement seedlings. Two dead barley plants were also replaced with new seedlings after 10 days from the beginning of the experiment.

Experimental design

The greenhouse experiment was conducted in Jokioinen between 10th February and 8th May 2009. The experiment was conducted in four greenhouses of which two had a temperature regime of 20/10 °C (18/6 h) (hereafter, current) and the other two 23/13 °C (18/6 h) (hereafter, elevated). The temperature regimes were randomized among greenhouses. The temperature regime with lower values was in line with the long-term (1971–2000) average minimum and maximum temperatures for the summer months (June–August) recorded at Jokioinen meteorological station (Drebs et al. 2002). The 3 degree elevation in temperature conforms to the predicted median temperature value for summer months (June-August) for the time period 2040–2069 according to four climate scenarios (Jylhä et al. 2004). The light/dark regime was 19/5 h for both temperature regimes, equivalent to the day length for Jokioinen in June.

The experiment included the following treatments: 1) *A. retroflexus* seedling planted on the 1st day of the experiment, no barley, 2) *A. retroflexus* seedling planted and barley sown on the 1st day of the experiment, 3) *A. retroflexus* seedling planted on the 7th and barley sown on the 1st day of the experiment, 4) *A. retroflexus* seedling planted on the 14th and barley sown on the 1st day of the experiment, 5) *A. retroflexus* seedling planted on the 21st and barley sown on the 1st day of the experiment and 6) Barley sown on the 1st day of the experiment, no *A. retroflexus*. Treatments 1–5 were placed on the same table as a row column design with three replicates (10 cm between pots). Four such tables were placed in each greenhouse (n = 12 for each treatment per greenhouse). The distance between the tables was about 1 metre. Barley control (treatment 6) consisted of two pots placed in close proximity to each table (n = 8 per greenhouse).

Measurements and data analyses

At the end of the experiment, plant height, above ground biomass (air-flow drying at 40 °C) and number and weight of seeds of *A. retroflexus* were recorded. The height of each barley plant and the above ground biomass of 12 barley plants per pot were also measured. Prior to analyses, the heights of barley plants were averaged and the data were pooled for treatments 1–5. The averages for barley controls were calculated for above ground biomass and height.

The data were analysed using linear mixed models. The treatment and greenhouse were fixed factors and the interaction of greenhouse and table a random factor in the models used for the analyses of all barley data sets and the height of *A. retroflexus*. However, for the data sets of seed number and weight, as well as for the biomass of *A. retroflexus*, comparisons within treatment 1 only were possible due to missing data (seeds) or highly skewed data distributions (biomass). In these analyses, the greenhouse was a fixed factor and the interaction of greenhouse and table a random factor. In both analyses, the paired comparisons between temperatures within treatment or between treatments within temperature were made using two-sided t-tests. All the *A. retroflexus* data were square root-transformed and the height and biomass data for barley (treatments 1–5) log (x+1) transformed prior to analyses. The statistical analyses were performed using the MIXED procedure in SAS (Littell et al. 2006).

Results

Seed production of *A. retroflexus* was affected both by competition with barley and temperature. The impact of competition was so strong that only 9 *A. retroflexus* plants in treatment 2, 2 plants in treatment 3 and a single plant in treatments 4 and 5 produced seeds. The majority of these cases were in the greenhouses at an elevated temperature: only one plant produced seeds in competition with barley at the current temperature. Due to the scattered data for seed production, the impact of competition and the interaction of competition and temperature could not been verified using statistical testing. In the comparison of treatment 1 (i.e. no competition with barley) at different temperatures, a greater number (1655 ± 896 vs. 5465 ± 2711 seeds per plant, t = 4.3, df = 12, p < 0 .001) and weight (0.7 ± 0.4 vs. 2.1 ± 1 g per plant, t = 4.2, df = 12, p < 0.01) of seeds were associated with an elevated rather than a current temperature (Fig. 1).

The biomass of *A. retroflexus* did not differ between temperature treatments (treatment 1: t = 1.8, df = 12, p < 0.05). The impact of temperature on the height of *A. retroflexus* was dependent on the competition treatment (treatment and temperature interaction $F_{4, 48}$ = 4.8, p < 0.01), the height being greater (t = -5.61, df = 59.3, p < 0.001) only for treatment 2 (Fig. 2). For barley, the elevated temperature resulted in both lower biomass and reduced height for all treatments (biomass: t = 3.6-4.1, df = 46.2, P < 0.001; height: t = 5.7-6.9, df = 17.7, p < 0.001). The same pattern was detected in control barleys, where both height (63.3 ± 3.6 vs. 55.6 ± 2.8 cm) and biomass (34.8 ± 2.3 vs. 30.8 ± 1.8 g) were higher at current rather than at an elevated temperature (height: t = -5.2, p < 0.001; biomass: t = -4.8, P < 0.001).

