

Research Article

Performance of *Ambrosia artemisiifolia* and its potential competitors in an experimental temperature and salinity gradient and implications for management

Hana Skálová^{1,*}, Wen-Yong Guo¹, Lenka Moravcová¹ and Petr Pyšek^{1,2}

¹Institute of Botany, The Czech Academy of Sciences, Zámek 1, CZ-252 43 Průhonice, Czech Republic

²Department of Ecology, Faculty of Science, Charles University, Viničná 7, CZ-128 44 Prague, Czech Republic

Author e-mails: hana.skalova@ibot.cas.cz (HS), guowyhgy@gmail.com (WYG), lenka.moravcova@ibot.cas.cz (LM), pysek@ibot.cas.cz (PP)

*Corresponding author

Citation: Skálová H, Guo W-Y, Moravcová L, Pyšek P (2019) Performance of *Ambrosia artemisiifolia* and its potential competitors in an experimental temperature and salinity gradient and implications for management. *Management of Biological Invasions* 10(2): 359–376, <https://doi.org/10.3391/mbi.2019.10.2.10>

Received: 26 September 2018

Accepted: 20 March 2019

Published: 14 May 2019

Handling editor: Catherine Jarnevich

Copyright: © Skálová et al.

This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International - CC BY 4.0).

OPEN ACCESS

Abstract

As it produces large quantities of allergenic pollen that has a serious effect on human health *Ambrosia artemisiifolia* (common ragweed) is among the most noxious invasive plant species in Europe. It is most widespread in southern parts of Eastern and Central Europe and likely to spread into other regions. Thus its suppression is highly desirable. To identify species with a potential to suppress this invasive species, we carried out a growth chamber experiment to investigate the performance (height and weight) of *A. artemisiifolia* and 10 native Central-European species (six grasses and four herbaceous plants), growing in similar habitats and hence potential competitors of ragweed. Two factors were investigated in order to determine the processes that are likely to affect the future spread of *A. artemisiifolia* in Central Europe, i.e. increasing temperatures and winter treatment with salt of roads that serve as dispersal corridors. The plants were reared at five temperatures ranging from 10 to 26 °C and three levels of salinity. The height and weight of *A. artemisiifolia* increased with increasing temperature over the whole range of temperatures tested, with most native species growing best at 22 °C. This indicates that *A. artemisiifolia* will perform better in a warming climate and its spread will be facilitated by the poor performance of native species growing at suboptimal temperatures. As the largest differences in size between *A. artemisiifolia* and the native species were recorded at 10 and 14 °C we recommend that native seed mixtures are sown at ragweed invaded sites early in spring, or the previous autumn, to provide the competitors with a growth advantage at lower temperatures when *A. artemisiifolia* plants are still small and thus competitively weak. With respect to the other factor tested, *A. artemisiifolia* was suppressed similarly by high salinity as most of the native species tested, which indicates that the ragweed spread along roads is not primarily facilitated by its high tolerance of salinity. Different tolerances of native species to salinity indicates that this should be reflected in the selection of species for roadside seeding.

Key words: plant invasions, common ragweed, management, climate change, plant height, biomass, competition, native species, thermal optimum

Introduction

Eradication and prevention of the spread of invasive plants is among the highest priorities of invasion biologists and managers (e.g. Panetta 2015; Daehler et al. 2016; McGeoch et al. 2016; Pergl et al. 2016). Traditionally a

wide variety of methods have been used to eradicate invasive plants, such as manual removal, mechanical methods and herbicides (Randall 1996; Gardener et al. 2010; Panetta 2015). Recently it was shown that native species can act as a filter and using them in ecological restoration may adversely affect the performance of invasive species (Bakker and Wilson 2004; Endress et al. 2008; Carter and Blair 2012; Falk et al. 2013; Jones et al. 2013; Gornish and dos Santos 2016). As the resistance to invasion depends on the identity of the native species planted (Bakker and Wilson 2004; Abella et al. 2011; Allen and Meyer 2014) selection of appropriate species to be used for restoring local plant communities is crucial. Suppression of invasive species by restored communities is especially suitable in areas where plant conservation is the main goal (e.g. in protected areas), or where regular management is difficult (e.g. steep slopes, difficult access and use of machinery) or there is a risk of water contamination (e.g. populations located by water streams). In addition, it is suitable at other sites and especially for controlling species with persistent seed banks that provide an opportunity for populations to survive over time (Goria et al. 2012; Goria and Pyšek 2016). In such species continuous long-term application of traditional methods is needed, which can be costly. Searching for an effective method of suppression is especially desirable for species that have a great socioeconomic impact (Pyšek and Richardson 2010; Pergl et al. 2016).

Ambrosia artemisiifolia L. (common ragweed) is a typical candidate for intensive suppression (Lambdon et al. 2008; DAISIE 2009; Pergl et al. 2016), mainly because it produces large quantities of allergenic pollen (Kazinczi et al. 2008) and causes up to 80% loss in the yield of certain crops (Essl et al. 2015). This annual herbaceous plant was originally introduced into Europe from North America in the 18th century through botanical gardens (Bullock et al. 2012), and then repeatedly as a contaminant of agricultural products (Brandes and Nitzsche 2006; Chauvel et al. 2006). It began to spread and naturalize in Europe in the 1930s, these processes accelerated from the 1960s onward and since the 1990s there has been a rapid spread and increase in abundance of local invasive populations. The largest, recently-recorded European populations are on the Pannonian Plains in Hungary, Croatia, Serbia and Ukraine. There has also been a considerable increase in abundance in southern and central France and northern Italy (Essl et al. 2015). It colonizes mainly anthropogenic habitats such as agricultural and ruderal areas, abandoned fields and roadsides (Chauvel et al. 2006). Populations of *A. artemisiifolia* dominate the early stages of succession in disturbed areas, especially in areas with a warm continental climate (Fumanal et al. 2008). It is predicted that the species will spread further in Europe, favoured by ongoing global warming (Cunze et al. 2013; Richter et al. 2013; Chapman et al. 2014; Storkey et al. 2014; Leiblein-Wild et al. 2016; Mang et al. 2018).

This species reproduces exclusively by seed, with thousands produced per plant and most falling within 1 m of the source plant (Essl et al. 2015). Long-distance seed dispersal is mainly due to human activities, such as the transport of contaminated litter, soil, agricultural products (e.g. crops and bird feed) or with agricultural and construction machinery that inadvertently distributes the seed along transport corridors (Bullock et al. 2012). Seed germination is ~ 90% and decreases with the depth of burial; none of the seeds buried at 10 cm or deeper germinate (Guillemin and Chauvel 2011). The seeds are able to survive in the seed bank for up to 40 years (Darlington 1922). Besides the large seed production and long-term seed survival, spread is facilitated by this species' wide ecological amplitude, tolerance to stress and phenotypic plasticity (Paquin and Aarssen 2004; Fumanal et al. 2008; Leskovšek et al. 2012; Qin et al. 2012; Onen et al. 2017; Yair et al. 2017).

Ambrosia artemisiifolia can be reasonably well controlled in all major crops by chemical and/or mechanical measures (Kazinczi et al. 2008; Buttenschøn et al. 2009; Smith et al. 2013). Well-designed mechanical control seems to be effective along roadsides (Milakovic et al. 2014; Milakovic and Karrer 2016), but for other habitats an effective management still needs to be found. Because of its long persistent seed bank (Darlington 1922), the focus is on searching for cost-efficient measures that remain effective over long periods of time. In this respect, biological control (Guo et al. 2011; Zhou et al. 2014) or suppression by co-occurring highly competitive plants seem most promising (Buttenschøn et al. 2009). The suppression of *A. artemisiifolia* by *Erigeron* species in early successional fields in its native range is reported (Raynal and Bazzaz 1975). A similar result is reported for pot experiments with native European species (e.g. Leskovšek et al. 2012; Laube et al. 2015; Yannelli et al. 2017a, b) and with seed mixtures in the field (Gentili et al. 2015, 2017; Cardarelli et al. 2018).

These results suggest that the negative effects on *A. artemisiifolia* are likely to increase if the competitive seed mixtures are designed specifically for this purpose, and reflect the ecological demands of the target invader. *Ambrosia artemisiifolia* is a thermophilous species and it is predicted that increasing temperatures will facilitate its future spread (Cunze et al. 2013; Richter et al. 2013; Chapman et al. 2014; Storkey et al. 2014; Leiblein-Wild et al. 2016). Thus, the potential competitors should match the demands of *A. artemisiifolia* not only in terms of soil, water and irradiation requirements but also temperature. Because in Europe *A. artemisiifolia* often occurs along roads where winter treatment with salt has been traditionally applied (Milakovic et al. 2014; Essl et al. 2015; Hrabovský et al. 2016; Skálová et al. 2017), its strong performance in this habitat may be due to its salt tolerance (DiTommaso et al. 2000; DiTommaso 2004; Eom et al. 2013). To optimize the competitive mixtures, the potential competitors need to be tested also for their tolerance of salt.

