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ORIGINAL PAPER

# Alien plant species favoured over congeneric natives under experimental climate warming in temperate Belgian climate

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**Abstract** Climate warming and biological invasions by alien species are two key factors threatening the world's biodiversity. To date, their impact has largely been studied independently, and knowledge on whether climate warming will promote invasions relies strongly on bioclimatic models. We therefore set up a study to experimentally compare responses to warming in native and alien plant species. Ten congeneric species pairs were exposed to ambient and elevated temperature (+3°C) in sunlit, climate-controlled chambers, under optimal water and nutrient supply to avoid interaction with other factors. All species pairs combined, total plant biomass reacted differently to warming in alien versus native species, which could be traced to significantly different root responses. On average, native species became less productive in the warmer climate, whereas their alien counterparts showed no response. The three alien species with the strongest warming response (*Lathyrus latifolius*, *Cerastium tomentosum* and *Artemisia verlotiorum*) are currently non-invasive but all originate from regions with a warmer climate. Still, other alien species that also originate from warmer regions became less or remained equally productive. Structural or ecophysiological acclimation to warming was largely absent, both in native and alien species, apart from light-saturated photosynthetic rate, where warming tended to restrain the native but not the alien species. A difference in the capacity to acclimate photosynthetic rates to the new climate may therefore have caused the contrasting biomass response. Future experiments are needed to ascertain whether climate warming can effectively tip the balance between native and alien competitors.

**Keywords** Climate warming · Plant invasions · Global change · Alien species · Congeneric species · Temperature acclimation

## Introduction

Climate change and biological invasions are two of the most urgent ecological concerns facing the world today, and synergies between these two global changes have been identified as a possible new threat to biodiversity (Chown et al. 2007; Ward and Masters 2007; Pyke et al. 2008). However, the nature of and the mechanisms underlying such synergies are poorly explored (Stachowicz et al. 2002; Chown et al. 2007). Insight into these mechanisms is needed to help curb the exponential increase of economic and environmental damage inflicted by biological invasions (Ward and Masters 2007).

Future invaders will very likely not experience the climate of today. Global surface temperatures are

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projected to increase by 1.1–6.4°C over the next 100 years, in reaction to the rising atmospheric concentrations of greenhouse gases (IPCC 2007). There are several reasons to assume that invasive plant species will react differently to warming than their native counterparts (Dukes and Mooney 1999; Walther et al. 2002; Hellmann et al. 2008). Alien species often exhibit a greater plasticity in their response to environmental changes and disturbances (Alpert et al. 2000; McDowell 2002). Consequently, they may have a greater capacity to shift their physiological optimum to a range that is favourable in the new climate (Richards et al. 2006; Maron et al. 2007). Furthermore, in the absence of acclimation, alien species, especially those originating from regions with a warmer climate, may already be closer to optimal physiological functioning under elevated than under ambient temperatures. This may enhance their future competitiveness relative to natives. Climate warming could therefore, on the one hand, be a trigger for many ‘slumbering’ alien species that are currently part of the flora without expanding, and may on the other hand strengthen the invasive potential of many alien species that are already invasive (Sutherst 2000).

In recent years, our understanding of the responses to climate warming of plants in general has significantly increased owing to a growing number of experimental and modelling studies. Under warming, stimulation of growth and primary productivity is possible mainly through altered reaction kinetics (Larcher 2003), acclimation to changing temperatures and water availability (Luo et al. 2001; Wythers et al. 2005) and improved access to nutrients (Rustad et al. 2001). Adverse effects of warming on the productivity of plants can, among others, arise from increased temperature stress (White et al. 2000) and from water shortage as a result of increased evapotranspiration (Saleska et al. 1999; De Boeck et al. 2008). Species-specific effects of warming on productivity and competitiveness may lead to changes in plant community composition (Levy et al. 2004; Niu et al. 2008).

The response of invasive plant species to climate warming, on the other hand, has only been investigated in a handful of studies. Techniques used so far include: (1) experimentally growing plants across elevational gradients (Willis and Hulme 2002), (2) analysing the natural distribution of invasive plants across elevational gradients (McDougall et al. 2005), (3) climate envelope modelling (Thuiller et al. 2005), (4) ecological niche modelling (Peterson et al. 2008), and (5) models of vegetation dynamics (Gritti et al. 2006). While these methodologies deliver information on the possible consequences of warming for invasive species, they are less pointed at identifying the plant traits or other underlying causes involved. Moreover, because several of the available studies are based on modelling, there is a lack of experimental confirmation on how invasive alien species actually respond.