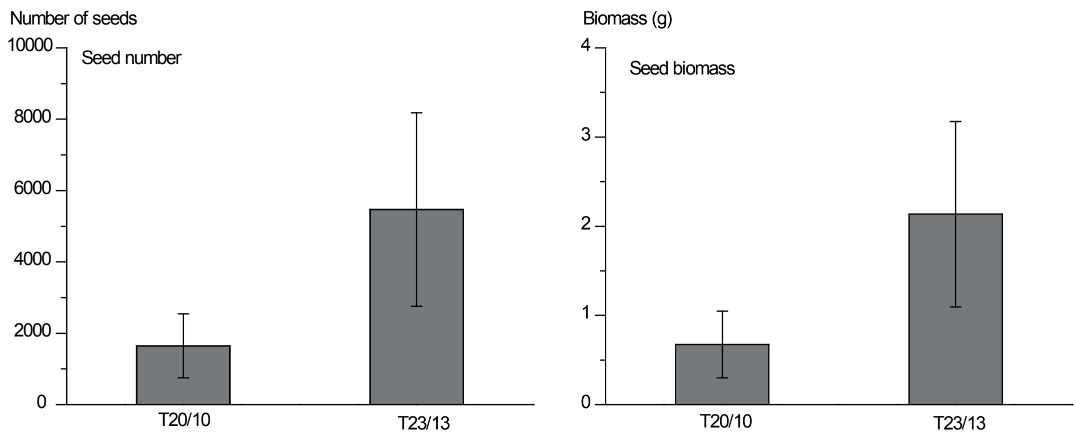

Fig. 1. The number and biomass of *Amaranthus retroflexus* seeds per plant (mean and SD) at the two temperature regimes.

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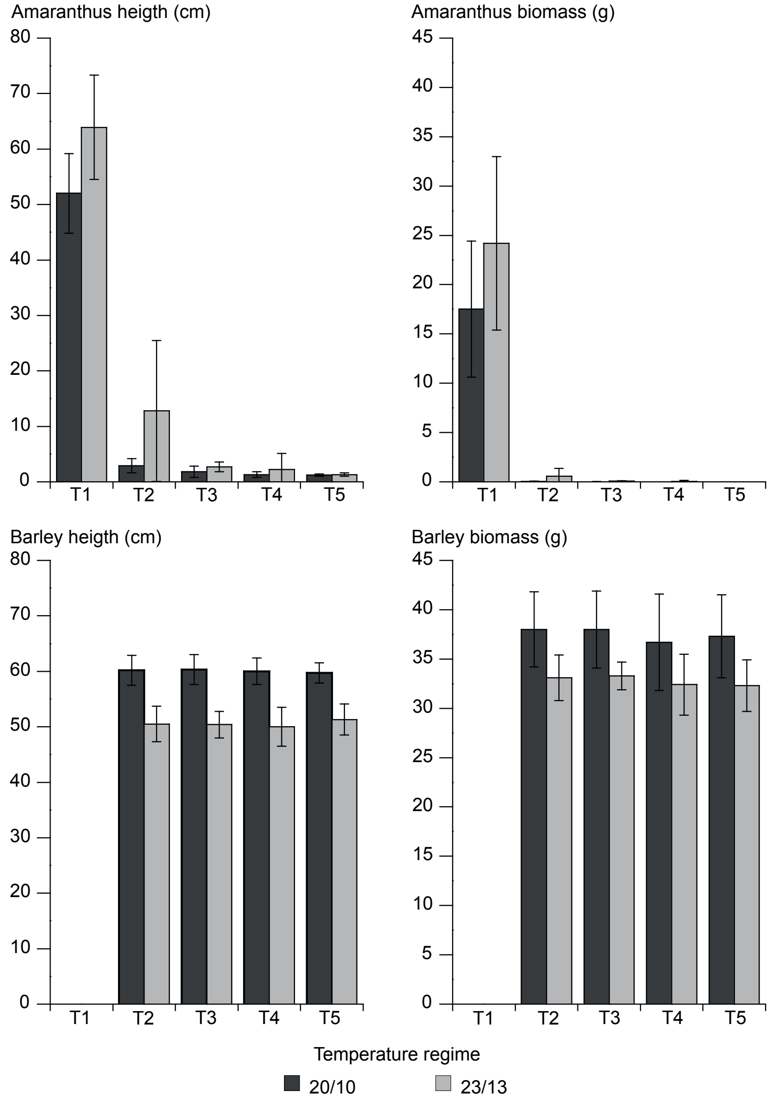

Fig. 2. The height and biomass of *Amaranthus retroflexus* and barley individuals (mean and SD). In T1, no barley included. The treatments T2-T5 differed in terms of sowing date of *A. retroflexus*.