To take into account the above factors we used 12 potential competitors (six herbaceous plants and six grasses) of *A. artemisiifolia*, which are widespread species native to Europe with similar ecological demands to *A. artemisiifolia*, and determined their performance relative to that of *A. artemisiifolia* in growth chambers at different temperatures and salinities. We performed a series of experiments to determine (i) what is the optimum temperature for growth of *A. artemisiifolia*? (ii) does its optimal temperature range overlap with that of potential native competitors? (iii) is this species more tolerant to salt than potential native competitors?

Materials and methods

Selection of competitive species

Potential competitors of *Ambrosia artemisiifolia* were chosen from species that are native or archaeophytes in the Czech Republic (hereafter referred to as native). Archaeophytes are species that were introduced into the Czech Republic before AD 1500, mostly from the Mediterranean region and are a permanent component of the local flora (Pyšek et al. 2002, 2012). The selected species are widespread and have similar ecological demands to *A. artemisiifolia*, which were assessed using Ellenberg indicator values (Ellenberg 1992), occur in the same habitat and compete with *A. artemisiifolia* (G. Karrer, pers. comm.). We chose six species of grass (*Agropyron repens*, *Arrhenatherum elatius*, *Bromus erectus*, *Festuca rubra*, *Phleum pratense* and *Poa compressa*) and six herbaceous plants (*Achillea millefolium*, *Atriplex sagittata*, *Falcaria vulgaris*, *Lotus corniculatus*, *Plantago media* and *Tanacetum vulgare*); see Table 1 for details. The species names follow Kubát et al. (2002).

Seeds of these species were collected at various localities in the Czech Republic in the summer and autumn of 2015. *Ambrosia artemisiifolia* and *T. vulgare* were collected at a ruderal site in the north-western suburb of the town of Pečky (50°5'36.800"N; 15°1'5.822"E), *A. repens* at a ruderal site in the eastern suburb of the village of Průhonice (50°0'3.796"N; 14°34'14.093"E) and *A. sagittata* at a ruderal site close to the railway station in the street Pod Pařankou, Prague 7 (50°6'54.863"N; 14°23'31.066"E). Seeds of the remaining species were obtained from Planta naturalis (<http://planta-naturalis.com>); the seeds come from plants grown in the cultivation garden close to the village of Markvartice (50°25'46"N; 15°11'54"E).

Experimental conditions

Seeds of *Ambrosia artemisiifolia* and *Falcaria vulgaris* were cold-stratified on wet sand in the dark at 4 °C for 2 months and then germinated at a diurnally fluctuating temperature of 25/10 °C (day/night cycle 12/12 h) together with the seeds of the other species. As none or a very low percentage of the seed of *F. vulgaris* and *Tanacetum vulgare* germinated they

Table 1. Characteristics of the species included in this study; H = herbaceous plant, G = grass, A = annual, P = perennial; Ellenberg indicator values: L = light availability, N = nutrient (N) availability, T = temperature, W = water availability; n = not defined mostly due to wide amplitude.

Species	Herb/Grass	Life span	L	N	T	W
<i>Ambrosia artemisiifolia</i>	H	A	9	6	7	4
<i>Achillea millefolium</i>	H	P	8	5	n	4
<i>Agropyron repens</i>	G	P	7	7	6	n
<i>Arrhenatherum elatius</i>	G	P	8	7	5	n
<i>Atriplex sagittata</i>	H	A	9	7	7	n
<i>Bromus erectus</i>	G	P	8	3	5	3
<i>Falcaria vulgaris</i>	H	P	7	n	7	3
<i>Festuca rubra</i>	G	P	n	n	n	6
<i>Lotus corniculatus</i>	H	P	7	3	n	4
<i>Phleum pratense</i>	G	P	n	7	n	5
<i>Plantago media</i>	H	P	n	3	n	4
<i>Poa compressa</i>	G	P	n	3	n	3
<i>Tanacetum vulgare</i>	H	P	6	5	6	5

Table 2. Average, minimum and maximum temperatures (°C) in the individual regimes.

Average	Maximum	Minimum
10	14	6
14	18	9
18	22.5	13
22	27.5	17
26	30	21

were not included in the experiment. Germinated seeds with a radicle or a first leaf (in grasses) of length 1–10 mm were individually transplanted to 39 ml containers filled with pure silica sand. Ten to 24 germinated seeds were planted, giving at least five individuals harvested for all the species at each temperature and salinity, except for *Poa compressa* at 10 °C (two plants) and 22 °C (four plants), and *A. artemisiifolia*, *Plantago media* and *P. compressa* at the high salinity (four, two and no plants, respectively), which was due to extremely poor growth and high mortality of the plants under these conditions. A total of 835 plants were harvested.

The plants were grown in growth chambers (Vötsch 1014 by VÖTSCH Industrietechnik GmbH, Federal Republic of Germany) with identical irradiation: day/night regime 13 h/7 h with a corresponding full light/dark alternation and 2 × 2 h gradual change between dark and full light; full light was characterized by photosynthetically active radiation of 360 µmol m⁻² s⁻¹, red radiation (R, λ = 660 nm) of 26 µmol m⁻² s⁻¹ and far-red radiation (FR, λ = 730 nm) of 15 µmol m⁻² s⁻¹, R/FR 1.73; which was measured using a SPh 2020 photometer from Optické dílny Turnov, Czech Republic, and 80% air moisture. The temperatures used simulated the gradually changing daily temperature recorded in the field in the Czech Republic in spring and summer and were possible to maintain in the growth chambers used for experimentation. The average temperature in individual regimes was 10, 14, 18, 22 and 26 °C (for details see Table 2).

The plants were supplied with 50% Knop nutrient solution. For the plants subjected to different salinities a solution of NaCl was added to achieve 25 mMol and 75 mMol. These plants were kept only at 14 °C. We used this regime as it corresponds to the temperature in time of seedling growth in Central Europe. To achieve a stable nutrient supply and salinity levels, conductivity of the solutions was measured on Monday, Wednesday, Friday of each week and nutrient solution or demineralized water was added to keep the conductivity at 1770, 6500 and 15,500 µS cm⁻¹, respectively. In addition, the solution was completely changed every week.

Characteristics measured

The plants were monitored on Monday, Wednesday, and Friday of each week and the appearance of the first real leaf or leaf pair was recorded. Four weeks after the appearance of leaves the plants were cut at the surface of the sand, and their height and width (measured as the horizontal distance of the two most distant parts of the canopy) was recorded, as well as the length of the longest leaf, measured as the distance from the leaf base to the tip. We also recorded the number of branches (or daughter tillers where applicable) and the number of leaves on the main stem or tiller. After these measurements, soil was washed from the roots, plants were divided into shoots and roots, dried at 70 °C for 8 h and then weighed. Root/shoot ratio was calculated. For plants with very small roots that were impractical to weigh, the weight of the roots was arbitrarily set at 0.0001 g and the root/shoot ratio was not calculated.

Data analysis

All analyses were carried out in R (v. 3.3.2, R Core Team 2016), with packages/functions specified in each analysis. We ran a principal component analysis (PCAs), including all the variables measured, to determine the similarity of the species in each treatment and detect the most important factors or contributors influencing response. PCAs were run using *prcomp* function in R.

To determine the responses of specific traits to treatments, we further ran linear models for each response variable with species and treatments (either temperature or salinity) as fixed factors. For continuous response variables, the normality and homogeneity of variances were checked and further certified using diagnostic plots. For count variables, i.e. numbers of leaves and branches, generalized linear models (GLM) with a logit link function and Poisson distribution of errors were used. R package *lme4* (Bates et al. 2015) was used in this analysis. Due to the high correlations between traits (Figure 1), we focused below on the two most important traits: total weight and plant height. The differences among species, treatments and their interaction were post hoc tested using Tukey HSD

