Preslia 87: 31–53, 2015

Tolerance of alien plant species to extreme events is comparable to that of their native relatives

Nepůvodní druhy jsou schopny tolerovat extrémní projevy klimatu v míře srovnatelné s příbuznými původním druhy

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Laube J., Ziegler K., Sparks T. H., 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

In addition to increases in temperature and CO_2, other features of climate change, such as extreme events and short-term variations in climate are thought to be important. Some evidence indicates that invasive plant species might benefit from climate change via these features. However, apart from theory-based predictions, knowledge of the tolerance of invasive species to short-term climatic stress is very limited. We investigated whether three naturalized alien plant species in central Europe, *Ambrosia artemisiifolia*, *Hieracium aurantiacum* and *Lysimachia punctata* perform better under stressful conditions than comparable native species. A greenhouse experiment with a fixed stress sequence of frost, drought and water logging was set up. We applied this stress treatment to two life history stages (seedling and adult plants), plants grown in monoculture (mild intraspecific competition) and in a highly competitive setting with intra- and interspecific competition. Whilst small differences in plant responses were detected the alien species overall were not more tolerant to stress. The responses of alien and native congeners/confamilials to stress in all treatments (monoculture, competition, adult, seedling) were similar, which indicates that stress thresholds are phylogenetically conserved. All species were more vulnerable to stress at the seedling stage and when subject to competition. Our data indicates that results obtained from experiments using only monocultures and one development stage are not appropriate for drawing generalizations about lethal thresholds. Moreover, rather abrupt species-specific thresholds exist, which indicates that a prediction of species responses based on just two stress levels, as is the case in most studies, is not sufficient.

Keywords: alien, climate change, climatic stress, drought, precipitation, frost, greenhouse experiment, life history stage, competition

Introduction

Biological invasions are increasing worldwide. Since the 1970s there has been an increase in the number of species, speed of spread (Lockwood et al. 2010) and extensions in the altitudinal and latitudinal range limits of invasive species (Pauchard et al. 2009). In addition to other factors, ongoing climate change has been proposed as a cause of this trend (Walther et al. 2009). There are important reasons to expect invasive plant species to benefit, or at least suffer less, from climate change than native species, as several recent reviews on this topic suggest (Dukes et al. 1999, Thuiller et al. 2007, Vilà et al. 2007, Hellmann et al. 2008, Walther et al. 2009, Diez et al. 2012). Amongst other reasons, invasive species might benefit because of their broad ecological niches, high phenotypic plasticity, short generation times and high dispersal ability. But while our knowledge of the invasion risk following increasing temperatures and CO_2 levels, or changing mean precipitation, remains limited, our knowledge of the effects of extreme events or response to climatic stress is scarce (Bradley et al. 2010, Diez et al. 2012, Verlinden et al. 2013). While over 10,000 papers on invasions were published over the last 30 years (Moles et al. 2012), a detailed search at ISI Web of Science for experiments on this topic yields only 30 papers (search string within “Topic”: (stress OR extreme) AND climate change AND experiment AND ((alien OR invasi*) AND plant), 07/2014) – some additional experimental studies exist, which do not use the word “experiment” in either the title, abstract or keywords.

This lack of studies seems problematic, since several types of extreme events and short-term variability in climate are expected to increase in frequency and intensity (IPCC 2007), and the probability that several climatic stressors occur within one year at the same site will increase in the future (Reyer et al. 2013). An increase in the risk of late spring frosts is expected, and for Europe, a higher frequency and intensity of summer drought is also expected, since increasing temperatures will not be compensated for by higher precipitation (IPCC 2007). A general intensification of the water cycle, with changes in amount, timing, variability and extremes (Huntington 2006, Min et al. 2011) is likely to result in a higher frequency of extreme precipitation events and floods.

Given that the importance of climatic extremes in shaping the composition of species is well known (Damgaard 1998, Reyer et al. 2013), the question has to be raised whether a higher frequency of climatic stress situations might facilitate plant invasions. Many invasive species are reported to have short generation times and high dispersal ability (Thuiller et al. 2007, Hellmann et al. 2008, Bradley et al. 2010), which are likely to enable them to spread quickly into disturbed areas and take advantage of increased resource availability and reduced competition after such events (Davis et al. 2000, Thuiller et al. 2007, Moles et al. 2012). A highly positive effect on invasive species is expected if invaded sites prove less prone to disturbance than uninvaded sites (Moles et al. 2012) – i.e. if invaded sites on average differ with respect to microclimate – if invasive species withstand disturbance better than native species, or recover faster (Diez et al. 2012).

Invasive plant species are often able to tolerate rather broad range of climatic conditions (Vilà et al. 2007, Hellmann et al. 2008), show rather high phenotypic plasticity (Davidson et al. 2011; for contradictory results see Godoy et al. 2011, Palacio-Lopez & Gianoli 2011)) and are capable of fast adaptation and/or acclimatization to new environments (Vilà et al. 2007, Hellmann et al. 2008, Bradley et al. 2010, Alexander 2013), which might translate into higher tolerance of climatic stresses. Moreover, many invasive species have high potential growth rates (Vilà & Weiner 2004, Pyšek & Richardson 2007, van Kleunen et al. 2010b, Moles et al. 2012; but see Daehler 2003), which should facilitate fast recovery from non-lethal stress. Furthermore, invasive species seem to be capable of taking advantage of short or irregular fluctuations in the availability of resources (fluctuating resource theory; Davis et al. 2000, Moles et al. 2012), for which there is strong experimental evidence for the highly invasive *Fallopia japonica* (Parepa et al.

2013). Different types of climatic events, such as frost, drought or flood, lead to great variability in the availability of resources (water) and consequential resource flushes (nutrients). This might additionally contribute to tolerance of and faster recovery after, climatic stress. Anecdotal evidence suggests that heat waves (White et al. 2001), heavy rainfall (Bradley et al. 2010), or severe drought (Scott et al. 2010, Jimenez et al. 2011) can promote plant invasions. Analysis of a large-scale field survey showed that changes in disturbance regimes, in particular, rather than disturbance per se promoted terrestrial plant invasions, despite not being the primary predictor (Moles et al. 2012). Hence, changes in the magnitude and frequency of climatic stresses might also be expected to promote invasions.

It is widely accepted that biotic interactions determine the diversity, structure and dynamics of plant communities (Grime 1979, Gibson et al. 1999, Levine et al. 2004, Maestre et al. 2005, Brooker 2006) and influence the spread of species (Brooker 2006). High competitive ability has been shown to be an important factor in the success of invasive species (Vilà & Weiner 2004) and environmental changes often affect communities indirectly via changes in the competitive abilities of some species (Brooker 2006). The stress gradient hypothesis suggests that the strength and direction of biotic interactions change with environmental productivity, with dominance of competitive effects in highly productive environments and reduced competitive or facilitative effects in unproductive or stressful environments (Goldberg et al. 1999, Maestre et al. 2005, Brooker 2006, Lortie & Callaway 2006, Mangla et al. 2011, He et al. 2013). However, if the relative importance of competition decreases with an increase in abiotic stress, then one of the main advantages of invasive species might diminish. It is generally assumed that the competitive ability of native species will be reduced by climate change, since they are adapted ideally to current conditions (Thuiller et al. 2007, Hellmann et al. 2008) and that a reduced competitiveness of native species, or a delayed recovery of competitive ability, will indirectly promote invasions ("invasion window"; Diez et al. 2012). For example, Collinge et al. (2011) record that invasive species profited from a decrease in competition after flooding and drought in a long-term restoration experiment of vernal pool communities. A high effect of reduced competition in facilitating invasions has also been shown in a phytotron experiment using species of grass (White et al. 2001). But only a few competition experiments with invasive species have included environmental gradients (Vilà & Weiner 2004), hence empirical evidence of changed competitive ability under climate change and knowledge of changes in competitive ability under climatic stress is scarce. In conclusion, existing knowledge on the effects of increased climatic stress and extreme events on the dispersal and success of invasive species is minimal. Theory indicates that net effects could be positive, negative or zero.