The current study is the first to our knowledge to investigate the responses of multiple alien versus closely related native species to experimentally induced temperature increase in controlled conditions. Ten congeneric species pairs were screened, with the alien component including both invasive and non-invasive species. We looked for changes in plant biomass and in plant structural and ecophysiological characteristics related to growth and productivity. The following questions were addressed: (1) Does experimental warming favour alien species over their native counterparts in terms of biomass production? (2) Can the observed patterns be explained by differences in structural and ecophysiological acclimation to warming?

## Materials and methods

### Experimental site and design

The experimental site was located at the Drie Eiken Campus of the University of Antwerp (Belgium, 51°09′N, 04°24′E). Average annual precipitation at this site is 776 mm, equally distributed over the year. Average annual air temperatures ($T_{\mathrm{air}}$) vary around 9.6°C, and mean monthly air temperatures are between 2.2°C (January) and 17.0°C (July). Plants were grown in four sunlit, climate-controlled chambers, facing south. The interior surface area was $150 \times 150\ \mathrm{cm}^2$, the height at the north side 150 cm and at the south side 120 cm. The top of the chambers was covered with a colourless polycarbonate plate (4 mm thick), while the sides were made of polyethylene film (200 µm thick), both UV transparent. Belowground, the soil inside the chamber area was fenced off at the sides by 40-cm-deep concrete plates.

Half of the chambers were exposed to the ambient $T_{air}$ (unheated chambers), while the other half (heated chambers) were continuously heated 3°C above fluctuating ambient values. Each chamber had its individual air control group and temperature regulation. The conditioned air was evenly distributed throughout the chambers by means of aerators with regulated flow. The air temperature and the air relative humidity was measured with a combined humdity-temperature sensor (Siemens, type QFA66, Germany) and all measurements were monitored and logged every 30 min on a computer with GE Fanuc Cimplicity software 150 I/O (Scada, MA, USA).

Each chamber contained 80 plants, sown (9 May 2005) individually in containers (grey PVC-tubes of 13.5 cm inner diameter and 25 cm height), filled with sand. To avoid unnatural soil temperatures in the containers, they were buried into the surrounding soil. Holes in the lids sealing the bottom of the containers ensured that water could drain freely, while anti-root mats prevented roots from growing outside. In order to investigate the response to temperature in the absence of confounding factors, plants were grown under optimal water and nutrient supply. To this end the plants were watered daily with 100 ml and fertilized weekly with a modified (70%) Hoagland solution (3.02 mM $Ca(NO_3)_2 \times 4\ H_2O$, 3.98 mM $KNO_3$, 0.19 mM $KH_2PO_4$, 0.27 mM $MgSO_4 \times 7\ H_2O$, 2 µM $MnSO_4 \times H_2O$, 0.85 µM $ZnSO_4 \times 7\ H_2O$, 0.15 µM $CuSO_4 \times 5\ H_2O$, 20 µM $H_3BO_3$, 0.25 µM $Na_2MoO_4 \times H_2O$ and 40.48 µM $C_{10}H_{12}N_2O_8NaFe$ (Fe-EDTA)).

## Plant species

Ten congeneric species pairs, each consisted of one terrestrial alien plant species and one closely related native counterpart, were selected (Table 1). We first chose alien species that were able to grow in the greenhouse conditions (chamber height). Next, closely related native congeners were selected by the method of phylogenetically independent contrasts (Felsenstein 1985). Species pairs were further chosen based on the size similarity of the congeners. The species set that left comprised only a few invasive alien species, which were all selected as we aimed to include both invasive and non-invasive alien species (which can be considered future high-risk species if they respond strongly to warming). Finally, the alien species had to originate from regions varying in climate.

Congeneric species pairs were used as an alternative to randomly selected species, thereby avoiding chance overrepresentation of specific adaptations that govern the response to warming in either the native or the alien group. Because of potential confounding between ecological differences and phylogenetic effects, the value of multiple-species comparisons is greatly strengthened if they are made between congeners (Hamilton et al. 2005; Richards et al. 2006). The 10 chosen species pairs do not reflect a particular community from a specific habitat, but can be seen—within certain limitations—as a model for temperate herbaceous plant communities in general. In each treatment, eight replicate plants per species were arranged at random positions within the chambers (four per chamber).

## Measurements

We examined the influence of warming on a range of structural and ecophysiological plant characteristics related to growth rate and productivity, in order to explain possible changes in biomass of alien versus native species. Ecophysiological characteristics were measured from 19 till 26 August 2005 with a portable gas exchange system (LI-6400, Li-cor, NE, USA) on four randomly chosen replicates per species (two per chamber). They included leaf light-saturated photosynthetic rate ($P_{max}$, µmol $m^{-2}$ $s^{-1}$), dark respiration rate ($R_d$, µmol $m^{-2}$ $s^{-1}$), stomatal conductance ($g_s$, mmol $m^{-2}$ $s^{-1}$) and transpiration rate (Tr, mmol $m^{-2}$ $s^{-1}$). All measurements were made on the youngest fully expanded leaves (allowing minimum 5 min of stabilization to give them enough acclimation time), between 10 and 16 h local time, at a $CO_2$ concentration of 380 µmol $mol^{-1}$ and at 22°C to approximate temperature optima for plant growth in temperate regions (Larcher 2003). This temperature was also the local average maximum temperature for August. Measurements of $P_{max}$, $g_s$ and Tr were made at saturating irradiance (1,800 µmol $m^{-2}$ $s^{-1}$). Since the ecophysiological parameters were measured at constant temperature, any changes would reflect acclimation. Due to logistical limitations, we were not able to carry out the multitude of measurements required to detect direct temperature effects