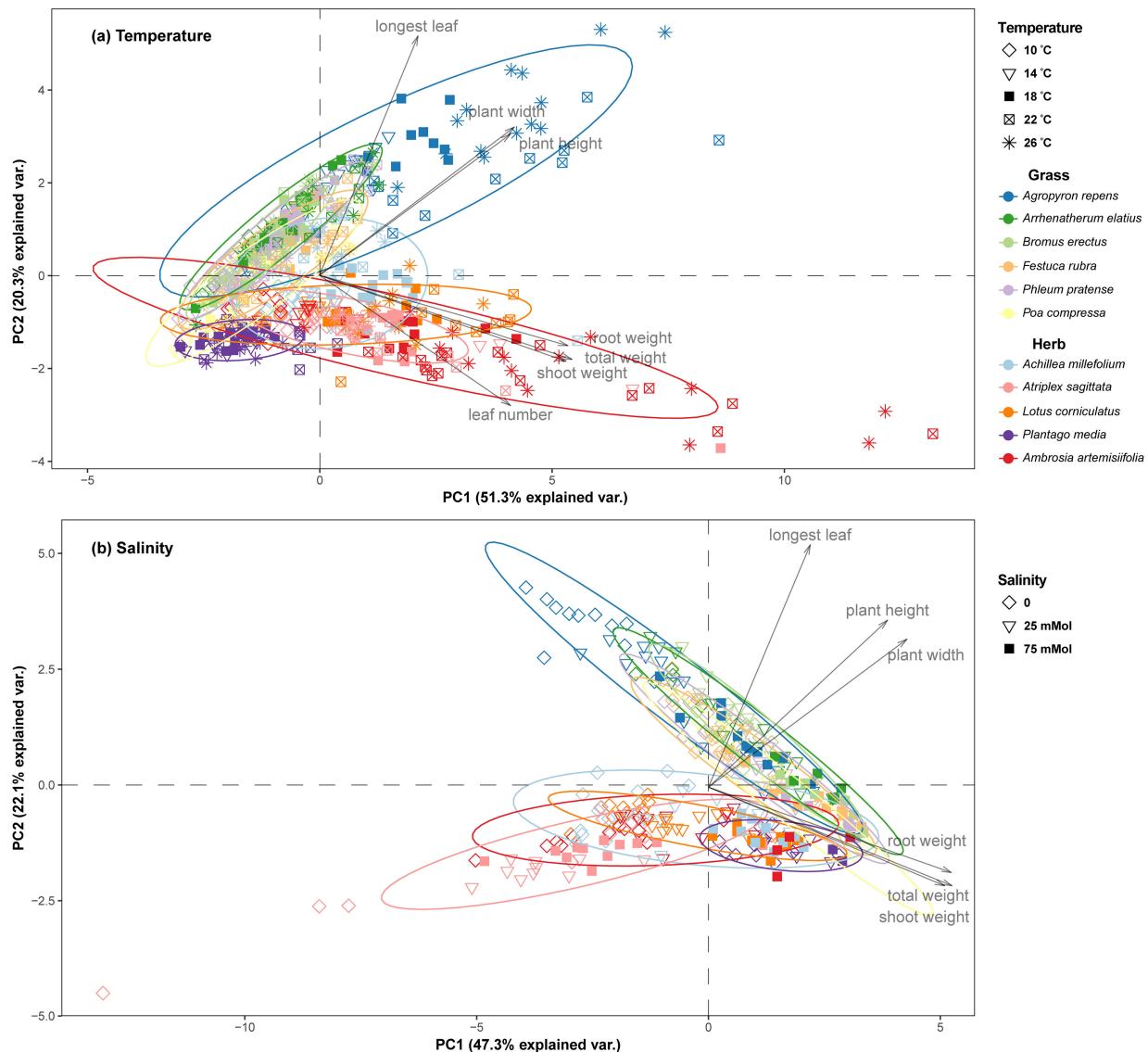


Figure 1. Principal component analysis (PCA) of the plant characteristics measured at different temperatures and salinities. Different colours indicate different species and shapes indicate treatment levels. The ellipses define the 95% confidence intervals of the species. Factor loadings from the principal components analyses of (a) temperature and (b) salinity are shown. The arrows indicate traits with coefficients higher than 0.6.

pairwise comparison of least-square (LS) means and the *lsmeans* package (Lenth 2016). The LS means and the confidence intervals were back-transformed to original measurements of the traits for ease of interpretation.

To assess the degree of plasticity, the environmentally standardized plasticity index (ESPI) was calculated as follows:

$$ESPI = \frac{\max - \min}{\text{distance}}$$

where *max* and *min* were the maximum and minimum values of the means of the trait recorded in each treatment and *distance* was the absolute difference between the treatment levels at which maximum and minimum mean values were recorded (Valladares et al. 2006). The ESPI is often used for quantifying the phenotypic change for a given environmental change. ESPIs were calculated for both treatments.

Table 3. Effects of species (*Ambrosia artemisiifolia* and native *Achillea millefolium*, *Agropyron repens*, *Arrhenatherum elatius*, *Atriplex sagittata*, *Bromus erectus*, *Festuca rubra*, *Lotus corniculatus*, *Phleum pratense*, *Plantago media*, *Poa compressa*), salinity and temperature on the traits measured (F-values). Significance of the effects was tested using two-way ANOVAs, with ** indicating $p < 0.01$, *** $p < 0.001$ and ns non-significant difference; df = degree of freedom.

	Temperature			Salinity		
	Species (df = 10)	Temperature (df = 4)	Species × Temperature (df = 40)	Species (df = 10)	Salinity (df = 2)	Species × Salinity (df = 19)
Shoot weight (g)	122.46***	85.21***	3.91***	55.31***	93.63***	2.96***
Root weight (g)	95.27***	43.79***	3.40***	45.32***	95.04***	3.73***
Total weight (g)	119.54***	75.69***	3.76***	55.84***	100.78***	3.19***
Root / shoot ratio	69.19***	32.57***	5.50***	21.64***	13.10***	6.54***
Plant height	83.70***	74.67***	4.30***	30.51***	89.68***	2.00**
Plant width (mm)	57.04***	76.75***	4.41***	25.96***	105.21***	2.19**
Longest leaf (mm)	213.52***	74.52***	3.68***	68.13***	94.10***	2.98***
Number of leaves	200.01***	170.99***	9.05***	64.80***	36.12***	4.29***
Number of branches	104.60***	54.98***	9.31***	22.43***	45.72***	1.62 ns

Results

Temperature and salinity had significant effects on all the variables measured as did species and species × treatments interactions (Table 3). Principal component analysis revealed the similarity between species in each treatment (Figure 1), and separated two groups of variables, the first related to weight and the second to plant shape. Thus, total weight and plant height responses are described in more detail below.

Temperature

Overall, *Ambrosia artemisiifolia* performed better than the native species as assessed by plant growth rate over increasing temperature regimes. Its weight and height increased with increasing temperature (Figures 1a, 2). At 26 °C, only *A. artemisiifolia*, *Festuca rubra* and *Agropyron repens* achieved significantly increased weight, while that of the other species was lower. Except for *Achillea millefolium* which achieved its maximum weight at 18 °C, the other native species reached their maxima at 22 °C. At 26 °C only two species (*A. repens* and *Atriplex sagittata*) were similar in weight to *A. artemisiifolia*, and at lower temperatures this was the case also for *A. millefolium* and *Lotus corniculatus*. Only once was the weight of a native species greater than that of *A. artemisiifolia*, i.e. for *A. sagittata* at 10 °C (Figure 2a). The response of *A. artemisiifolia* to temperature in terms of weight was the most plastic, followed by *A. sagittata*, *A. repens* and *L. corniculatus* (Figure 3a).

Agropyron repens was the only native species in which height increased with temperature and it was also taller than *A. artemisiifolia* at all temperatures (Figure 2b). At 26 °C only three other species (*Arrhenatherum elatius*, *F. rubra* and *L. corniculatus*) were comparable to *A. artemisiifolia*, at lower temperatures this was the case for most of the other species and *A. elatius* and *L. corniculatus* were sometimes even taller (Figure 2b). The most plastic response in terms of height was recorded in *A. repens*, *L. corniculatus*, *Poa compressa* and *Phleum pratense*, which were more plastic than *A. artemisiifolia* (Figure 3a).