The objective of this study, therefore, was to compare the response of three alien species with that of native congener or confamilial, co-occurring species to an increase in short-term climatic stress. We investigated whether alien taxa are generally more resistant to climatic stress and how their resistance is modulated by competition. As age-specific responses to climatic stress are generally assumed but rarely proven (Mangla et al. 2011, Beier et al. 2012) we subjected different life-history stages (seedling and adult plants) to climatic stress.

Materials and methods

Outline

We tested the resistance to stress and performance of three naturalized and currently spreading alien species in Germany, *Ambrosia artemisiifolia, Lysimachia punctata* and *Hieracium aurantiacum* in a greenhouse experiment. *Ambrosia* is an annual and the other two species are perennial herbaceous plants. Three ecologically similar and taxonomically closely related native competitors were chosen for comparison (Table 1). Reponses of these species to climatic stresses were tested at two developmental stages (Fig. 1A), each grown in monoculture, in which they only competed intraspecifically, or subject to strong intra- and interspecific competition from both congener/confamilial species and grasses, which resulted in a higher overall plant density per pot (Fig. 1B). We refer to the different developmental stages at the start of the stress application as either "seedling" or "adult" when plants were, respectively, at the seedling stage or 3 weeks later at the adult stage.

A screening experiment was used in this study because both the choice and timing of climate change scenarios and controls are far from trivial (Beier et al. 2012), even if the focus is on mean values, and the predictions of short-term variations in climate and extreme climatic events are both highly uncertain and variable in space (Reyer et al. 2013). We follow recent suggestions that the reactions of organisms to climatic stress should be measured using gradients of stress and include mortality thresholds, rather than try to simulate highly uncertain predictions (Kreyling et al. 2014). The results obtained can be analysed using regression techniques, which generally are statistically more robust than ANOVA (Cottingham et al. 2005). We exposed the species to a gradient of increasing climatic variability with five different levels of stress including the control. For each level of stress we applied a fixed sequence of climatic stress conditions one after another, starting with frost, followed by drought and ending with water logging (Table 2 and Fig. 1A). The level of severity of climatic stress was determined by the duration of each stress condition. The different climatic stresses were chosen to mimic some of the unfavourable weather conditions that are predicted to increase in frequency and variability with climate change. In central Europe, an earlier start of the vegetative period (Menzel et al. 2006) may expose plants to frost more frequently in the future. In addition, the expectation is that the intensity and frequency of summer droughts will also increase (Kundzewicz et al. 2006, Beniston et al. 2007, Sillmann et al. 2008, Estrella & Menzel 2013) along with extreme precipitation events, especially in autumn and winter (Sillmann et al. 2008, Estrella & Menzel 2013).

As mortality thresholds are of high importance, but usually not well studied (Beier et al. 2012), we chose a steep stress gradient, which included the expected mortality thresholds. Mortality was the main response variable. As biomass is a good proxy of the uptake of resources such as nutrients, water or light (Goldberg & Werner 1983) and usually a good predictor of overall fitness, at least for annuals (Gibson et al. 1999) it was the second response variable. The percentage of individuals that flowered was used as a proxy of reproductive success.

Table 1. – Information on the species used in the experiment. Ellenberg indicator values: L, light (1: deep shade, to 9: full light), T, temperature (1: cold, to 9: extremely warm), F, moisture (1: extreme dryness, to 12: submerged, * water level fluctuation indicator species), R, reaction (1: extreme acidity, to 9: basic reaction), N, nitrogen (1: extremely infertile sites, to 9: extremely rich sites), x: indifferent behaviour. Ellenberg values are those cited by Ellenberg et al. (2001), habitat according to BfN (2013).

Type	Species	Habitats	Ellenberg values				
			L	T	F	R	N
alien	*Hieracium aurantiacum*	meadows, heathland, ruderal habitats	8	3	5*	4	2
native	*Hieracium pilosella*	meadows, heathland, ruderal habitats	7	x	4	x	2
alien	*Ambrosia artemisiifolia*	ruderal habitats	9	7	4	8	6
native	*Achillea millefolium*	ruderal habitats, meadows	8	x	4	x	5
alien	*Lysimachia punctata*	tall herbaceous plant fringe, ruderal wetlands	6	7	7	8	4
native	*Lysimachia vulgaris*	tall herbaceous plant fringe, wet meadows	6	x	8*	x	x
grass	*Holcus lanatus*		7	6	6	x	4
grass	*Dactylis glomerata*		7	x	5	x	6
grass	*Arrhenatherum elatius*		8	5	5	7	7
grass	*Luzula campestris*		7	x	4	3	2
grass	*Anthoxanthum odoratum*		x	x	x	5	x

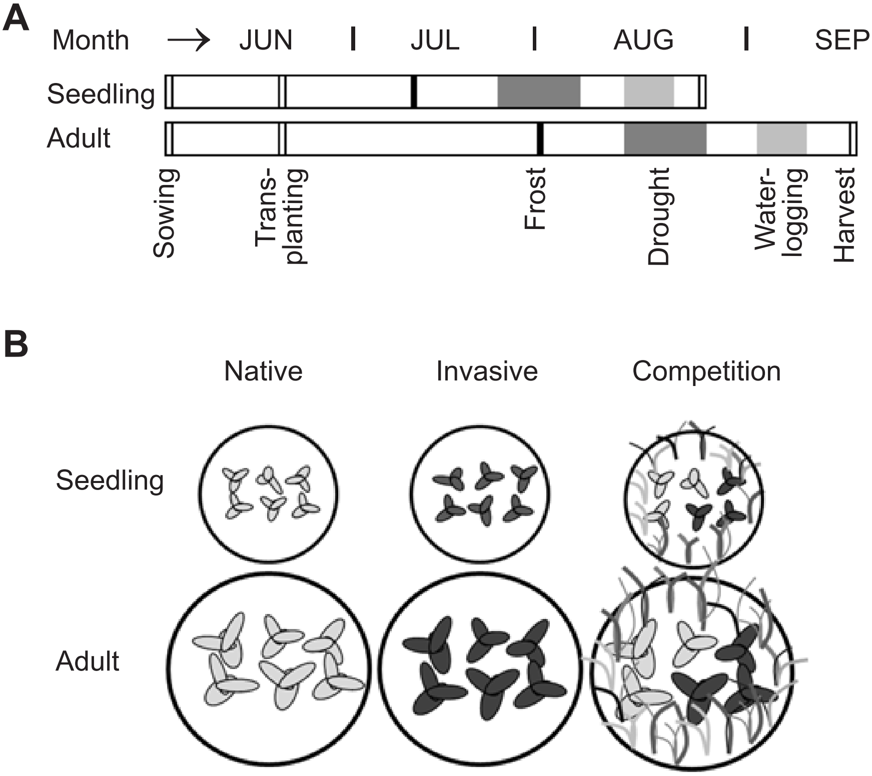

Fig. 1. – Schematic diagram of the timing and developmental stage/species combination in each treatment. (A) Timeline of the occurrence of stress applications for each of the developmental stages. (B) Planting schemes for the different treatments.

Table 2. – Stress factors and stress levels applied.