**Table 1** Species pairs used

| Alien species | Native species | Family | Native range of the alien species | Temperature preference of the alien species | Abbreviation |
|---|---|---|---|---|---|
| *Artemisia verlotiorum* Lamotte (E) | *Artemisia vulgaris* L. | Asteraceae | S-China | 7 | *Ave-Avu* |
| *Bidens frondosa* L. (E) | *Bidens tripartita* L. | Asteraceae | N-America | 6 | *Bf-Bt* |
| *Barbareae stricta* Andrz. (E) | *Barbareae vulgaris* R. Br. | Brassicaceae | M-, N-, E-Europe; W-, M-Asia | 6 | *Bs-Bv* |
| *Cerastium tomentosum* L. (E) | *Cerastium arvense* L. | Caryophyllaceae | M-, S-Italy | 8 | *Ct-Ca* |
| *Impatiens glandulifera* Royle (I) | *Impatiens noli-tangere* L. | Balsaminaceae | Himalaya | 7 | *Ig-In* |
| *Lathyrus latifolius* L. (E) | *Lathyrus pratensis* L. | Fabaceae | S-, E-Europe | 8 | *Ll-Lp* |
| *Lepidium draba* L. (E) | *Lepidium campestre* R. Br. | Brassicaceae | S-Europe, SW-Asia, N-Africa | 7 | *Ld-Lc* |
| *Rumex scutatus* L. (E) | *Rumex acetosa* L. | Polygonaceae | S-Europe, SW-Asia, N-Africa | 7 | *Rs-Ra* |
| *Senecio inaequidens* DC. (I) | *Senecio jacobaea* L. | Asteraceae | S-Africa | 7 | *Si-Sj* |
| *Solidago gigantea* Ait. (I) | *Solidago virgaurea* L. | Asteraceae | N-America | 6 | *Sg-Sv* |

Letters in parentheses indicate the alien species' status in Flanders according to Verloove (2002): *I* invasive, *E* established. Temperature preference (according to Ellenbergh et al. 1992): 5, moderate thermophilous; 6, between 5 and 7; 7, thermophilous; 8, between 7 and 9; 9, extreme thermophilous

(i.e. simultaneous, replicated temperature response curves of 20 species in two treatments).

Among the structural characteristics we determined were specific leaf area (SLA), calculated as leaf area/dry leaf mass ($cm^2\ g^{-1}$), and leaf nitrogen concentration ([N], $g\ m^{-2}$), measured with an NC element analyzer (NC-2100, Carlo Erba Instruments, Italy). Both were assessed on the leaf samples used for the $P_{max}$ measurements. From these measurements, two more ecophysiological traits were derived: instantaneous photosynthetic nitrogen use efficiency, calculated as PNUE = $P_{max}$/[N] (mol $CO_2$ $mol^{-1}$ N $s^{-1}$), and instantaneous water use efficiency, calculated as WUE = $P_{max}$/Tr (μmol $CO_2$ $mmol^{-1}$ $H_2O$). Because not all leaf samples had sufficient mass for leaf nitrogen analyses, sample size for [N] and consequently also for PNUE was lower than for the other ecophysiological parameters. We will not present the Tr data themselves, since at constant temperature they correlate with $g_s$.

From 6 till 16 October 2005, all plants were harvested, dried for a minimum 48 h at 60°C and weighed. The total biomass ($B_{plant}$) of each individual plant was separated into below- and aboveground biomass ($B_{below}$ and $B_{above}$), and $B_{above}$ of four replicates per species was divided further into stems and leaves ($B_{stem}$ and $B_{leaf}$). Three additional structural plant traits were derived from this: root/shoot ratio (RSR), the ratio of below- to aboveground biomass, and leaf and stem mass ratio (LMR and SMR), the ratio of leaf and stem biomass, respectively, to total plant biomass.