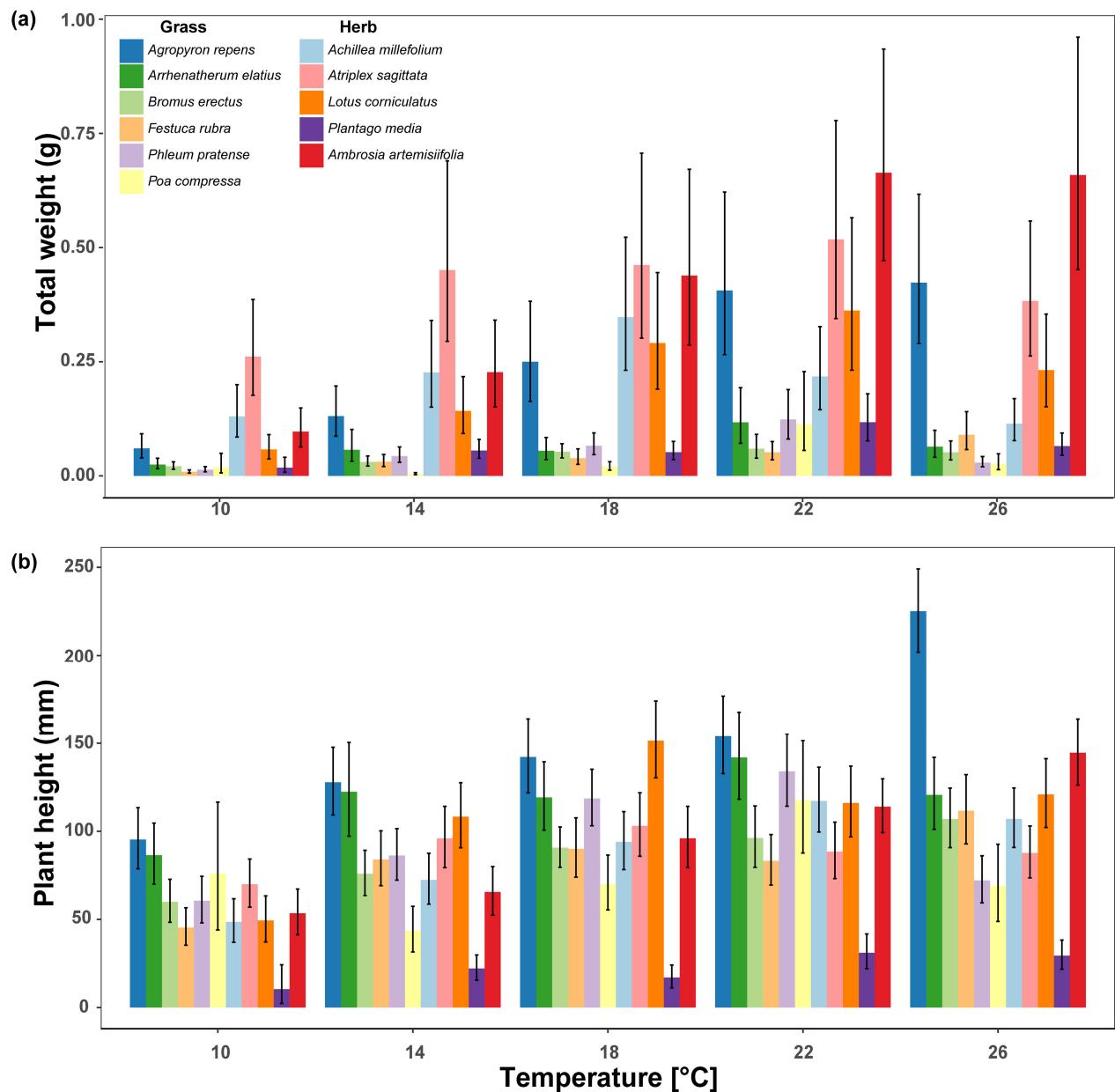


Figure 2. Total weight (a) and height (b) of species recorded at the different temperatures tested. Data are least square (LS) means and 95% confidence intervals (CI), which were back transformed to the units in which the original measurements were made. No overlap between the CIs indicates significant difference between the corresponding species.

Salinity levels

The performance of *Ambrosia artemisiifolia* at the different levels of salinity was comparable to that of the native species. Its weight and height decreased with increasing salinity (Figures 1b, 4) and the same was true for the other species, except *Atriplex sagittata* whose height and weight was the same at all the salinities tested and *Poa compressa* that was not able to grow at the high salinity (75 mMol NaCl). *Ambrosia artemisiifolia* was among the species with the highest weight in the control conditions and at low salinity (25 mMol NaCl) together with *Achillea millefolium*, *Agropyron repens*, *A. sagittata* and *Lotus corniculatus*, while at high salinity its weight was comparable with that of the other species except *A. sagittata*, which was

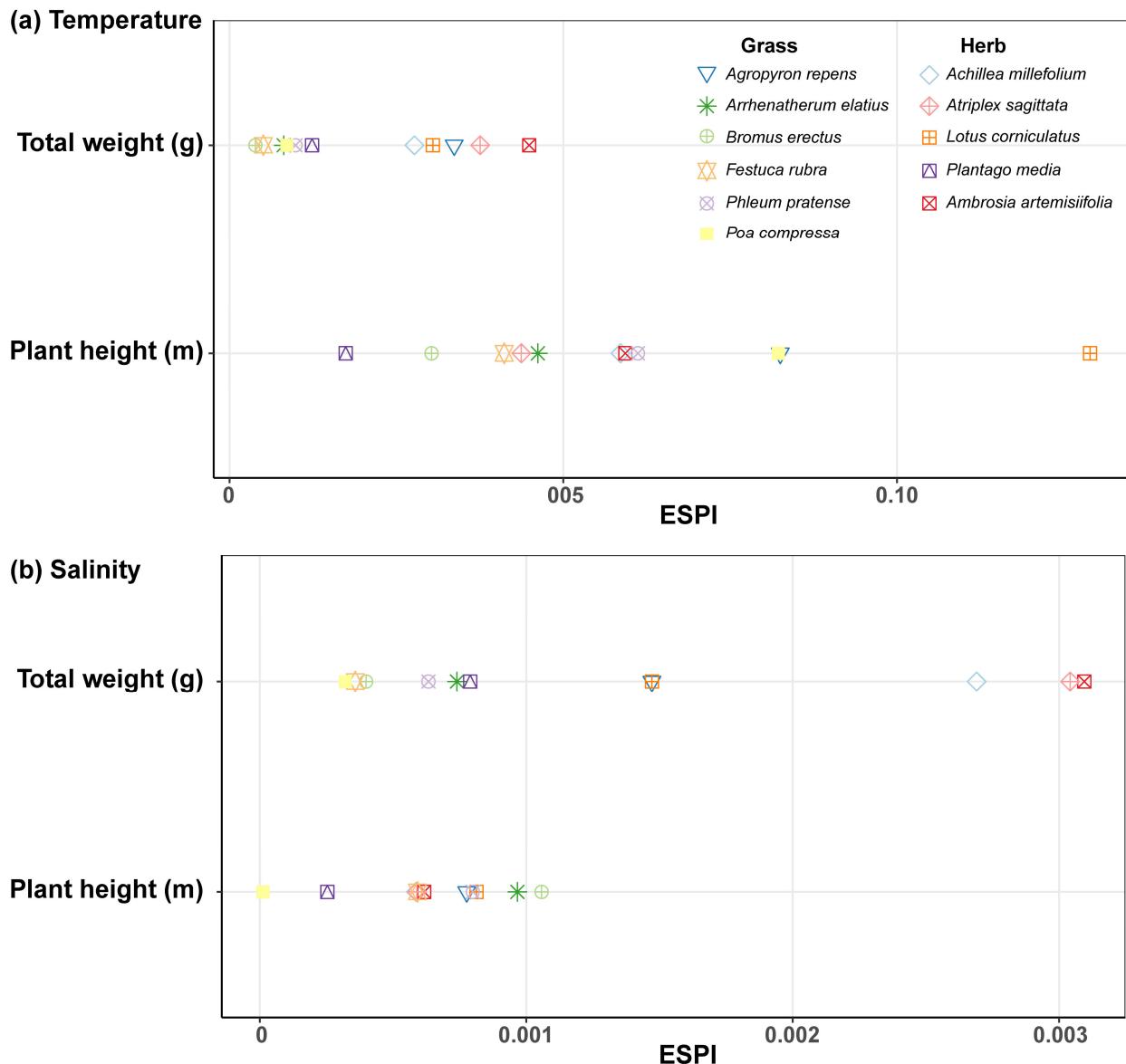


Figure 3. Environmentally standardized plasticity index (ESPI) of each species in the temperature and salinity treatments. Note plant height is different from that in the other tables/figures.

heavier (Figure 4a). *Ambrosia artemisiifolia* responded to salinity, in terms of weight, most plastically, followed by *A. sagittata*, and *A. millefolium* (Figure 3b). The pattern in plant height was similar at both levels of salinity (Figure 4b), e.g. *A. repens*, *Arrhenatherum elatius*, *A. sagittata* and *L. corniculatus* were taller than *A. artemisiifolia* at both levels of salinity and the other species, except *Plantago media*, were similar in height. Like its response to temperature, *A. artemisiifolia* was moderately plastic in terms of height (Figure 3b).