Stress factor/level	Frost	Drought (duration 14 days)	Duration of water logging
Stress 0 (control)	none	regular irrigation	none
Stress 1	–6 °C / 2 h	irrigation every 2nd day	2 days
Stress 2	–6 °C / 4 h	irrigation every 4th day	4 days
Stress 3	–6 °C / 6.25 h	irrigation once/week	6 days
Stress 4	–6 °C / 8 h	no irrigation	8 days

Selection of species

We studied the tolerance of *Ambrosia artemisiifolia*, *Hieracium aurantiacum* and *Lysimachia punctata*, three naturalized alien species currently spreading in Germany (Table 1). *Ambrosia artemisiifolia* originates from North America, is highly allergenic and a serious agricultural weed. This species was first introduced accidentally with clover and soya seed and has spread more widely recently as it is a contaminant of bird seed. In Germany this synanthropic species is established in 9% of the grid cells, each of which is about 30 km^2 (BfN 2013). It is also an established alien species in the Czech Republic, Denmark, Finland, France, Germany, Hungary, Italy, Norway, Poland, Romania, Spain, Sweden and Turkey (DAISIE 2014). The subalpine distribution of *Hieracium aurantiacum* in Europe is disjunct (Tutin et al. 1972, Meusel & Jäger 1992), with native records for Germany only from the alpine region (a population on the Bohemian Massif is probably of synanthropic origin; Gaggermeier 1996). It was spread as an ornamental plant, and already occurs in 25% of all the grid cells in Germany as an established or synanthropic alien species (BfN 2013). For Bavaria, it is included in the Black List of invasive species (Bayerisches Landesamt für Umwelt 2014). It is also an established alien plant in other European countries (Belgium, Great Britain, Ireland; DAISIE 2014). *Lysimachia punctata*, whose native range is in southern and central-eastern Europe (Tutin et al. 1972), is known to have only one natural population in Germany (Berchtesgaden, south-eastern Bavaria (Merxmüller 1973)). It was equally widely distributed as an ornamental plant (Meusel & Jäger 1992). It is currently reported from 25% of the grid cells in Germany as an established or synanthropic alien species (BfN 2013), and is an established alien plant in Belgium, Czech Republic, France, Germany, Great Britain, Ireland, Norway, Poland and Sweden (DAISIE 2014). In Germany, the latter two species are currently spreading into sites of conservation value; *Hieracium* occurs in meso- and oligotrophic meadows, *Lysimachia* in tall fringes of herbaceous plants.

It is recognized that the results of past experiments on the competitive ability of invasive species, using highly dissimilar pairs of species, are difficult to interpret (Vilà & Weiner 2004, van Kleunen et al. 2010a). Some of the former studies are biased towards invasive species that are strong competitors and have high growth rates and native species that are threatened (often rare species) and usually with low growth rates (Lepš 2005). It is well known that it is difficult to compare species with different life-forms (Gibson et al. 1999, Vilà & Weiner 2004). But since different species co-occur in nature, hence all individuals in a community are potential competitors and share and compete for the same limited resources (Goldberg & Werner 1983), this issue is still disputed.

Not only differences in life form, but also initial differences in size might lead to biased results, since large individuals are likely to be favoured and comparable densities are hard to attain (Gibson et al. 1999). For competition, and even more for stress experiments, the niche of species is another important constraint. Different niches of species pose major drawbacks when comparing their responses to stress, since control treatments will not be optimum for all the species investigated. If the level of stress used is close to the limit of one species, but far from the limit of the other, the expectation is the species will react differently. Such confounding effects might make is very difficult to draw any conclusions about the tolerance of the species to stress.

We therefore chose native competitors with similar growth forms, phylogenies, sizes, preferred habitats and ecological niches (Table 1). For the invasive *Ambrosia artemisiifolia*, no matching native annual *Asteraceae* with similar Ellenberg values exists (BfN 2013): of the seven *Asteraceae* with comparable Ellenberg values native to Germany, we excluded the two species that inhabit salt marshes, four species that differ in size (three are considerably smaller and one considerably taller) and chose *Achillea millefolium* as the closest comparable, although perennial, species. The *Hieracium* and *Lysimachia* pairs were highly comparable in terms of size (BfN 2013), growth-form and life-form, while for the *Ambrosia-Achillea* pair the best possible compromise in terms of matching habitat requirements, taxonomic relatedness and size was chosen.

The comparison with species that most closely match the alien species reduces flaws due to phylogeny, life-cycle or differences in niche, and thus addresses the question whether increased tolerance to climatic stress is related to the invasive potential of a species (Pyšek & Richardson 2007). This approach, however, does not allow comparisons with other, less related co-occurring native species. It is thus not suitable for drawing conclusions about species changes in communities, where trait differences could be related to changes in the tolerance of the species to stress.

Rather than the effect of simple pairwise interactions, the performance of the focal species in an environment of competitive interactions was studied, since in natural communities competitive interactions are also highly diffuse (McGill et al. 2006). All alien and native species occur in open habitats, where grass species usually co-occur. Thus, we used five additional species of grass in the interspecific competition treatments. Grass species were chosen that occur in different ecological niches (from species usually occurring in dry habitats to species occurring in rather wet habitats), to ensure that despite the possible death of single species strong competition from the remaining species was assured. Seeds of all species were obtained from commercial seed suppliers.

Experimental setup

We used a mixed substrate of commercial peat, quartz sand and loam in a volume ratio of 1.2/0.8/1.0. The high proportion of inorganic matter and a more natural distribution of particle sizes ensured a close-to-natural substrate reaction with respect to frost, drying and rewetting, which is not possible with commercial peat mixtures. Diameters of the pots were 15 cm (volume 1.4 l) for seedlings and 23 cm (volume 8 l) for adult plants. Base irrigation (before and after the application of stress) was regulated so as to provide an optimal supply of water (watered daily to approximately field capacity), using a drip irrigation for adult plants and a flow/ebb system for seedlings. Mean volumetric water contents were logged using TDR Loggers (Hobo Data Logger H21, 1 per stress level), with around 0.2 m^3/m^3 during base irrigation for both seedlings and adult plants. Seedlings were sown in a seed bed (commercial peat) and were transplanted after germination and assigned randomly to the different treatments. Each pot contained six individuals of the target species; for the competition treatment a fixed number (seedlings: 11, adult plants: 16) of grasses were added (Fig. 1B). When necessary, insecticides and fungicides were applied equally to all treatments and species.

We applied frost treatments in cold climate chambers (Heraeus Vötsch). Drought treatments consisted in a pause in watering, i.e. removal of drip irrigation (adult plants) or raising the seedlings above the flow/ebb system on the days of drought. Mean relative water contents were reduced to 89% of the average water content in the control (stress level 0) and 13% for stress level 4 for adult plants. Pots with seedlings showed a comparable decrease in water content, of from 82% (stress level 0) to 10% (stress level 4). The decrease in soil moisture in the control (stress level 0) during the drought treatment most likely resulted from the high temperatures experienced during the drought period by both seedling (about +3 °C) and adult plants (about +2 °C) compared to the overall temperature average.

Water logging treatments were applied using constantly flooded tables (seedling), or constantly flooded tables and additional drip irrigation (adult, drip irrigation to correct for the reduced capillary rise in large pots). Pots without or with short flood duration were raised above the water and irrigated by hand. The mean water content changed by –2% (stress level 0) and +48% (stress level 4) of the average water content. Descriptions of the stress levels used are given in Table 2.