## Statistical analysis

Microclimatic data were analyzed with repeated measure analysis of variance (RM-ANOVA) with date of measurement as within-subject factor and climate as between-subject factor. The effects of climate, chamber (nested within climate), species pair, origin (native or alien, nested within species pair) and their interactions on all structural and ecophysiological parameters and on plant biomass were tested with a nested univariate analysis of variance (ANOVA). Chamber was treated as random, other factors as fixed. The nesting of 'chamber' within 'climate' avoids pseudo replication. The chamber factor was omitted from the analysis if not significant (which was the case for all factors except $B_{plant}$, $B_{below}$ and $P_{max}$). Origin is nested within species pair because ‘native’ and ‘alien’ are different species in each pair. When the interaction between origin and treatment was found, separate ANOVAs with the factors climate, chamber (nested within climate) and species were carried out for native and alien species. Variables were examined for normality and heterogeneity of variance and log-transformed if necessary. Differences were considered significant at $P < 0.05$. Linear regressions were used to analyse relationships between biomass and structural or ecophysiological parameters. All statistics were performed using SPSS 13.0 (SPSS Science, Woking, UK).

## Results

### Microclimate

During the entire growing season (sowing to harvest), the average temperature of the unheated chambers was equal to the ambient $T_{air} + 0.56 \pm$ (SD) 1.63°C; the average temperature of the heated chambers was equal to the ambient $T_{air} + 3.22 \pm$ (SD) 1.28°C. During the same period, the average vapour pressure deficit (VPD) was 693 ± (SE) 59.3 and 791 ± (SE) 49.6 Pa in the unheated and heated chambers, respectively. There was no significant difference in VPD between the two treatments (RM-ANOVA, $F_{1,169} = 1.247$, $P > 0.05$).

### Biomass

There were significant effects of species pair on total plant biomass and all of its components, expressing the considerable variation in productivity between genera (Table 2). Native species had on average a significantly higher $B_{plant}$, $B_{below}$ and $B_{leaf}$, while $B_{stem}$ was significantly higher in the alien species (Fig. 1; Table 2, significant origin effects).

All species pairs combined, alien and native species responded differently to warming for total plant biomass and belowground biomass (significant climate × origin interaction in Table 2; Fig. 1a, b) In native species, warming negatively affected both $B_{plant}$ and $B_{below}$ (ANOVA on native species only, $F_{1,92} = 3.944$, $P < 0.05$; $F_{1,92} = 7.716$, $P < 0.05$, respectively). In alien species, on the other hand, none of the biomass variables reacted to warming (ANOVA on alien species only, $P > 0.05$).

**Table 2** *F*-values and significance levels of ANOVAs of total plant biomass ($B_{plant}$), belowground biomass ($B_{below}$), leaf biomass ($B_{leaf}$), stem biomss ($B_{stem}$); structural parameters: root/shoot ratio (RSR), leaf mass ratio (LMR), stem mass ratio (SMR), specific leaf area (SLA), leaf nitrogen concentration ([N]); and ecophysiological parameters: leaf light-saturated photosynthetic rate ($P_{max}$), dark respiration rate ($R_d$), stomatal conductance ($g_s$), water use efficiency (WUE), and photosynthetic nitrogen use efficiency (PNUE) with factors climate, species pair and origin (native or alien, nested within species pair)

| | Climate | Species pair | Origin (species pair) | Climate × origin (species pair) |
|---|---|---|---|---|
| $B_{plant}$ | $F_{1,2} = 0.058$ | $F_{9,214} = 21.390$*** | $F_{10,214} = 5.159$*** | $F_{10,214} = 2.245$* |
| $B_{below}$ | $F_{1,2} = 0.249$ | $F_{9,214} = 17.738$*** | $F_{10,214} = 2.176$* | $F_{10,214} = 2.710$** |
| $B_{leaf}$ | $F_{1,131} = 0.011$ | $F_{9,131} = 17.803$*** | $F_{10,131} = 3.619$*** | $F_{10,131} = 0.639$ |
| $B_{stem}$ | $F_{1,131} = 4.212$* | $F_{9,131} = 47.093$*** | $F_{10,131} = 16.504$*** | $F_{10,131} = 1.620$ |
| RSR | $F_{1,216} = 0.241$ | $F_{9,216} = 14.805$*** | $F_{10,216} = 8.312$*** | $F_{10,216} = 1.550$ |
| LMR | $F_{1,131} = 0.994$ | $F_{9,131} = 13.099$*** | $F_{10,131} = 1.982$* | $F_{10,131} = 1.102$ |
| SMR | $F_{1,131} = 3.023$ | $F_{9,131} = 57.698$*** | $F_{10,131} = 6.626$*** | $F_{10,131} = 0.625$ |
| SLA | $F_{1,106} = 0.494$ | $F_{9,106} = 10.588$*** | $F_{10,106} = 4.106$*** | $F_{10,106} = 0.807$ |
| [N] | $F_{1,98} = 0.002$ | $F_{9,98} = 1.107$ | $F_{10,98} = 1.528$ | $F_{10,98} = 1.415$ |
| $P_{max}$ | $F_{1,2} = 0.110$ | $F_{9,104} = 5.779$*** | $F_{10,104} = 1.941$* | $F_{10,104} = 1.690$ |
| $R_d$ | $F_{1,106} = 2.693$ | $F_{9,106} = 15.561$*** | $F_{10,106} = 2.237$* | $F_{10,106} = 1.124$ |
| $g_s$ | $F_{1,106} = 1.860$ | $F_{9,106} = 5.773$*** | $F_{10,106} = 0.592$ | $F_{10,106} = 0.392$ |
| WUE | $F_{1,106} = 1.518$ | $F_{9,106} = 1.530$ | $F_{10,106} = 0.634$ | $F_{10,106} = 0.469$ |
| PNUE | $F_{1,98} = 0.653$ | $F_{9,98} = 5.124$*** | $F_{10,98} = 1.377$ | $F_{10,98} = 1.330$ |