Discussion

Temperature

In this study the weight and height of *Ambrosia artemisiifolia* increased with temperature, which together with the previously reported increase in

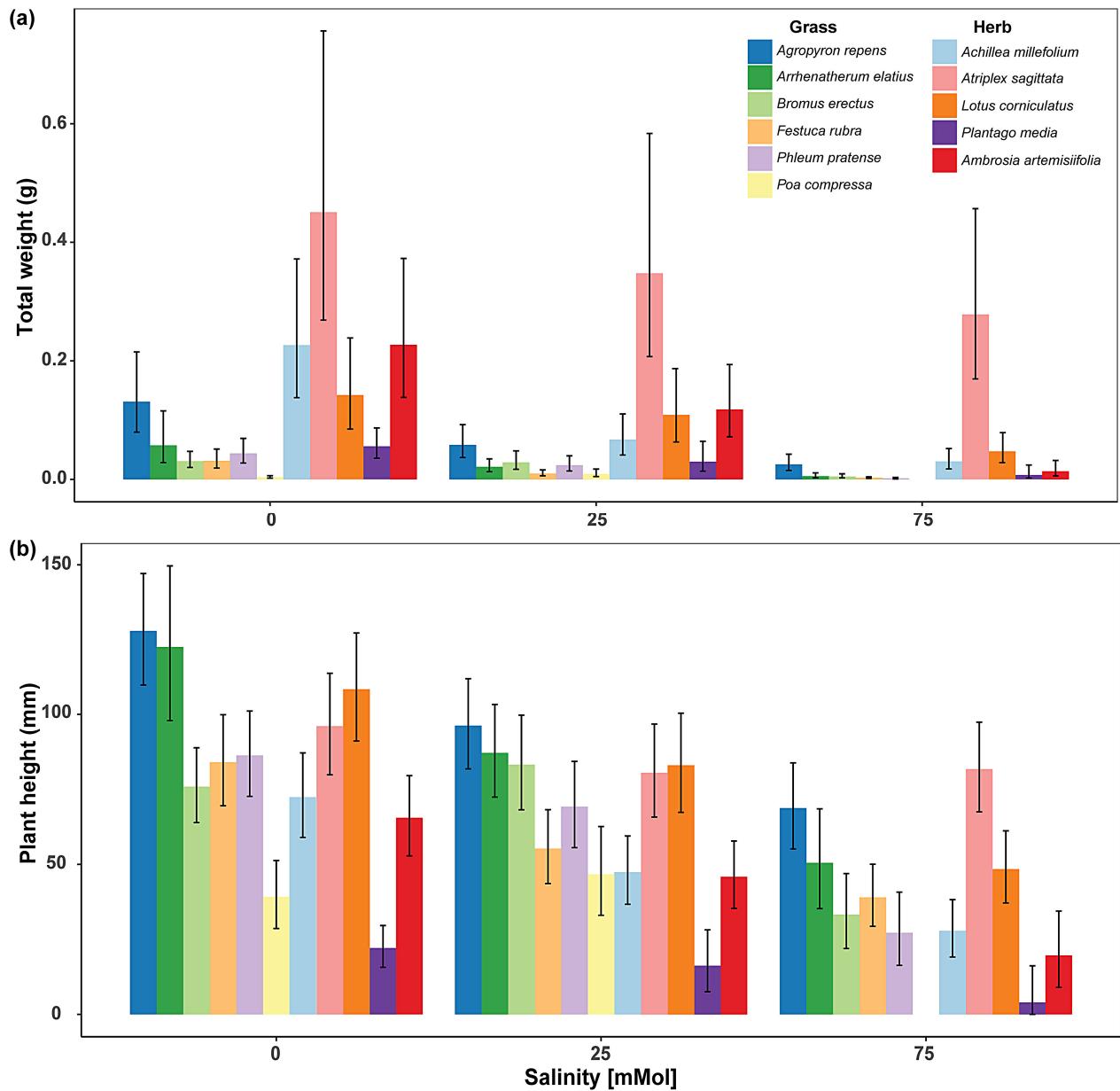


Figure 4. Total weight (a) and height (b) of species grown at different salinities. Data are least square (LS) means and 95% confidence intervals (CI), which were back transformed to the units in which the original measurements were made. No overlap between the CIs indicates significant difference between the corresponding species.

rate of development (Deen et al. 1998; Skálová et al. 2015) may account for the successful invasion of this species in the warmer areas of Central Europe (Essl et al. 2009; Skálová et al. 2017). On the other hand, most of the species native to Europe (including archaeophytes) that we considered to be potential competitors were tallest and achieved greater weight at the lower temperature of 22 °C, which corresponds to the mean temperature in late spring / early summer in warm regions in the Czech Republic (Tolasz et al. 2007). Even in terms of best performance only one species, *Agropyron repens*, was taller than *A. artemisiifolia* and most other species were similar in height and only three species were of similar weight. This suggests the strong competitive potential of *A. artemisiifolia* under warm conditions under natural settings. The greatest differences in size between *A. artemisiifolia*

and the native species were recorded at 10 or 14 °C. Thus any competitive advantage of the native species is likely to be greatest in spring or autumn, so the seeds of these species should be sown early in spring, or even the previous autumn, so that they can germinate and reach a large size before *A. artemisiifolia* germination starts in late April.

An established plant community can limit the germination of seed in long-lived seed banks (Darlington 1922; Gioria et al. 2014) and reduce the abundance and growth of *A. artemisiifolia* (e.g. Gentili et al. 2017; Cardarelli et al. 2018). Species with similar ecological demands to *A. artemisiifolia* are likely to suppress it during its development as they are similar in size and weight and establish a canopy before the peak of germination of *A. artemisiifolia*. Five of the 10 species tested proved to be potential competitors of common ragweed. The annual *Atriplex sagittata* is suitable only for early spring sowing, because it was the only species that increased in weight more than *A. artemisiifolia* at low temperatures. However, *A. sagittata* responded to high temperatures by shedding leaves, which will probably limit its competitiveness when temperatures increase. Perennial species, especially those that germinate in autumn, are particularly suitable. *Agropyron repens* appears to be the best potential competitor, is similar in weight to *A. artemisiifolia* and is taller at all the temperatures tested. *Lotus corniculatus* and *Achillea millefolium*, with similar weights and slightly less or similar heights at 22 °C, and *Arrhenatherum elatius*, that is taller than *A. artemisiifolia* at low temperatures, are also suitable for including in competitive seed mixtures. The other species are less suitable as they are shorter in stature. However, other characteristics such as tolerance of environmental stress or allelopathy, which is documented for *A. artemisiifolia* (Novak et al. 2018), may play a role under field conditions. This study focused on the growth of young plants that may differ from that of adult plants. On the other hand, the performance of juveniles may influence the success of alien species in the field (Sans et al. 2004; Richardson 2006; Grotkopp and Rejmánek 2007; van Kleunen and Johnson 2007; Skálová et al. 2012; Čuda et al. 2016).

The success of some invasive plants is related to their plasticity (Richards et al. 2006), which is greater than that of native species (Funk 2008; Davidson et al. 2011; but see Palacio-Lopez and Gianoli 2011; Liu and van Kleunen 2017). This is likely to be true for *A. artemisiifolia*, which in our study had the highest plasticity index for weight and an intermediate one for height compared to native species. Other studies also report that the development of *A. artemisiifolia* is very plastic (e.g. Paquin and Aarssen 2004; Leskovšek et al. 2012; Ortmans et al. 2016; Onen et al. 2017), but only rarely is it compared with that of native species (e.g. Qin et al. 2012). These studies showed that *A. artemisiifolia* can tolerate unfavourable conditions, which probably further facilitates its success as an invasive species (Richards et al. 2006; Davidson et al. 2011).

The increase in weight and height of *A. artemisiifolia* with increase in temperature could facilitate its further spread, as temperatures are predicted to increase due to global warming (Cunze et al. 2013; Richter et al. 2013; Chapman et al. 2014; Storkey et al. 2014; Leiblein-Wild et al. 2016). Its spread may be facilitated not only by improved performance, but also by the poorer performance of native species as they will probably experience suboptimal temperatures. Global warming will probably result in shifts of thermophilous species or ecotypes northwards or even evolution of locally adapted genotypes. However, the northward shift of native species due to climate warming will be probably slower than that of aliens, similarly to the upward spread of native and alien plant species in mountains (Dainese et al. 2017). Aliens generally spread faster than climate is changing, are very phenotypically plastic and well adapted to new selection pressures (Hulme 2014). Using thermophilous species or genotypes native to southern regions of Europe in competitive seed mixtures may be relevant, as warm-adapted genotypes perform better than local genotypes in transplant experiments (Schreiber et al. 2013; Hancock and Hughes 2014; Lu et al. 2014; Wilczek et al. 2014, but see Beierkuhnlein et al. 2011; Bucharová et al. 2016).

Salinity

Increasing salinity resulted in a decrease in weight and height in all species including *A. artemisiifolia*. In addition, *A. artemisiifolia* had the highest plasticity in weight and moderate plasticity in height in response to salinity, which indicate that it suffered similarly or even more than the natives. This contradicts reports of a higher salt tolerance of *A. artemisiifolia* compared to potential competitors in North America (e.g. DiTommaso et al. 2000). However, the cited study is of roadside populations of *A. artemisiifolia* exposed to winter treatment with salt, which were later shown to be more tolerant of salt than field populations (DiTommaso 2004; Eom et al. 2013). Seeds used in our experiment were collected at one ruderal site not exposed to salt treatment. Our results suggest that the spread of *A. artemisiifolia* along European roads (Essl et al. 2015; Hrabovský et al. 2016; Milakovic and Karrer 2016; Skálová et al. 2017) is not primarily facilitated by its high tolerance of salinity but further study with additional roadside populations are warranted to determine their tolerance. It is likely that other factors like propagule transport by vehicles (von der Lippe and Kowarik 2007), disturbance (Gelbard and Belnap 2003; Jodoin et al. 2008; Kalwij et al. 2008) and possibly high temperature due to high absorption of radiation by the dark surface of the road is also important (Delgado et al. 2007). However, further evolution of tolerant populations cannot be excluded, as indicated by their existence in its native range (DiTommaso 2004; Eom et al. 2013).