Discussion

Contrary to expectations, elevation in the temperature enhanced seed production and had a minor impact on the growth of the C_4 weed *A. retroflexus*. The growth and seed production of *A. retroflexus* in competition with a C_3 crop, spring barley, was minimal although barley growth was decreased by the elevation in temperature. The results indicate that climate change could improve the success of *A. retroflexus* populations but success in spring barley is unlikely.

Previous studies showed C_4 weeds to respond positively to elevation in temperature (Guo and Al-Khatib 2003). However, the temperature optimum for photosynthesis of C_4 plants is typically high (Sage and Kubien 2007); for *A. retroflexus* over 35 °C (Pearcy et al. 1981). This suggests that the maximum temperature used in the present study (23 °C) was too low to give an advantage to *A. retroflexus* in terms of photosynthetic rate. Interestingly, the 3 degree elevation in temperature used in the present study was high enough to limit the growth of barley, in accordance with earlier findings (Peltonen-Sainio et al. 2010, 2011). This suggests a decline in the competitive ability of spring cereals against weeds, in a future climate. For C_4 weeds this would mean potential improvement in the success in the crop rotations typical of boreal regions. The results of the present study, however, suggest that even these changes will not promote the success of *A. retroflexus* in competition with spring cereals in the boreal region.

Previous competition experiments (e.g. Knezevic et al. 1997) showed considerable yield losses due to competition by *A. retroflexus*. In the present study, yield loss was not evident but *A. retroflexus* was unable to effect any decline in the biomass of barley either. Previous studies included crops other than spring cereals as study species. Under field conditions *A. retroflexus* is more common in such crops than in cereals (e.g. Costea et al. 2004), which suggests the growth patterns to be more alike with these species. One of the factors related to growth patterns is the germination temperature which determines the emergence patterns of seedlings. In the present study, the germination temperature (35 °C) was high compared with the day temperatures used during growth (20 or 23 °C). Under field conditions, *A. retroflexus* would have germinated later than barley. Therefore, the treatment used in the study benefited *A. retroflexus*. However, the seedlings of *A. retroflexus* were germinated on Petri dishes and the seedlings planted in the pots to ensure the same germination date for each individual within treatments. This procedure appeared not to be successful since one third of the seedlings had to be replaced with new seedlings during the experiment. This likely contributed to the poor success of *A. retroflexus* in competition with barley.

Even though *A. retroflexus* did not affect decrease in barley biomass, seed production showed a positive response to elevation in temperature. The finding was contradictory to previous findings by Weaver (1984), who reported an increase in seed production when the temperature regime was changed from 28/22 °C to 22/14 °C. The latter temperature regime is comparable with the elevated temperature regime used in this study. Therefore, the results are not entirely contradictory. The seed production level recorded in the present study was lower compared with those reported earlier (Weaver 1984, Costea et al. 2004). The increase in seed production at the elevated temperature suggests an improvement in the success of establishment of permanent populations. The finding suggests that some individual plants could produce seeds even in competition with barley. However, the building up of the populations, which would effect considerable yield losses, would require a crop rotation including a crop species less competitive against *A. retroflexus* (e.g. sugar beet). Even though the present study focused only on seed production, neglecting many components of the population demography (e.g. Morse and Bazzaz 1994), the suggestion is that *A. retroflexus* could survive under these conditions.

Range expansion of C_4 weeds into the boreal region of Europe as a consequence of global warming is of concern. Several C_4 weed species comprise an important part of the weed community in central Europe, but C_4 weed species typically occur in C_4 crops (Schroeder et al. 1993). The results of the present study suggest that *A. retroflexus* is unlikely to take hold in spring cereals. This is confirmed by the field observations: none of the 188 weed species found in a Finnish weed survey (Salonen et al., 2001) was a C_4 species. In addition, none of the C_4 species belong to the most important weeds of C_3 crops in Europe (Schroeder et al. 1993). The results suggest that even though the 3 degree elevation in average temperature decreased the growth of a C_3 crop and improved the seed production of a C_4 weed, C_3 crop species could act as a barrier to invasion by the "world's worst weeds" into the

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boreal region. Furthermore, climate warming will advance the sowing times of C_3 crops (Kaukoranta and Hakala 2008), thus reinforcing the competitive benefit of C_3 crops in spring time. The invasion of C_4 weeds cannot be expected to take place before the introduction of C_4 crops (e.g. maize), which has been predicted to occur not before the end of this century in Finland (Peltonen-Sainio et al. 2009).

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