*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$, otherwise not significant

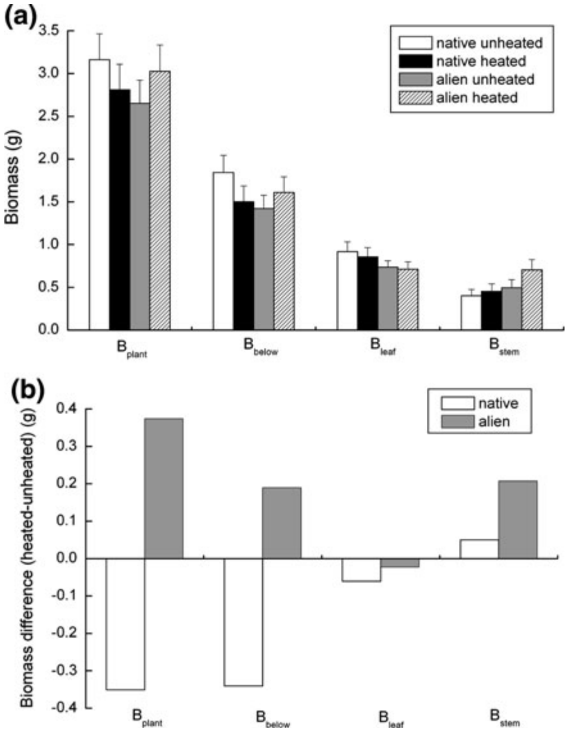

**Fig. 1** Total plant biomass ($B_{plant}$), belowground biomass ($B_{below}$), leaf biomass ($B_{leaf}$) and stem biomass ($B_{stem}$). **a** Mean absolute values ± SE for the native and alien species in the unheated and the heated (+3°C) chambers. **b** Response to warming: mean absolute difference between heated and unheated chambers for the alien and native plant species