In considering plant/plant or plant/community interactions for suppression, an ideal competitive seed mixture for roadsides should consist of tall, vigorously growing species with low plasticity and high tolerance of salt. From our native species set, the perennials *L. corniculatus* and *A. elatius* best match these criteria, followed by *A. repens*, *Bromus erectus*, *Festuca rubra* and *Phleum pratense*. *Atriplex sagittata* performs better than *A. artemisiifolia* at high salinities but being an annual and intolerant of high temperatures may decrease its competitive effectiveness.

Acknowledgements

Our thanks are due to Vendula Havlíčková, Marie Brůnová and Zuzana Sixtová for technical assistance. Tony Dixon kindly improved our English. The study was supported by project LD15157 from Ministry of Education, Youth and Sports of the Czech Republic, grant no. 19-20405S by GACR, long-term research development project RVO 67985939 (The Czech Academy of Sciences), and EXPRO grant no. 19-28807X (Czech Science Foundation). We also acknowledge support from EU COST Action FA1203 ‘Sustainable management of *Ambrosia artemisiifolia* in Europe (SMARTER)’. Our thanks are also due to three reviewers who provided us valuable suggestions to improve the manuscript.

References

- Abella SR, Craig DJ, Chiquoine LP, Prengaman KA, Schmid SM, Embrey TM (2011) Relationships of native desert plants with red brome (*Bromus rubens*): toward identifying invasion-reducing species. *Invasive Plant Science and Management* 4: 115–124, <https://doi.org/10.1614/ipsm-d-10-00013.1>
- Allen PS, Meyer SE (2014) Community structure affects annual grass weed invasion during restoration of a shrub-steppe ecosystem. *Invasive Plant Science and Management* 7: 1–13, <https://doi.org/10.1614/ipsm-d-13-00021.1>
- Bakker JD, Wilson SD (2004) Using ecological restoration to constrain biological invasion. *Journal of Applied Ecology* 41: 1058–1064, <https://doi.org/10.1111/j.0021-8901.2004.00962.x>
- Bates D, Mächler M, Bolker BM, Walker SC (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67: 1–48, <https://doi.org/10.18637/jss.v067.i01>
- Beierkuhnlein C, Thiel D, Jentsch A, Willner E, Kreyling J (2011) Ecotypes of European grass species respond differently to warming and extreme drought. *Journal of Ecology* 99: 703–713, <https://doi.org/10.1111/j.1365-2745.2011.01809.x>
- Brandes D, Nitzsche J (2006) Biology, introduction, dispersal, and distribution of common ragweed (*Ambrosia artemisiifolia* L.) with special regard to Germany. *Nachrichtenblatt des Deutschen Pflanzenschutzdienstes* 58: 286–291
- Bucharová A, Durka W, Hermann JM, Holzel N, Michalski S, Kollmann J, Bossdorf O (2016) Plants adapted to warmer climate do not outperform regional plants during a natural heat wave. *Ecology and Evolution* 6: 4160–4165, <https://doi.org/10.1002/ece3.2183>
- Bullock J, Chapman D, Schaffer S, Roy D, Girardello M, Haynes T, Beal S, Wheeler B, Dickie I, Phang Z, Tinch R, Čivić K, Delbaere B, Jones-Walters L, Hilbert A, Schrauwen A, Prank M, Sofiev M, Niemelä S, Räisänen P, Lees B, Skinner M, Finch S, Brough C (2012) Assessing and controlling the spread and the effects of common ragweed in Europe. European Commission, Brussels. Final Report ENV.B2/ETU/2010/0037, 456 pp
- Buttenschøn RM, Waldspühl S, Bohren C (2009) Guidelines for management of common ragweed, *Ambrosia artemisiifolia*. http://internationalragweedsociety.org/smarter/wp-content/uploads/Ambrosia-management-guidelines-2009_AMBROSIA-EUPHRESCO_eng.pdf
- Cardarelli E, Musacchio A, Montagnani C, Bogliani G, Citterio S, Gentili R (2018) *Ambrosia artemisiifolia* control in agricultural areas: effect of grassland seeding and herbivory by the exotic leaf beetle *Ophraella communa*. *NeoBiota* 38: 1–22, <https://doi.org/10.3897/neobiota.38.23562.suppl1>
- Carter DL, Blair JM (2012) High richness and dense seeding enhance grassland restoration establishment but have little effect on drought response. *Ecological Applications* 22: 1308–1319, <https://doi.org/10.1890/11-1970.1>
- Chapman DS, Haynes T, Beal S, Essl F, Bullock JM (2014) Phenology predicts the native and invasive range limits of common ragweed. *Global Change Biology* 20: 192–202, <https://doi.org/10.1111/gcb.12380>
- Chauvel B, Dessaint F, Cardinal-Legrand C, Bretagnolle F (2006) The historical spread of *Ambrosia artemisiifolia* L. in France from herbarium records. *Journal of Biogeography* 33: 665–673, <https://doi.org/10.1111/j.1365-2699.2005.01401.x>

- Čuda J, Skálová H, Janovský Z, Pyšek P (2016) Juvenile biological traits of *Impatiens* species are more strongly associated with naturalization in temperate climate than their adult traits. *Perspectives in Plant Ecology, Evolution and Systematics* 20: 1–10, <https://doi.org/10.1016/j.ppees.2016.02.007>
- Cunze S, Leiblein MC, Tackenberg O (2013) Range expansion of *Ambrosia artemisiifolia* in Europe is promoted by climate change. *ISRN Ecology* 2013: 610126, <https://doi.org/10.1155/2013/610126>
- Daehler CC, van Kleunen M, Pyšek P, Richardson DM (2016) EMAPi 2015: Highlighting links between science and management of alien plant invasions. In: Daehler CC, van Kleunen M, Pyšek P, Richardson DM (eds), Proceedings of 13th International EMAPi Conference, Waikoloa, Hawaii. *NeoBiota* 30: 1–3, <https://doi.org/10.3897/neobiota.30.9594>
- Dainese M, Aikio S, Hulme PE, Bertolli A, Prosser F, Marini L (2017) Human disturbance and upward expansion of plants in a warming climate. *Nature Climate Change* 7: 577–580, <https://doi.org/10.1038/nclimate3337>
- DAISIE (2009) Handbook of Alien Species in Europe. Springer, Dordrecht, The Netherlands, 399 pp
- Darlington HT (1922) Dr. W. J. Beal's seed-viability experiment. *American Journal of Botany* 9: 266–269, <https://doi.org/10.1002/j.1537-2197.1922.tb05672.x>
- Davidson AM, Jennions M, Nicotra AB (2011) Do invasive species show higher phenotypic plasticity than native species and, if so, is it adaptive? A meta-analysis. *Ecology Letters* 14: 419–431, <https://doi.org/10.1111/j.1461-0248.2011.01596.x>
- Deen W, Hunt LA, Swanton CJ (1998) Photothermal time describes common ragweed (*Ambrosia artemisiifolia* L.) phenological development and growth. *Weed Science* 46: 561–568
- Delgado JD, Arroyo NL, Arévalo JR, Fernández-Palacios JM (2007) Edge effects of roads on temperature, light, canopy cover, and canopy height in laurel and pine forests (Tenerife, Canary Islands). *Landscape and Urban Planning* 81: 328–340, <https://doi.org/10.1016/j.landurbplan.2007.01.005>
- DiTommaso A (2004) Germination behavior of common ragweed (*Ambrosia artemisiifolia*) populations across a range of salinities. *Weed Science* 52: 1002–1009, <https://doi.org/10.1614/ws-04-030r1>
- DiTommaso A, Choy J, Watson AK (2000) Seed germination of common ragweed (*Ambrosia artemisiifolia* L.) roadside populations and of potential competitor species under saline conditions. *Weed Science Society of America Abstracts* 40: 17–18
- Ellenberg H (1992) Zeigerwerte von Pflanzen in Mitteleuropa [Handbook of Central European plant species]. *Scripta Geobotanica* 18: 1–258
- Endress BA, Parks CG, Naylor BJ, Radosevich SR (2008) Herbicide and native grass seeding effects on sulfur cinquefoil (*Potentilla recta*)-infested grasslands. *Invasive Plant Science and Management* 1: 50–58, <https://doi.org/10.1614/ipsm-07-005.1>
- Eom SH, DiTommaso A, Weston LA (2013) Effects of soil salinity in the growth of *Ambrosia artemisiifolia* biotypes collected from roadside and agricultural field. *Journal of Plant Nutrition* 36: 2191–2204, <https://doi.org/10.1080/01904167.2013.836226>
- Essl F, Dullinger S, Kleinbauer I (2009) Changes in the spatiotemporal patterns and habitat preferences of *Ambrosia artemisiifolia* during its invasion of Austria. *Preslia* 81: 119–133
- Essl F, Biro K, Brandes D, Broennimann O, Bullock JM, Chapman DS, Chauvel B, Dullinger S, Fumanal B, Guisan A, Karrer G, Kazinczi G, Kueffer C, Laitung B, Lavoie C, Leitner M, Mang T, Moser D, Muller-Scharer H, Petitpierre B, Richter R, Schaffner U, Smith M, Starfinger U, Vautard R, Vogl G, von der Lippe M, Follak S (2015) Biological flora of the British Isles: *Ambrosia artemisiifolia*. *Journal of Ecology* 103: 1069–1098, <https://doi.org/10.1111/1365-2745.12424>
- Falk AD, Fulbright TE, Smith FS, Brennan LA, Ortega-Santos AJ, Benn S (2013) Does seeding a locally adapted native mixture inhibit ingress by exotic plants? *Restoration Ecology* 21: 474–480, <https://doi.org/10.1111/j.1526-100x.2012.00918.x>
- Fumanal B, Girod C, Fried G, Bretagnolle F, Chauvel B (2008) Can the large ecological amplitude of *Ambrosia artemisiifolia* explain its invasive success in France? *Weed Research* 48: 349–359, <https://doi.org/10.1111/j.1365-3180.2008.00627.x>
- Funk JL (2008) Differences in plasticity between invasive and native plants from a low resource environment. *Journal of Ecology* 96: 1162–1173, <https://doi.org/10.1111/j.1365-2745.2008.01435.x>
- Gardener MR, Atkinson R, Rentería JL (2010) Eradications and people: lessons from the plant eradication program in Galapagos. *Restoration Ecology* 18: 20–29, <https://doi.org/10.1111/j.1526-100x.2009.00614.x>
- Gelbard JL, Belnap J (2003) Roads as conduits for exotic plant invasions in a semiarid landscape. *Conservation Biology* 17: 420–432, <https://doi.org/10.1046/j.1523-1739.2003.01408.x>
- Gentili R, Gilardelli F, Ciappetta S, Ghiani A, Citterio S (2015) Inducing competition: intensive grassland seeding to control *Ambrosia artemisiifolia* L. *Weed Research* 55: 278–288, <https://doi.org/10.1111/wre.12143>
- Gentili R, Montagnani C, Gilardelli F, Guarino MF, Citterio S (2017) Let native species take their course: *Ambrosia artemisiifolia* replacement during natural or “artificial” succession. *Acta Oecologica-International Journal of Ecology* 82: 32–40, <https://doi.org/10.1016/j.actao.2017.05.007>