The stress treatments started 3 weeks after transplanting the seedlings and 6 weeks in the case of adult plants (Fig. 1A). At the beginning of the stress treatments, seedlings had four or five leaves (*Ambrosia* pair), six leaves (*Hieracium* pair) and two leaves (*Lysimachia* pair) on average. The adult plants of *Ambrosia*, *Hieracium* and *Lysimachia* had two side-branches, two stolons and seven leaves, respectively. Initially there were no differences in developmental stages of the seedlings and adults subjected to the different stress treatments (Kruskal-Wallis tests per species and developmental stage, all $P > 0.85$). After subjection to frost plants were allowed to regenerate for two weeks before being subjected to drought, followed by one week of regeneration before being subjected to water logged conditions. The short breaks between being subjected to different stresses were designed to give plants some possibility to regenerate, but not fully recover. Surviving above ground biomass of individual target plants as well as of grasses was harvested 1 week after being subjected to the last stress ended, dried at 60 °C for at least 48 h and weighed (Sartorius balance with a precision of 0.1 mg, with 5 replicate measures).

The experimental design was a randomized block design, with blocks in adjacent identical compartments within one greenhouse divided by a glass wall. Different pot sizes and different irrigation systems were used for the two developmental stages (seedling/adult). Species combination/stress levels were fully randomized within blocks (Fig. 1B). The number of replicates was 5, resulting in a total of 150 pots (5 stress levels × 2 development stages × 3 species combinations × 5 replicates) and 900 individuals per species pair.

The experiment was conducted from 22 May to 19 September 2012 in a greenhouse belonging to GHL Dürnast, Freising, Bavaria. Greenhouse temperatures were close to natural conditions, with mean values of 19.1 °C (6.3–37.9 °C minimum-maximum) for seedlings, 20.5 °C (6.9–42.2 °C) for adults and outside air temperature of 19.1 °C

(3.8–36.0 °C). Relative humidity in the greenhouses was 66.7% and 69.6% (seedlings/adults).

Data collection

Biomass of individual plants at harvest and total biomass of competing species of grass were recorded as dry weights. After subjection to each type of stress the percentage of intact (not damaged) above ground tissue of individuals of each of the plants tested was estimated to the nearest 5%. These estimates take into account the newly damaged tissue, since frost damaged leaves were rapidly shed, which is mostly also true for drought damaged leaves. However, confounding effects have to be considered, and values are thus interpreted with care. The survival of individuals was recorded at harvest, 1 week after experiencing the last type of stress.

The developmental stages of all individuals were recorded using a German phenological system (BBCH-codes according to Meier 2001) before the start of the stress treatments. Reproductive fitness was recorded as the number of flowering individuals per pot at harvest (adult group only).

Statistical analysis

Since we were interested in differences between closely related and co-occurring species, but not all species differences, the three species pairs were analysed separately. We used mean values per pot to avoid pseudo replication (Hurlbert 1984). Mortality rates were analysed using logistic regression, relevant predictors (species identity, developmental stage, competition treatment, stress level) were chosen using backward model selection based on chi-square tests. The results for the controls (stress levels 0) were chosen as the reference value. Starting (full) models included all primary predictors and interactions up to the 3 way interaction term (stress × species × age; stress × species × competition). Goodness of fit for final models was estimated using pseudo R^2 (1-(deviance of final model)/(deviance of null model)) following Menard (2000). The main regression analysis assumed stress levels to be equally spaced. Since departures from this assumption are possible, the procedure was repeated with stress level as a factor to validate the results.

For biomass at harvest, effects of developmental stage, competition, species identity (as a factor) and stress level (as a scalar predictor) were analysed using ANCOVA. Observations were weighted by the number of surviving individuals. To meet the assumption of normality, log-transformed weight was used as the response variable. Analysis of biomass was based on surviving individuals, i.e. dead individuals were not included in the analysis. Predictors were chosen by backward model selection with respect to chi-square tests and the Akaike Information Criterion (AIC values). Residuals of final models were checked for normality. As for mortality, the main analysis assumed equidistant stress levels as predictors, but tests were also repeated with stress level as a factor (ANOVA).

The influence of stress level on the percentage of flowering individuals was assessed using Spearman's rank correlation based on the subset of adult plants (assuming an ordinal data type for stress level).

The estimates of intact tissue were used to assess the effect of single applications of stress. We analysed the differences between species in response to different levels of stress using linear mixed models, with species and stress level as fixed effects, and developmental stage and competition as random factors (R-package nlme). Reanalysis with stress level as a factor did not give a different result. In addition, differences between species recorded at the most severe stress level (level 4) were analysed separately (with species as fixed, and developmental stage and competition as random factors), since we expected species-specific differences to be most pronounced at the severest level of stress. All analyses were done in R.

Results

Effect of competition and age on the controls

Baseline percentage mortality (Table 3) did not differ significantly between the congeners/confamilials of any of the three species pairs. We also found no significant differences in percentage mortality between native and alien species for different developmental stages. Baseline percentage mortality between native and alien species did not differ between competition treatments for the *Hieracium* and *Lysimachia* pair, but native *Achillea* performed significantly worse when subjected to competition than *Ambrosia* ($P = 0.035$).

Baseline biomass of individuals (Table 4) was higher for invasive *Ambrosia* than for *Achillea* ($P < 0.001$), and very slightly higher for alien *Hieracium aurantiacum* than for *H. pilosella* (close to significance at $P = 0.088$). Biomass did not differ significantly within the *Lysimachia* pair. That of *Achillea* was lighter when subjected to competition than the invasive *Ambrosia* ($P < 0.001$). The reduction in biomass recorded when subjected to competition did not differ between the congeners of the *Hieracium* and *Lysimachia* pair.

Not surprisingly, the biomass of seedlings of all species pairs at harvest was less than that of adult individuals, and the biomass of all three species pairs was less when they were subjected to competition (each $P < 0.001$). For the *Hieracium* and *Lysimachia* pairs, the increases in biomass from seedling to adult did not differ between congeners, whereas native *Achillea* grew more slowly than *Ambrosia* ($P = 0.008$).

Mortality and stress levels

Mean overall percentage mortality recorded for the *Lysimachia* pair of 43% (±48% SD) was greater than that recorded for both the *Ambrosia* (27±41% SD)) and *Hieracium* (27±44% SD) pairs. Mean percentage mortality varied considerably between stress levels, with very low values for the control (stress level 0) (*Ambrosia*: 0±0% SD, *Hieracium*: 0±0% SD, *Lysimachia* 13±32% SD) and high values for stress level 4 (*Ambrosia*: 73±41% SD, *Hieracium*: 74±44% SD, *Lysimachia*: 65±43% SD). Percentage mortality of all species pairs increased with increase in stress (Fig. 2) with odds of mortality increasing by 21% (species pair *Hieracium*) to 149% (pair *Lysimachia*) per increase in stress level (Table 3).

We found no significant species × stress level, stress level × competition or stress level × developmental stage interactions for the *Hieracium* and *Lysimachia* pairs. The difference in percentage mortality between confamilials was significant for the *Ambrosia* pair. While *Achillea* suffered a higher overall percentage mortality with increase in stress level

Table 3. – Results of the final logistic regression analysis of the percentage mortality recorded for each of the species. For Species*. coefficients for native *Achillea millefolium* are given. Coefficients on the logit-scale, P-values (significant in bold) and number of observations (based on individual pots; n) are shown. Intercepts refer to the reference group (alien, stress 0, adult plants, monoculture). Only the results of the final models are presented.