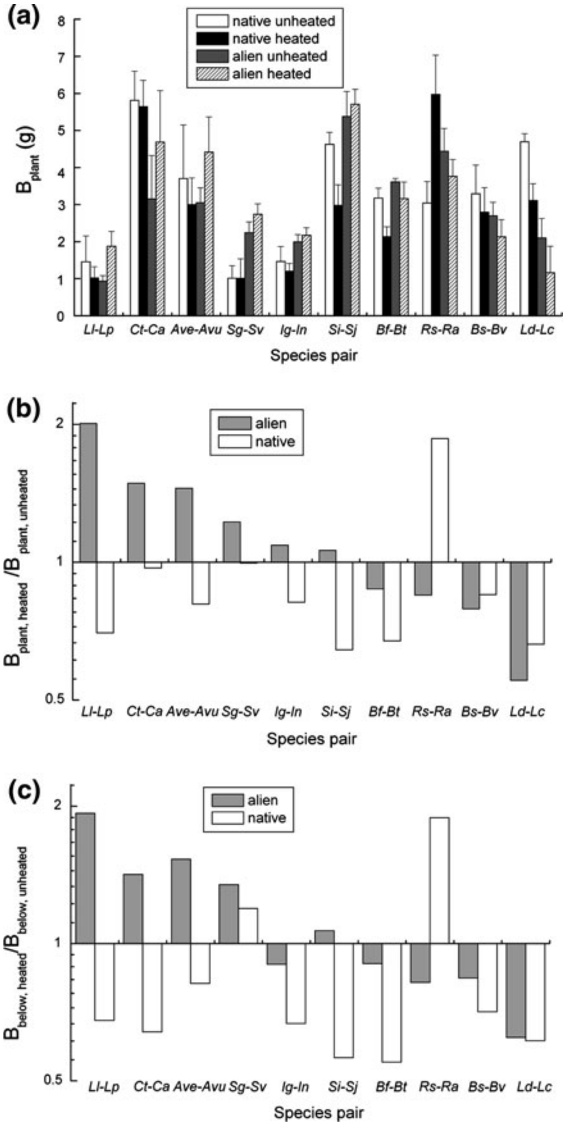

**Fig. 2** Mean absolute values ± SE of total plant biomass for all native and alien plant species in the unheated and the heated (+3°C) chambers (**a**). Response to warming: ratio of total plant biomass (**b**) and belowground biomass (**c**) in heated to unheated chambers for all alien and native plant species. Species: *Ll*, *Lathyrus latifolius*; *Lp*, *Lathyrus pratensis*; *Ct*, *Cerastium tomentosum*; *Ca*, *Cerastium arvense*; *Ave*, *Artemisia verlotiorum*; *Avu*, *Artemisia vulgaris*; *Sg*, *Solidago gigantea*; *Sv*, *Solidago virgo-aurea*; *Ig*, *Impatiens glandulifera*; *In*, *Impatiens noli-tangere*; *Si*, *Senecio inaequidens*; *Sj*, *Senecio jacobaea*; *Bf*, *Bidens frondosa*; *Bt*, *Bidens tripartita*; *Rs*, *Rumex scutatus*; *Ra*, *Rumex acetosa*; *Bs*, *Barbarea stricta*; *Bv*, *Barbarea vulgaris*; *Ld*, *Lepidium draba*; *Lc*, *Lepidium campestre*

We next focus on whether the contrasting responses of total biomass to warming in alien versus native species were consistent across species pairs (Fig. 2a). Although the statistical analyses are based on absolute differences, we also depict the relative effects in order to show responses to warming independent of plant size (Fig. 2b). In agreement with the analysis on all species combined in Table 2 and Fig. 2b shows no clear trend in the response of alien species to climate warming. Some species were favoured by an increase in temperature and this was significant for *Lathyrus latifolius*, *Cerastium tomentosum* and *Artemisia verlotiorum* (separate ANOVAs by species with factors climate and chamber, $P < 0.05$, $F_{1,12} = 4.762$; $F_{1,7} = 5.629$; $F_{1,9} = 5.564$, respectively). However, other alien species showed an opposite trend, which was significant for *Lepidium draba* ($F_{1,9} = 5.774$, $P < 0.05$). The native species, on the other hand, responded more consistently in a negative direction (Fig. 2b). In separate ANOVAs by species, this was significant for *Senecio jacobaea*, *Bidens tripartita* and *Lepidium campestre* ($P < 0.05$, $F_{1,10} = 7.204$; $F_{1,10} = 4.984$; $F_{1,11} = 6.655$, respectively). Only one species

(*Rumex acetosa*) showed the opposite response ($F_{1,10} = 9.165$, $P < 0.05$).

The three alien species with the strongest warming response (*L. latifolius*, *C. tomentosum* and *A. verlotiorum*) are currently non-invasive but all originate from regions with a warmer climate. Still, several other alien species used in this experiment that also originate from warmer regions showed no (*Senecio inaequidens* and *Rumex scutatus*) or a negative response (*L. draba*) to warming, hinting that there need not be a consistent relationship between response to warming and climate in the native range.

The species-specific response pattern of total biomass in Fig. 2b was clearly driven by changes in the root and stem compartments. In particular, the same alien species exhibited more positive values than their native counterparts in $B_{plant}$ and $B_{below}$ (Fig. 2c). A similar pattern was found in $B_{stem}$ (not shown).

## Structural and ecophysiological parameters

There were significant effects of species pair on all structural and ecophysiological parameters except for WUE (Table 2). The selected genera were thus characterized by considerable physiological and structural variation. All species pairs combined, alien species had significantly higher RSR, SMR, $P_{max}$ and $R_d$, and significantly lower SLA and LMR (significant origin effect in Tables 2, 3). However, we did not find significant climate effects or climate × origin interaction effects on any of the ecophysiological and structural parameters, indicating a general lack of acclimation to temperature. Nevertheless, we did find a nearly significant climate × origin effect on $P_{max}$ (Table 2, $P = 0.074$) and a trend of $P_{max}$ in native species being negatively affected by climate warming (Table 3). Furthermore, when combining data of all species and treatments, a significant positive relationship emerged between $B_{plant}$ and $P_{max}$, not affected by warming or origin (Fig. 3, linear regression, $F_{1,40} = 7.264$, $P < 0.05$). Combined, these observations suggest that photosynthesis drove the (significant) contrasting warming responses of native versus alien species biomass in this study. Relationships between $B_{plant}$ and other structural or