- Gioria M, Pyšek P (2016) The legacy of plant invasions: changes in the soil seed bank of invaded plant communities. *BioScience* 66: 40–53, <https://doi.org/10.1093/biosci/biv165>
- Gioria M, Pyšek P, Moravcová L (2012) Soil seed banks in plant invasions: promoting species invasiveness and long-term impact on plant community dynamics. *Preslia* 84: 327–350
- Gioria M, Jarošík V, Pyšek P (2014) Impact of invasions by alien plants on soil seed bank communities: emerging patterns. *Perspectives in Plant Ecology, Evolution and Systematics* 16: 132–142, <https://doi.org/10.1016/j.ppees.2014.03.003>
- Gornish ES, dos Santos PA (2016) Invasive species cover, soil type, and grazing interact to predict long-term grassland restoration success. *Restoration Ecology* 24: 222–229, <https://doi.org/10.1111/rec.12308>
- Grotkopp E, Rejmánek M (2007) High seedling relative growth rate and specific leaf area are traits of invasive species: phylogenetically independent contrasts of woody angiosperms. *American Journal of Botany* 94: 526–532, <https://doi.org/10.3732/ajb.94.4.526>
- Guillemin JP, Chauvel B (2011) Effects of the seed weight and burial depth on the seed behavior of common ragweed (*Ambrosia artemisiifolia*). *Weed biology and Management* 11: 217–223, <https://doi.org/10.1111/j.1445-6664.2011.00423.x>
- Guo J-Y, Zhou Z-S, Zheng X-W, Chen H-S, Wan F-H, Luo Y-H (2011) Control efficiency of leaf beetle, *Ophraella communa*, on the invasive common ragweed, *Ambrosia artemisiifolia*, at different growing stages. *Biocontrol Science and Technology* 21: 1049–1063, <https://doi.org/10.1080/09583157.2011.603823>
- Hancock N, Hughes L (2014) Turning up the heat on the provenance debate: testing the “local is best” paradigm under heatwave conditions. *Austral Ecology* 39: 600–611, <https://doi.org/10.1111/aec.12122>
- Hrabovský M, Ščevková J, Mičieta K, Lafférsová J, Dušička J (2016) Expansion and erobiology of *Ambrosia artemisiifolia* L. in Slovakia. *Annals of Agricultural and Environmental Medicine* 23: 141–147, <https://doi.org/10.5604/12321966.1196854>
- Hulme PE (2014) Alien plants confront expectations of climate change impacts. *Trends in Plant Science* 19: 547–549, <https://doi.org/10.1016/j.tplants.2014.05.003>
- Jodoin Y, Lavoie C, Villeneuve P, Theriault M, Beaulieu J, Belzile F (2008) Highways as corridors and habitats for the invasive common reed *Phragmites australis* in Quebec, Canada. *Journal of Applied Ecology* 45: 459–466, <https://doi.org/10.1111/j.1365-2664.2007.01362.x>
- Jones CC, Dreyer GD, Barrett N (2013) Evaluating the success of seed sowing in a New England grassland restoration. *Natural Areas Journal* 33: 214–221, <https://doi.org/10.3375/043.033.0211>
- Kalwij JM, Milton SJ, McGeoch MA (2008) Road verges as invasion corridors? A spatial hierarchical test in an arid ecosystem. *Landscape Ecology* 23: 439–451, <https://doi.org/10.1007/s10980-008-9201-3>
- Kazinczi G, Béres I, Novák R, Biró K, Pathy Z (2008) Common ragweed (*Ambrosia artemisiifolia*). A review with special regards to the results in Hungary. II. Importance and harmful effect, allergy, habitat, allelopathy and beneficial characteristics. *Herbologia* 9: 93–118
- Kubát K, Hrouda L, Chrtěk J jun, Kaplan Z, Kirchner J, Štěpánek J (2002) Klíč ke květeně České republiky. [Key to the Flora of the Czech Republic]. Academia, Praha, 928 pp
- Lambdon PW, Pyšek P, Basnou C, Hejda M, Arianoutsou M, Essl F, Jarošík V, Pergl J, Winter M, Anastasiu P, Andriopoulos P, Bazos I, Brundu G, Celesti-Grapow L, Chassot P, Delipetrou P, Josefsson M, Kark S, Klotz S, Kokkoris Y, Kuehn I, Marchante H, Perglová I, Pino J, Vilà M, Zikos A, Roy D, Hulme PE (2008) Alien flora of Europe: species diversity, temporal trends, geographical patterns and research needs. *Preslia* 80: 101–149, <https://doi.org/10.17011/conference/eccb2018/107390>
- Laube J, Ziegler K, Sparks TH, Estrella N, Menzel A (2015) Tolerance of alien plant species to extreme events is comparable to that of their native relatives. *Preslia* 87: 31–53
- Leiblein-Wild MC, Steinkamp J, Hickler T, Tackenberg O (2016) Modelling the potential distribution, net primary production and phenology of common ragweed with a physiological model. *Journal of Biogeography* 43: 544–554, <https://doi.org/10.1111/jbi.12646>
- Lenth RV (2016) Least-squares means: the R package lsmeans. *Journal of Statistical Software* 69: 1–33
- Leskovšek R, Eler K, Batič F, Simončič A (2012) The influence of nitrogen, water and competition on the vegetative and reproductive growth of common ragweed (*Ambrosia artemisiifolia* L.). *Plant Ecology* 213: 769–781, <https://doi.org/10.1007/s11258-012-0040-6>
- Liu Y, van Kleunen M (2017) Responses of common and rare aliens and natives to nutrient availability and fluctuations. *Journal of Ecology* 105: 1111–1122, <https://doi.org/10.1111/1365-2745.12733>
- Lu P, Parker WH, Cherry M, Colombo S, Parker WC, Man R, Roubal N (2014) Survival and growth patterns of white spruce (*Picea glauca* [Moench] Voss) rangewide provenances and their implications for climate change adaptation. *Ecology and Evolution* 4: 2360–2374, <https://doi.org/10.1002/ece3.1100>
- Mang T, Essl F, Moser D, Dullinger S (2018) Climate warming drives invasion history of *Ambrosia artemisiifolia* in central Europe. *Preslia* 90: 59–81, <https://doi.org/10.23855/preslia.2018.059>