	Ambrosia pair		*Hieracium* pair		*Lysimachia* pair	
Predictors:	Coeff.	P	Coeff.	P	Coeff.	P
Intercept	–5.0	**< 0.001**	–4.3	**< 0.001**	–6.3	**< 0.001**
Stress	0.4	0.279	0.2	0.526	0.9	**0.001**
Species*	–2.7	0.134	–		–	
Age	–3.2	**0.003**	–14.6	**< 0.001**	–0.6	0.198
Competition	–1.3	0.450	0.8	0.412	5.3	**< 0.001**
Stress × Species*	1.4	**0.009**	–		–	
Stress × Age	1.7	**< 0.001**	5.4	**< 0.001**	0.8	**< 0.001**
Stress × Competition	2.0	**0.001**	1.7	**< 0.001**	1.1	**0.006**
Species* × Competition	4.9	**0.035**	–		–	
Stress × Species* × Competition	–2.3	**0.003**	–		–	
Model fit:						
Deviance/df	220.9/189		182.3/194		241.1/194	
Null deviance/df	796.1/198		922.6/199		1001.9/199	
Pseudo R^2	0.72		0.80		0.76	
n	199		200		200	

Table 4. – Results of the ANCOVA of the biomass of the surviving individuals. Calculations are based on means per pot. Species* – values for native *Achillea millefolium* and *Hieracium pilosella* are given; P-values (significant in bold) and number of observations (n) are given. Intercepts refer to the reference group (alien, stress 0, adult plants, monoculture). Only the results for the final models are presented.

	Ambrosia pair		*Hieracium* pair		*Lysimachia* pair	
Predictors:	Estimate	P	Estimate	P	Estimate	P
Intercept	2.24	**< 0.001**	1.23	**< 0.001**	0.51	**< 0.001**
Stress	–0.36	**< 0.001**	–0.29	0.158	–0.19	**< 0.001**
Species*	–1.09	**< 0.001**	–0.30	0.088	–	
Age	–1.78	**< 0.001**	–0.97	**< 0.001**	–1.34	**< 0.001**
Competition	–1.33	**< 0.001**	–3.20	**< 0.001**	–4.27	**< 0.001**
Stress × Species*	–		0.22	**< 0.001**	–	
Stress × Age	–		–0.17	**0.009**	–	
Species* × Age	0.50	**0.008**			–	
Species* × Competition	–1.57	**< 0.001**			–	
Model fit:						
Deviance / df	223.7/152		146.4/139		152.3/117	
Null deviance /df	1597.6/158		1824.7/145		1409.6/120	
AIC	302.8		212.8		192.4	
R^2	0.86		0.92		0.89	
n	159		146		121	

(odds ratio 305%, P = 0.009), it performed better than *Ambrosia* when subjected to competition (species × stress × competition interaction, P = 0.003). The goodness of fit was

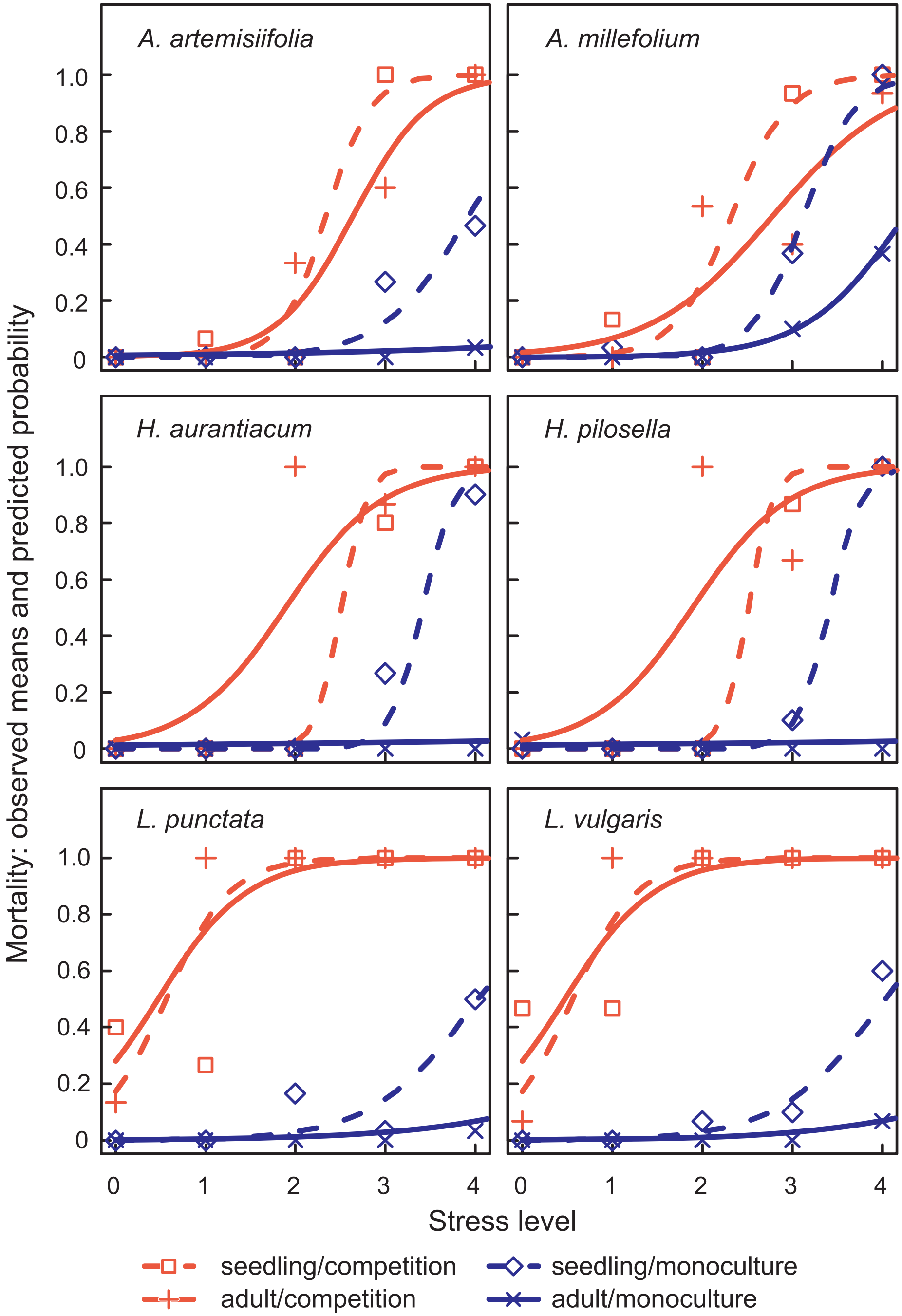

Fig. 2. – Average percentage mortality recorded for the two developmental stages of each species at each level of stress. Points indicate the mean percentage mortality recorded at each level of stress and lines the predictions of the model (probability of death) for the different groups. Stress levels used range from 0 (control) to 4 (most severe). The graphs for the alien species are on the left and native species on the right.

reasonable for all final models, with pseudo R^2 values of 0.76 for *Lysimachia*, 0.80 for *Hieracium* and 0.72 for the *Ambrosia* pair.

For all three species pairs, the increase in mortality with stress level was steeper for seedlings (stress × age interaction highly significant for all species pairs at $P < 0.001$). Similarly, competition increased percentage mortality (stress × competition interaction significant for all species pairs, $P < 0.001$ for the *Hieracium* and *Ambrosia* pairs, $P = 0.006$ for the *Lysimachia* pair). For each unit increase in stress level, the odds of dying when subjected to competition was 197% for the *Lysimachia* pair and 620% for the *Ambrosia* pair.

A recalculation of this analysis with stress level as a factor did not change the main findings. For the *Ambrosia* pair the stress × species interaction was of only borderline significance ($P = 0.055$), and in line with this, the stress × species × competition interaction was not significant. As for the analysis with stress level as a scalar predictor, species identity was not a significant predictor for either the *Hieracium* or *Lysimachia* pair. For the *Lysimachia* pair the stress × competition interaction was not significant.