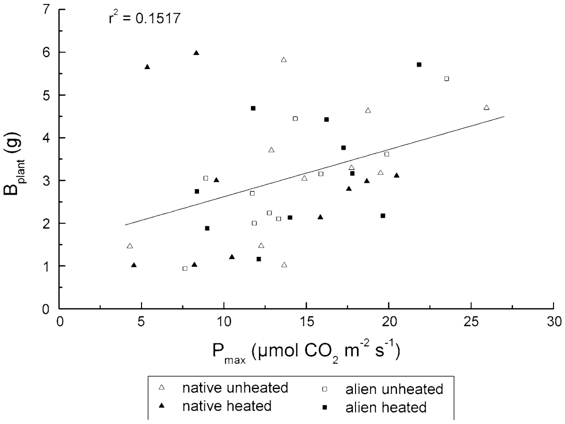

**Fig. 3** Linear regression of total plant biomass ($B_{plant}$) against light-saturated photosynthetic rate ($P_{max}$). Means per species

**Table 3** Structural parameters: root/shoot ratio (RSR), leaf mass ratio (LMR), stem mass ratio (SMR), specific leaf area (SLA), leaf nitrogen concentration ([N]); and ecophysiological parameters: leaf light-saturated photosynthetic rate ($P_{max}$), dark respiration rate ($R_d$), stomatal conductance ($g_s$), water use efficiency (WUE), and photosynthetic nitrogen use efficiency (PNUE)

| | Native unheated | Native heated | Alien unheated | Alien heated |
|---|---|---|---|---|
| RSR | 1.686 (±0.190) | 1.417 (±0.151) | 1.559 (±0.178) | 1.726 (±0.232) |
| LMR | 0.290 (±0.018) | 0.307 (±0.021) | 0.313 (±0.021) | 0.245 (±0.018) |
| SMR | 0.1434 (±0.023) | 0.165 (±0.029) | 0.142 (±0.022) | 0.196 (±0.030) |
| SLA ($cm^2\ g^{-1}$) | 269.5 (±31.7) | 252.4 (±28.9) | 239.3 (±17.0) | 235.1 (±15.7) |
| [N] ($g\ m^{-2}$) | 1.235 (±0.149) | 1.351 (±0.170) | 1.485 (±0.075) | 1.409 (±0.109) |
| $P_{max}$ ($\mu mol\ m^{-2}\ s^{-1}$) | 15.36 (±1.79) | 11.91 (±1.82) | 13.99 (±1.52) | 14.82 (±1.42) |
| $R_d$ ($\mu mol\ m^{-2}\ s^{-1}$) | 2.730 (±0.491) | 2.869 (±0.541) | 2.878 (±0.524) | 3.050 (±0.384) |
| $g_s$ ($mmol\ m^{-2}\ s^{-1}$) | 401.4 (±56.8) | 403.1 (±53.8) | 349.8 (±46.9) | 409.3 (±32.7) |
| WUE ($\mu mol\ CO_2\ mmol^{-1}\ H_2O$) | 6.570 (±0.691) | 5.551 (±0.909) | 6.207 (±0.670) | 5.283 (±0.820) |
| PNUE ($10^{-4}\ mol\ CO_2\ mol^{-1}\ N\ s^{-1}$) | 1.869 (±0.160) | 1.371 (±0.213) | 1.474 (±0.181) | 1.564 (±0.200) |

Means ± SE in the unheated and heated (+3°C) chambers for the native and alien plant species ecophysiological parameters were not significant (linear regressions, $P > 0.05$).

## Discussion

Experimentally induced climate warming had contrasting impacts on the total biomass of alien versus native species in ten congeneric species pairs (significant climate × origin interaction). On average, native species became less productive in the warmer climate, whereas their alien counterparts showed no overall response. Differences in root growth best explained the response.