- McGeoch MA, Genovesi P, Bellingham PJ, Costello MJ, McGrannachan C, Sheppard A (2016) Prioritizing species, pathways, and sites to achieve conservation targets for biological invasion. *Biological Invasions* 18: 299–314, <https://doi.org/10.1007/s10530-015-1013-1>
- Milakovic I, Karrer G (2016) The influence of mowing regime on the soil seed bank of the invasive plant *Ambrosia artemisiifolia* L. *NeoBiota* 28: 39–49, <https://doi.org/10.3897/neobiota.28.6838>
- Milakovic I, Fiedler K, Karrer G (2014) Management of roadside populations of invasive *Ambrosia artemisiifolia* by mowing. *Weed Research* 54: 256–264, <https://doi.org/10.1111/wre.12074>
- Novak N, Novak M, Baric K, Scepanovic M, Ivic D (2018) Allelopathic potential of segetal and ruderal invasive alien plants. *Journal of Central European Agriculture* 19: 408–422, <https://doi.org/10.5513/jcea01/19.2.2116>
- Onen H, Farooq S, Gunal H, Ozaslan C, Erdem H (2017) Higher tolerance to abiotic stresses and soil types may accelerate common ragweed (*Ambrosia artemisiifolia*) invasion. *Weed Science* 65: 115–127, <https://doi.org/10.1614/ws-d-16-00011.1>
- Ortmans W, Mahy G, Monty A (2016) Effects of seed traits variation on seedling performance of the invasive weed, *Ambrosia artemisiifolia* L. *Acta Oecologica-International Journal of Ecology* 71: 39–46, <https://doi.org/10.1016/j.actao.2016.01.008>
- Palacio-Lopez K, Gianoli E (2011) Invasive plants do not display greater phenotypic plasticity than their native or non-invasive counterparts: a metaanalysis. *Oikos* 120: 1393–1401, <https://doi.org/10.1111/j.1600-0706.2010.19114.x>
- Panetta FD (2015) Weed eradication feasibility: lessons of the 21st century. *Weed Research* 55: 226–238, <https://doi.org/10.1111/wre.12136>
- Paquin V, Aarsen LW (2004) Allometric gender allocation in *Ambrosia artemisiifolia* (Asteraceae) has adaptive plasticity. *American Journal of Botany* 91: 430–438, <https://doi.org/10.3732/ajb.91.3.430>
- Pergl J, Sádlo J, Petrušek A, Laštůvka Z, Musil J, Perglová I, Šanda R, Šefrová H, Šíma J, Vohralík V, Pyšek P (2016) Black, Grey and Watch Lists of alien species in the Czech Republic based on environmental impacts and management strategy. *NeoBiota* 28: 1–37, <https://doi.org/10.3897/neobiota.28.4824>
- Pyšek P, Richardson DM (2010) Invasive species, environmental change and management, and health. *Annual Review of Environment and Resources* 35: 25–55, <https://doi.org/10.1146/annurev-environ-033009-095548>
- Pyšek P, Sádlo J, Mandák B (2002) Catalogue of alien plants of the Czech Republic. *Preslia* 74: 97–186
- Pyšek P, Danihelka J, Sádlo J, Chrtěk J, Chytrý M, Jarošík V, Kaplan Z, Krahulec F, Moravcová L, Pergl J, Štajerová K, Tichý L (2012) Catalogue of alien plants of the Czech Republic (2nd edition): checklist update, taxonomic diversity and invasion patterns. *Preslia* 84: 155–255, <https://doi.org/10.1111/j.1472-4642.2009.00602.x>
- Qin Z, Mao DJ, Quan GM, Zhang JE, Xie JF, DiTomaso A (2012) Physiological and morphological responses of invasive *Ambrosia artemisiifolia* (common ragweed) to different irradiances. *Botany* 90: 1284–1294, <https://doi.org/10.1139/b2012-096>
- R Core Team (2016) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. <http://www.R-project.org/>
- Randall JM (1996) Weed control for the preservation of biological diversity. *Weed Technology* 10: 370–383, <https://doi.org/10.1017/s0890037x00040124>
- Raynal DJ, Bazzaz FA (1975) Interference of winter annuals with *Ambrosia artemisiifolia* in early successional fields. *Ecology* 56: 35–49, <https://doi.org/10.2307/1935298>
- Richards CL, Bossdorf O, Muth NZ, Gurevitch J, Pigliucci M (2006) Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. *Ecology Letters* 9: 981–993, <https://doi.org/10.1111/j.1461-0248.2006.00950.x>
- Richardson DM (2006) Pinus: a model group for unlocking the secrets of alien plant invasions? *Preslia* 78: 375–388
- Richter R, Berger UE, Dullinger S, Essl F, Leitner M, Smith M, Vogl G (2013) Spread of invasive ragweed: climate change, management and how to reduce allergy costs. *Journal of Applied Ecology* 50: 1422–1430, <https://doi.org/10.1111/1365-2664.12156>
- Sans FX, Garcia-Serrano H, Afán I (2004) Life-history traits of alien and native senecio species in the Mediterranean. *Acta Oecologica-International Journal of Ecology* 26: 167–178, <https://doi.org/10.1016/j.actao.2004.04.001>
- Schreiber SG, Ding C, Hamann A, Hacke UG, Thomas BR, Brouard JS (2013) Frost hardiness vs. growth performance in trembling aspen: an experimental test of assisted migration. *Journal of Applied Ecology* 50: 939–949, <https://doi.org/10.1111/1365-2664.12102>
- Skálová H, Havlíčková V, Pyšek P (2012) Seedling traits, plasticity and local differentiation as strategies of invasive species of *Impatiens* in central Europe. *Annals of Botany* 110: 1429–1438, <https://doi.org/10.1093/aob/mcr316>
- Skálová H, Moravcová L, Dixon AFG, Kindlmann P, Pyšek P (2015) Effect of temperature and nutrients on the growth and development of seedlings of an invasive plant. *AoB Plants* 7: plv044, <https://doi.org/10.1093/aobpla/plv044>

- Skálová H, Guo W-Y, Wild J, Pyšek P (2017) *Ambrosia artemisiifolia* in the Czech Republic: history of invasion, current distribution and prediction of future spread. *Preslia* 89: 1–16, <https://doi.org/10.23855/preslia.2017.001>
- Smith M, Cecchi L, Skjøth CA, Karrer G, Šikoparija B (2013) Common ragweed: a threat to environmental health in Europe. *Environment International* 61: 115–126, <https://doi.org/10.1016/j.envint.2013.08.005>
- Storkey J, Strattonovitch P, Chapman DS, Vidotto F, Semenov MA (2014) A process-based approach to predicting the effect of climate change on the distribution of an invasive allergenic plant in Europe. *PLoS ONE* 9: e88156, <https://doi.org/10.1371/journal.pone.0088156>
- Tolasz R, Míková T, Valeriánová A, Voženílek V (2007) Climate Atlas of Czechia. Czech Hydrometeorological Institute, Praha & Olomouc, 255 pp
- Valladares F, Sanchez-Gomez D, Zavala MA (2006) Quantitative estimation of phenotypic plasticity: bridging the gap between the evolutionary concept and its ecological applications. *Journal of Ecology* 94: 1103–1116, <https://doi.org/10.1111/j.1365-2745.2006.01176.x>
- van Kleunen M, Johnson SD (2007) South African Iridaceae with rapid and profuse seedling emergence are more likely to become naturalized in other regions. *Journal of Ecology* 95: 674–681, <https://doi.org/10.1111/j.1365-2745.2007.01250.x>
- von der Lippe M, Kowarik I (2007) Long-distance dispersal of plants by vehicles as a driver of plant invasions. *Conservation Biology* 21: 986–996, <https://doi.org/10.1111/j.1523-1739.2007.00722.x>
- Wilczek AM, Cooper MD, Korves TM, Schmitt J (2014) Lagging adaptation to warming climate in *Arabidopsis thaliana*. *Proceedings of the National Academy of Sciences of the United States of America* 111: 7906–7913, <https://doi.org/10.1073/pnas.1406314111>
- Yair Y, Sibony M, Rubin B (2017) Four *Ambrosia* species in Israel: invasive, naturalized and casual alien plants. *Israel Journal of Plant Sciences* 64: 93–98, <https://doi.org/10.1080/07929978.2017.1288399>
- Yannelli FA, Hughes P, Kollmann J (2017a) Preventing plant invasions at early stages of revegetation: the role of limiting similarity in seed size and seed density. *Ecological Engineering* 100: 286–290, <https://doi.org/10.1016/j.ecoleng.2016.12.001>
- Yannelli FA, Koch C, Jeschke JM, Kollmann J (2017b) Limiting similarity and Darwin's naturalization hypothesis: understanding the drivers of biotic resistance against invasive plant species. *Oecologia* 183: 775–784, <https://doi.org/10.1007/s00442-016-3798-8>
- Zhou Z-S, Chen H-S, Zheng X-W, Guo J-Y, Guo W, Li M, Luo M, Wan F-H (2014) Control of the invasive weed *Ambrosia artemisiifolia* with *Ophraella communis* and *Epiblema strenuana*. *Biocontrol Science and Technology* 24: 950–964, <https://doi.org/10.1080/09583157.2011.603823>