Biomass of surviving plants and stress level

Overall, increase in stress resulted in a decrease in biomass, with significant changes for the *Ambrosia* and *Lysimachia* pair (both $P < 0.001$), see Table 4. The decrease in weight with increase in stress level was significantly less for *H. pilosella* ($P < 0.001$) than for *H. aurantiacum*, while for the other two pairs the differences in response to stress were not significant. For both *Hieracium* species, seedlings performed worse with increase in stress ($P = 0.009$). The goodness of fit of final models was good, with R^2 for all species pairs above 0.86.

Reanalysis of the results with stress level as a factor changed the outcome only very slightly. For the *Ambrosia* pair, both stress level × age and stress level × competition interactions became significant ($P = 0.008$ and $P = 0.030$). For the *Hieracium* pair, the addition of the results for the controls (native *Hieracium pilosella* with significantly smaller biomass, $P < 0.001$) and the stress × competition interaction became significant ($P < 0.001$). Nothing changed for the *Lysimachia* pair, and results did not change with respect to stress × species interaction in any species pair.

While the biomass of competing grasses was strongly affected by treatment [mean of the control (stress level 0): 10.0g, stress level 4: 2.4 g], and developmental stage (seedling: 2.3 g, adult: 11.1 g), values for the three species pairs did not differ significantly (ANCOVA, stress effect $P < 0.001$, age effect $P < 0.001$, species pair effect $P > 0.05$, $n = 150$).

Reproduction

With increase in stress the percentage of individuals flowering was significantly reduced for both *Ambrosia* ($r_s = -0.39$, $P = 0.006$) and *Achillea* ($r_s = -0.35$, $P = 0.013$). Regression slopes of flowering against stress level were comparable for both species (Fig. 3). Increased stress had no effect on *Hieracium* species ($P > 0.05$ for both species). The number of pots with flowering plants was 46 for *Ambrosia*, 29 for *Achillea*, 16 for *H. aurantiacum* and *H. pilosella*. For the *Lysimachia* pair, only plants in one pot of *L. vulgaris* flowered before harvest.

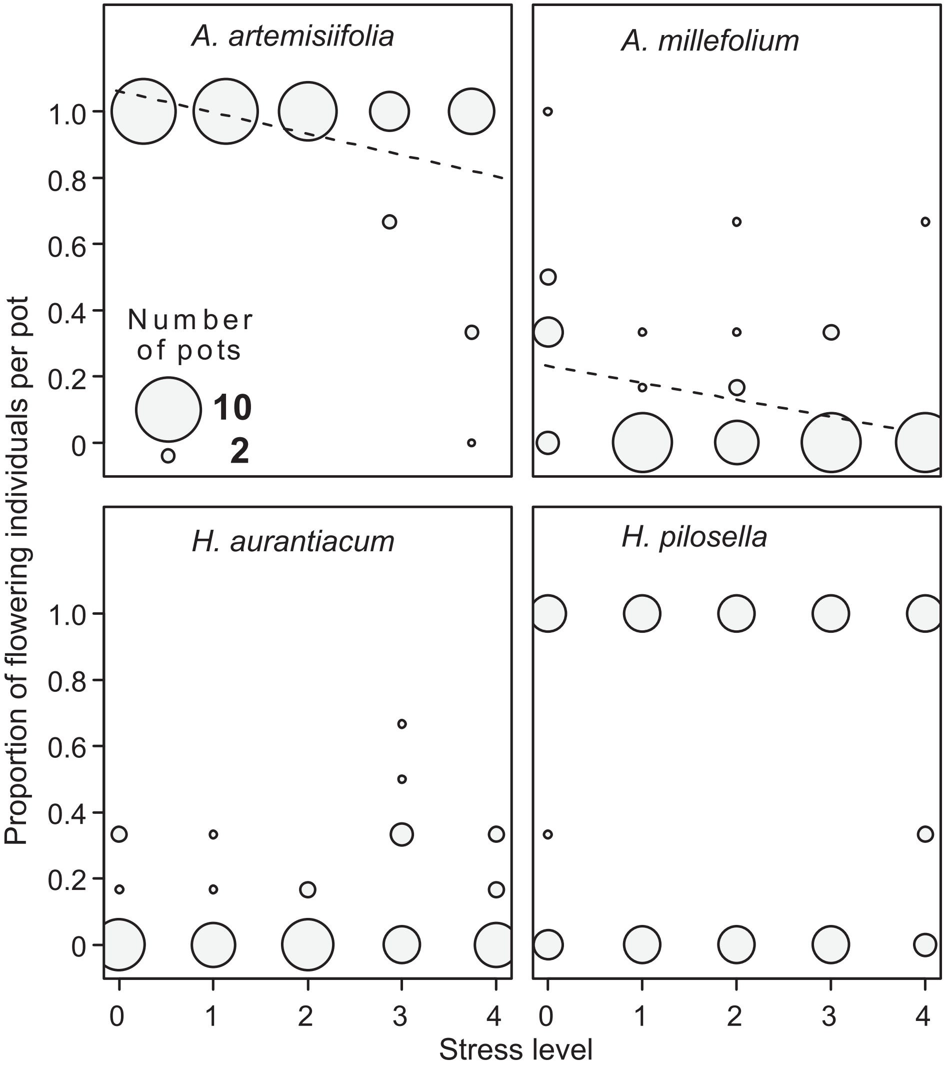

Fig. 3. – Proportion of the plants (*Ambrosia* and *Hieracium* pair) recorded flowering at each level of stress. Circle sizes indicate the number of pots (1 to 10) with flowering plants and the lines whether there were significant correlations with the level of stress. Number of observations 50 per species.

Effect of different types of stress

Estimates of the intact above ground plant tissues for stress level 4 after the plants were subjected to each of the different types of stress are given in Fig. 4. Within species-pair differences generally were rather small. For the *Ambrosia* pair, native *Achillea* performed significantly better following frost than invasive *Ambrosia* (coefficient *Ambrosia* = –14.5, coefficient *Achillea* = –6.7, P < 0.001). We found no overall significant species × stress level interactions for any other type of stress or species pair, and the outcome was