In explaining these observations, we can exclude indirect negative effects of warming resulting from soil drought induced by increased evapotranspiration (Norby and Luo 2004; Wan et al. 2004). Since all plants were watered daily with 100 ml, which exceeds the amount needed to replace even high typical summer evapotranspiration rates of 3–4 mm (Baguis et al. 2009), and since VPD (which affects transpiration as well as evaporation) was not significantly influenced by warming, it is unlikely that soil moisture was different between heated and unheated chambers. Indirect effects of warming through altered nutrient mineralisation and access to nutrients (Rustad et al. 2001) are unlikely to have contributed either, as the plants were grown in sand with optimal nutrient supply. Direct effects of warming through enhanced (in native species) or alleviated (in alien species) temperature stress on plant growth are thus the most likely origin of the observed patterns (White et al. 2000; Gielen et al. 2007). Roots are particularly sensitive to temperature, and soil warming has been shown to reduce both root number and mass due to increased root death as a consequence of higher maintenance respiration (Atkin et al. 2000; Edwards et al. 2004; Wan et al. 2004). Such mechanisms probably contributed strongly to the negative biomass response in our native species, as this could be clearly traced to roots. Alternatively, warming may have induced direct stress effects in leaves via greater transpiration at higher temperatures. This mechanism is known to reduce leaf turgor, and ultimately cell expansion and leaf growth (Larcher 2003). However, a strong contribution from this mechanism is unlikely, since warming did not significantly change leaf biomass or SLA. The warming effects on plant biomass were not mirrored by corresponding changes in structural traits. We infer that warming mainly affected the size of the plants, but not their organizational layout (RSR, LMR, SMR, SLA) or element composition (N concentration). Acclimation was not detected in ecophysiological characteristics either, such as stomatal conductance, WUE, PNUE or dark respiration rate (all measured at a common temperature). An exception was light-saturated leaf photosynthetic rate, in which we observed a trend in the response to increased temperatures similar to that in $B_{plant}$ (no response for alien and a decrease for native species). In addition, all species and treatments combined, $B_{plant}$ and $P_{max}$ were significantly positively coupled. This suggests that acclimatory adaptations in the photosynthetic apparatus were at the basis of the biomass responses to warming. Such adaptations could involve changes in the intercellular $CO_2$ concentration, in the temperature dependence of the maximum rate of RuBP (ribulose-1,5-biphospate) carboxylation and RuBP regeneration, or in the ratio of RuBP carboxylation to RuBP regeneration (Hikosaka et al. 2006; Ishikawa et al. 2007). Changes in the total amount of nitrogen invested in photosynthesis, on the other hand, can be excluded given the observed lack of change in leaf nitrogen concentration per unit area. The capacity to acclimate is considered a major difference between alien and native plant species (Daehler 2003; Maron et al. 2007). A possible greater acclimation in alien plants may enable them to successfully tolerate broad environmental conditions (Milberg et al. 1999; Sultan 2001; Sexton et al. 2002) and to occupy a wide geographic range in their native regions (Roy et al. 1991; Goodwin et al. 1999). The current data set on congeneric alien and native species exposed to warming seems to corroborate this hypothesis to some extent.

Obviously, regardless of acclimation, the instantaneous effect of a 3°C warming on $P_{max}$ will vary depending on whether ambient temperature is on average below or above the optimum for photosynthesis (Barnes et al. 1998). This is reflected in the literature by studies reporting either no changes (Loik et al. 2000; Llorens et al. 2003, 2004), decreases (Callaway et al. 1994; Pearson and Dawson 2003) or increases in photosynthetic rates (Apple et al. 2000; Lemmens et al. 2006). Our current findings to a large extent fit this simple explanatory framework. Assuming that native species would be well adapted to today's thermal regime of Western Europe, they would be expected to experience superoptimal temperatures for photosynthesis more often upon exposure to warming. This is in agreement with the observed reduction in their productivity. Conversely, alien species originating from regions with a warmer climate would in Western Europe experience temperatures below the photosynthetic optimum less often under warming, in agreement with the observed enhanced productivity in several of these species. However, we have no good explanation why alien species with a more southern native range showed no response or even became less productive (i.e. had an impaired carbon balance) in the simulated warmer climate. The species in question have a Mediterranean distribution, consequently they experience a considerably smaller seasonal sum of incident photosynthetically active radiation in Belgium compared with their native range. Perhaps, light limitations did not allow these species to fix sufficient additional carbon in photosynthesis to compensate for an enhanced respiratory carbon loss under warming.

To what extent can our findings shed light on how climate warming may affect the future invasiveness of alien plant species? Many prior studies of invasiveness have focused on the traits associated with the capacity of alien plant species to successfully invade new habitats (Pysek and Richardson 2006; Richardson and Pysek 2006) and apart from a broad native range, especially traits related to high growth rate under varying environmental conditions seem important (Durand and Goldstein 2001; Lake and Leishman 2004). Photosynthesis is such a trait (Pysek and Richardson 2006) and since increases in temperature can affect photosynthesis, warming could potentially lead to changes in invasiveness through this pathway (Patterson 1995). The results of the current study are thus in agreement with the hypothesis that climate warming might favour alien species over natives and enhance their invasion success (Dukes and Mooney 1999; Hellmann et al. 2008). We would like to emphasize though that simulating a realistic level of ecosystem complexity was outside our scope. For example, it is known that, in the current climate, a lower herbivory pressure on alien plants may contribute to their success (Keane and Crawley 2002). However, climate warming may increase leaf palatability (Dury et al. 1998) and consequently the level of herbivory (Roy et al. 2004), thus possibly reducing the capacity of alien plants to invade. A second reason for caution is that we have only tested the intrinsic reaction of individual species as single plants to rising temperatures. Larger biomass in individual plants does not always translate into enhanced competitive success in the field. Clearly, experiments on competing alien and native species are necessary to investigate whether climate warming will alter the competitive balance between them.

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