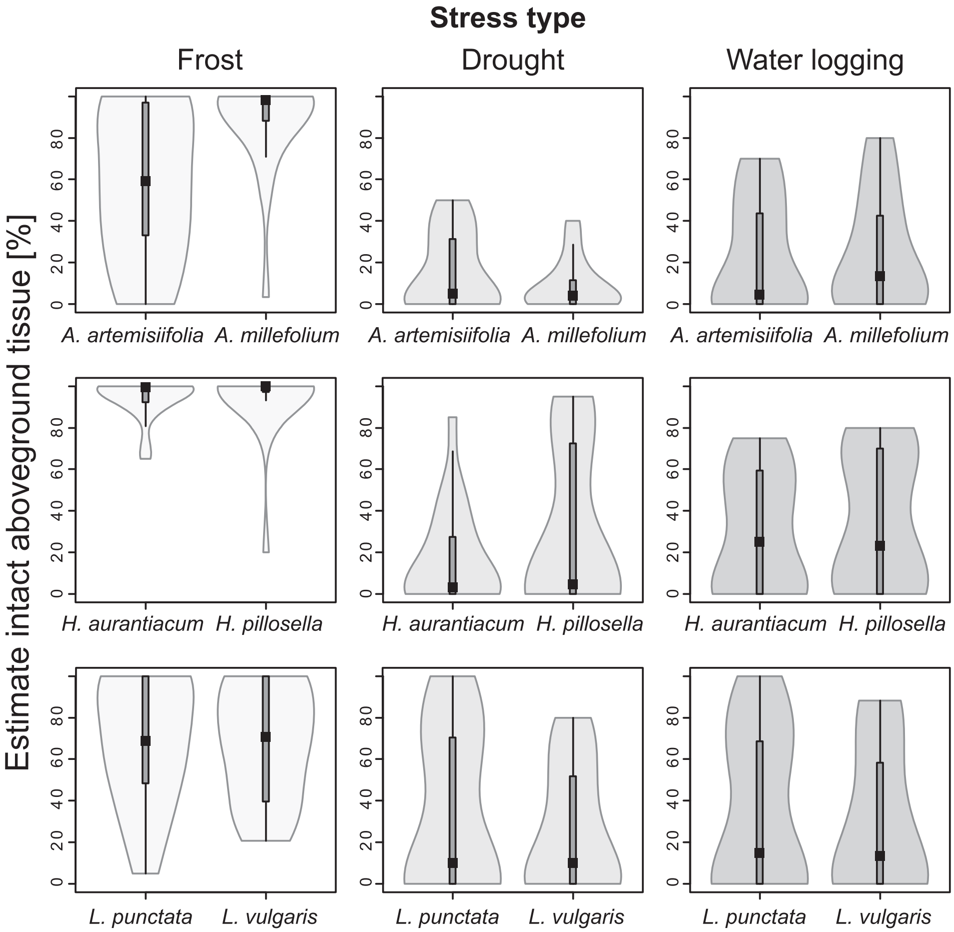

Fig. 4. – Effect of different stress events on the estimates of the above ground tissue recorded in each of the treatments. The violin plots show the estimates of the amount of intact above ground tissue recorded at the most severe level of stress (level 4), and give both boxplots (centre) and kernel density, that is, a non-parametric probability density estimate (surface). The graphs for the alien species are on the left and native species on the right. Bimodal frequency distributions (e.g. *Ambrosia artemisiifolia* for drought or *Hieracium* species for water logging) are due to the differences recorded for the two developmental stages and/or competition treatments.

the same if stress level was analysed as a factor. However, some species-specific significant differences do exist if calculated separately for the most severe stress level (level 4). There was significantly more intact tissue of *Achillea* remaining after frost (22% higher than *Ambrosia*, P = 0.008), but it was more damaged by drought (–8%, P < 0.001) and water logging (–9%, P = 0.043). Small, slightly significant differences were also recorded for the *Hieracium* pair, with more intact tissue of the native *H. pilosella* (+5%, P = 0.040) remaining after the drought treatment. No significant differences between congeners were recorded in the *Lysimachia* pair.

Discussion

Response of congener/confamilial species to the different levels of stress

Overall, we found no difference in the response to stress of congeners for the *Lysimachia* pair and only small differences for the *Ambrosia* and *Hieracium* pairs. In comparison with the congeners, the mortality of the invasive *Ambrosia artemisiifolia* increased slightly less and the biomass decrease of the native *Hieracium pilosella* was slightly lower with increase in the level of stress. Congeners/confamilials also reacted similarly to stress at the two different life history stages, and moreover, the response to stress when subject to competition differed only for *Achillea* (smaller increase in percentage mortality with increase in stress) and *Ambrosia*, but not for the other two species pairs. However, the overall percentage survival of the *Lysimachia* pair was very low when subject to competition (overall only 21%), hence results for interactions of competition with other factors might be underestimated. Nevertheless, these results are in line with a recent study on grass species, which found very similar responses of the congeners to drought and frost (Hofmann et al. 2013). In contrast, a study on native and invasive species of dandelion (Brock & Galen 2005) indicates that native congeners are more drought tolerant, and invasive balsams are less frost tolerant than the native congener (Skálová et al. 2011). Other studies, although not including congeners, indicate that invasive species suffer less than comparable native species from climatic extremes and are less affected by flooding (Collinge et al. 2011) or drought (Jimenez et al. 2011). Given these ambiguous results, it seems likely that the reaction of species to climatic extremes is highly species-specific and less associated with their invasive or native status (Jimenez et al. 2011).

To sum up, we found very little evidence for differences in the tolerance to stress of congeneric alien and native species at different developmental stages and when subjected to competition, and only small differences for the *Achillea*/*Ambrosia* confamilials. Differences in percentage mortality and biomass between native *Achillea* and invasive *Ambrosia* might be attributed to a greater phylogenetic distance and the fact that *Ambrosia* is an annual and *Achillea* a perennial. The baseline values indicated that *Achillea* grew more slowly and was less competitive than *Ambrosia*. In addition, the results for *Achillea* only reflect its ability to cope with stress and competition during the establishment phase in the first year. It is assumed that in subsequent years a larger and deeper rooting system and stored nutrients will increase its tolerance to stress, result in faster growth rates in spring and a higher competitive ability.

Effect of competition

Competition had a marked effect on the overall stress response of all three species pairs. However, several confounding effects have to be taken into consideration. Competition included rather mild intraspecific competition and competition from grass, which changed not only competing species identity, but also total plant density per pot (overall biomass per pot in monoculture was 7.2 g and in competition 8.0 g). Thus, competition changed the availability of resources per individual of the focal species.

A greater total biomass should not affect the severity of the frost treatments, but might affect the tolerance to frost via change in individual size and their ability to replace dead biomass from internal stores of nutrients. Clearly, a greater total biomass should result in increasing the severity of the drought treatments (greater total water demand and faster drying of the substrate). For the water logging treatment, higher total biomass should have decreased the severity of the stress, since a greater water demand due to higher transpiration, larger root volume and probably greater air volume within the substrate might have counter-balanced the effects of a too high level of soil moisture. Moreover, not only the focal species, but also the competitors were affected by the stress treatments. Thus competitiveness of the surrounding species may have decreased with increase in stress level. Some of these experimental interferences can be expected to also occur under natural conditions, such as faster soil desiccation, or reduced effects of water excess at higher plant densities.

As expected, focal species of all species pairs in the control with competition (stress level 0) achieved lower biomasses than in monoculture, and for the *Lysimachia* pair, percentage mortality also increased with competition. However, very strong increases in percentage mortality were recorded for all species pairs along with no decrease in surviving biomass for any of the species pairs (stress × competition interactions). We expected greater competition × stress level interactions for alien species, but this was only recorded for the least comparable species pair (*Achillea*/*Ambrosia*). Our results support the idea that invasive and naturalized alien species are not better at coping with competition and increased climatic stresses per se.

In a field study in which autumn precipitation was increased, which resulted in a decrease in climatic stress, biotic resistance dramatically reduced the invasive species' ability to profit from improved resource conditions (Eskelinen & Harrison 2014). Recent findings indicate that invasive species are not necessarily more competitive under mild drought stress (Verlinden et al. 2013), and winter warming and drought does not result in an overall better performance of invasive species of grass in Australia (Godfree et al. 2013). Similarly, a study using a modest level of water stress indicates that the invasive *Senecio inaequidens* is overall the most competitive congener, but that the competitive ability of the native species increases when subjected to water stress (Garcia-Serrano et al. 2007). Maybe there is a trade-off between high growth rates and resultant high competitive ability and their tolerance of stress (He et al. 2010). However, other studies have produced contrary results. Mild drought stress in Australian coastal dunes result in a strong decrease in the competitive ability of native species, whereas invasive species are less affected (Mason et al. 2012). Reduced competition from native species after being subjected to stress also favours invasive species in vernal pools (Collinge et al. 2011) and artificial grassland communities (White et al. 2001). A review by Daehler (2003) indicates that in low-nutrient environments the relative competitive performance of native species is increased in comparison with that of invasive species.

Effect of developmental stage

In this study the seedlings generally performed worse than adult plants. However, there was no evidence that the different life history stages of the alien congeners/confamilials were more tolerant of stress than those of the native plants (no significant species × age × stress interaction for any of the three species pairs). As for competition, coherent differences between life-history stages were also expected, since a later harvest and larger volume of substrate increase biomass (Poorter et al. 2012). But, in the competition treatments, we were mainly interested in changes in the stress × developmental stage interaction than in changes recorded in the control pots. The response of seedlings to stress was generally more pronounced (higher increase percentage mortality with increase in stress for all species pairs and the decrease in biomass was also significant for the *Hieracium* pair).

A considerable shortcoming of greenhouse studies is the unrealistic restriction of the rooting volume (Gibson et al. 1999), even more so when plants are subjected to drought conditions. To reduce the interference between large adults and small seedlings, we adjusted the available rooting volume of seedlings and adults by using different sized pots. In terms of the total biomass per pot volume, average values were well below the critical threshold of 2 $g \cdot l^{-1}$ (Poorter et al. 2012), which is supposed to restrict growth, for both seedlings and adults. Since the control values for the mortality of seedlings nevertheless were smaller than those for adult plants of the larger *Ambrosia* and *Hieracium* pairs, this experimental bias might have affected the baseline values (stress level 0, with highest biomass values). As in the competition treatments, limiting rooting volumes is assumed to have increased the severity of the drought conditions and decreased that of the flooding treatment. In the frost treatments, root frost damage should have occurred earlier (at lower stress levels) in the small pots. Under natural conditions, seedlings are likely to suffer greater root frost damage (with shallow roots) than the adult plants (with deeper rooting systems). Although little is known about the response to stress of the different developmental stages (Beier et al. 2012), it is likely that the low resistance of seedlings to stress might be due to a lower resistance of young leaves to stress or reduced storage pools. To conclude, the response to stress of seedlings and adults differed greatly, but there were no differences in the responses of alien and native congeners.

Response to single stress applications

There were only slight differences in the responses of congeners/confamilials to the different types of stress. As the levels of the different types of stress were not applied independently the responses are correlated (highly significant correlations for the damage estimates for all three types of stress). Individuals that had a high proportion of their above ground tissue killed by a particular stress event are likely to be less viable at the start of the next stress application, and thus more likely to respond more strongly to subsequent stress applications. On the other hand, correlations for the damage estimates for frost/drought and frost/water logging were rather small ($r_s = 0.34/0.26$), and only those for the drought/water logging treatments were strongly correlated ($r_s = 0.89$). Our rough interpretation of the relative effect of treatments, therefore, should provide an estimate of the relative effect of frost and drought, but is less useful for determining the relative effect of water logging.

The congeneric species responded similarly to single stress applications, although invasive *Ambrosia* was less tolerant of frost and slightly more tolerant of drought than native *Achillea*. *Ambrosia* in Hungary prefers humid regions (Pinke et al. 2011) and our experiment indicates that *Ambrosia* is not more vulnerable to drought than co-occurring and closely related native species.

Climate change implications

We applied a fixed sequence of climatic stresses, which roughly follows current central-European weather patterns (late spring frost, summer drought and heavy autumnal precipitation). It is predicted these events will increase in frequency and severity in the future. We cannot exclude the possibility that the order or duration of stress events or use of different planting densities in the competition treatment would have changed the main results. In addition, it is unwise to use the results of short term experiments to infer long-term outcomes (i.e. long-term success of a species), but should only be used as indicators of such trends (Gibson et al. 1999, Jolliffe 2000). However, in comparison to biomass, measurements of percentage mortality are a clear response and might indicate the likely long-term success of a species.

As Fig. 2 shows, there was not a slow and linear response to increase in stress. Our data indicate that there is a definite species-specific threshold, above which percentage mortality increase dramatically to almost 100%. A recent meta-analysis indicates that 95% of the studies on the effects of stress apply only two or three levels stress (including the control treatment), with an average decrease of 50% in performance recorded at the most severe level of stress (He et al. 2013). Our results indicate that this might not be appropriate for studying the effect of stress events. Moreover, species-specific thresholds were clearly influenced by competition and the timing of stress application. We conclude that results obtained from growing plants in monoculture and using adult plants probably cannot be used for drawing general conclusions (Verlinden et al. 2013). We agree with earlier studies, in recommending that the environmental tolerance of plants cannot be judged when growing them in monoculture (Woodward 1992), although this might not apply to several noxious invasive species with a strong tendency to establish large monocultures in the wild.

In terms of the climatic stresses, types of competition and life-history stages used the alien species of *Hieracium* and *Lysimachia* showed no overall higher tolerance of stress and *Ambrosia* performed only slightly better than the native confamilial. The responses of closely related species to level and type of stress were similar, which indicates that similarity of phylogenetically close species is not restricted to comparable traits (Harvey et al. 1995), or comparable phenotypic plasticity (Godoy et al. 2011, Palacio-Lopez & Gianoli 2011), but also to tolerance to stress. However, as we have focused on congeneric/confamilial species we cannot compare the stress tolerance of alien species with that of other, less-related co-occurring species. Thus our result that alien and native species respond similarly to stress events cannot be used to predict the changes that are likely to occur in communities following stress events.

The responses to the expected increase in the frequency of climatic stress with climate change are likely to be highly species-specific and will not necessarily favour alien species as a group. This does not imply, however, that alien species cannot benefit indirectly from an increase in climatic stress. Indeed, invasive species are well able to invade new environments, often have high dispersal abilities and high growth rates, which should facilitate a faster spread into and an establishment in sites, after stress events.

Acknowledgements

We thank Petra Scheuerer, Udo Ehlers, Ivonne Jüttner, F. Steinbacher and the team at TUM GHL Dürnast for the use of their facilities and technical help. Further thanks are due to Simeon Max, Marc Young, Irina Kozban and April Guo for help with harvesting, weighing and data entry. Our special thanks go to Tina Heger, who provided highly valuable feedback on the first draft of the manuscript. We thank the three reviewers and Tony Dixon for comments that improved the manuscript. With the support of the Technische Universität München –

Institute for Advanced Study, which is funded by the German Excellence Initiative and the European Research Council, under the European Union's Seventh Framework Programme (FP7/2007-2013)/ERC Grant agreement no. 282250.

Souhrn

Vedle nárůstu teploty a koncentrace CO_2 se připisuje značný význam i jiným projevům probíhajících klimatických změn, jako jsou extrémní projevy klimatu a jeho krátkodobé kolísání. Předpokládá se, že by lepší schopnost vyrovnat se s těmito faktory mohla představovat pro invazní druhy výhodu; naše znalosti toho, jak se invazní druhy dokáží vyrovnat s krátkodobým klimatickým stresem, jsou však velmi omezené. V článku jsme sledovali, zda tři ve střední Evropě naturalizované nepůvodní druhy *Ambrosia artemisiifolia*, *Hieracium aurantiacum* a *Lysimachia punctata* porostou ve stresujících podmínkách lépe, než jim příbuzné původní druhy. Skleníkový pokus sestával z postupného vystavení rostlin mrazu, suchu a zaplavení, všem těmto zásahům byly vystaveny rostliny ve dvou vývojových stádiích (semenáčky a dospělé rostliny), v monokulturách i směsích, suplujících silnou vnitrodruhovou i mezidruhovou kompetici. Zjistili jsme sice mírné rozdíly v reakci jednotlivých druhů, nepůvodní druhy však celkově nevykazovaly vyšší toleranci vůči stresu. Všechny druhy byly zranitelnější ve stadiu semenáčků. Výsledky studie naznačují, že z pokusů zahrnujících pouze monokultury a jediné vývojové stádium nelze usuzovat na hraniční hladiny stresových faktorů.

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Received 16 July 2014
Revision received 14 October 2014
Accepted 8 November 2014