GLOBAL CHANGE ECOLOGY - ORIGINAL PAPER

Plant–soil feedback of native and range-expanding plant species is insensitive to temperature

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Abstract Temperature change affects many aboveground and belowground ecosystem processes. Here we investigate the effect of a 5°C temperature increase on plant–soil feedback. We compare plant species from a temperate climate region with immigrant plants that originate from warmer regions and have recently shifted their range polewards. We tested whether the magnitude of plant–soil feedback is affected by ambient temperature and whether the effect of temperature differs between these groups of plant species. Six European/Eurasian plant species that recently colonized the Netherlands (non-natives), and six related species (natives) from the Netherlands were selected. Plant–soil feedback of these species was determined by comparing performance in conspecific and heterospecific soils. In order to test the effect of temperature on these plant–soil feedback interactions, the experiments were performed at two greenhouse temperatures of 20/15°C and 25/20°C, respectively. Inoculation with unconditioned soil had the same effect on natives and non-natives. However, the effect of conspecific conditioned soil was negative compared to heterospecific soil for natives, but was positive for non-natives. In both cases, plant–soil interactions were not affected by temperature. Therefore, we conclude that the temperature component of climate change does not affect the direction, or strength of plant–soil feedback, neither for native nor for non-native plant species. However, as the non-natives have a more positive soil feedback than natives, climate warming may introduce new plant species in temperate regions that have less soil-borne control of abundance.

Keywords Climate change · Neophyte · Plant–soil feedback · Range shift · Warming

Introduction

As a result of global climate change, ecological interactions between organisms are changing (e.g. Voigt et al. 2003; Roy et al. 2004; Visser and Both 2005). This is also true for the interaction between plants and the decomposer community in the soil (Walther 2004; Cornelissen et al. 2007). The soil community, however, does not just consist of the decomposer community, but also contains organisms that directly interact with plants, such as mutualists and pathogens (Bever 1994; Klironomos 2002; Wardle et al. 2004). The sensitivity of the interaction between plants and these groups of soil organisms to temperature changes is currently unknown.

Feedback effects between plants, soil organisms and physical–chemical soil conditions can play a major role in structuring the composition and dynamics of natural plant communities (van der Putten et al. 1993; Bever 1994;

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Ehrenfeld et al. 2005). Plants change biotic and abiotic characteristics of the soil in which they grow. This, in turn, can affect the performance of the plants, and this interaction is known as plant–soil feedback (Bever et al. 1997). Plant–soil feedback can be positive, through enhanced nutrient availability or the accumulation of mutualists in the rhizosphere, or negative due to depletion or immobilization of nutrients, or the accumulation of root herbivores and soil pathogens (Wardle et al. 2004). Plant–soil feedback includes direct interactions between plant roots and mutualists, herbivores and pathogens, but also indirect interactions between plants and decomposer organisms that are responsible for nutrient turnover (Wardle et al. 2004). Although both types of interactions can be affected by global warming, effects of temperature on indirect interaction-related pathways have received most attention, especially litter decomposition (Cornelissen et al. 2007). Decomposition, soil respiration and mineralization tend to increase with increasing ambient temperature (Bardgett et al. 1999; Davidson and Janssens 2006; Bengtson and Bengtsson 2007). Although the effects of increased temperature on individual pathogen and mutualist species have been studied, the resulting effect of increased temperature on the interaction between plants and the whole community of pathogens or mutualists plants are typically exposed to, has remained largely unresolved. In the present study the effects of ambient temperature on interaction between plants and the soil community as a whole is tested.

The effect of an ambient temperature increase on plant–soil feedback is the sum of the effects on many components and their interactions. The impact of plant–soil feedback on plant performance can therefore be positive, negative or neutral (Klironomos 2002; Kardol et al. 2006). A temperature increase can change this outcome through changes in decomposition and mutualistic effects, but it can also affect pathogenic activity. Therefore, it is difficult to predict the net effect of atmospheric temperature on plant–soil feedback.

Apart from local effects of climate warming on community composition and dynamics, warming also causes poleward shifts of many plants and other species groups (Parmesan and Yohe 2003; Tamis et al. 2005; Hickling et al. 2006). As not all species shift their range at the same speed, local biotic interactions between plants and other organisms can become disrupted (van der Putten et al. 2004; Visser et al. 2006). Plants with well-dispersed seeds can expand their range quite fast (Higgins and Richardson 1999), whereas soil-borne pathogens lack targeted dispersal (van der Putten et al. 2001). This may result in a temporary release from soil-borne enemies of range-expanding plant species, so called thermophilic neophytes (Tamis et al. 2005; van Grunsven et al. 2007; van Grunsven et al. 2010). While release from soil-borne enemies has

been reported for non-native plant species that colonize new continents (Klironomos 2002; Reinhart et al. 2003), such effects of climate warming on local plant–soil interactions have received little attention. Two studies showed that plant species from warmer climate regions had a less negative soil feedback in their new range than plants which are native in that range (van Grunsven et al. 2007; Engelkes et al. 2008). However, it is not known whether these plant–soil feedback effects are sensitive to temperature and if plants from temperate regions differ from plants from warmer climate regions in their soil feedback response to temperature.

The main question addressed in the present study is how plant–soil feedback may be affected by an elevated ambient temperature and whether warming affects soil feedback of native plants and non-native plants differently. As a null hypothesis, we expected no differences of warming on plant–soil feedback. Alternatively, warming can result in a change in plant–soil feedback, either in a positive or negative direction. Additionally, we expected plant species from warm climate regions to benefit more from a high ambient temperature than the plants that were native to the temperate zone.

Materials and methods

General setup

The experiment consisted of two parts, a conditioning and a feedback phase (Fig. 1). In the conditioning phase, plants were grown in soil inoculated with field soil in order to create specific soil communities for each plant species. A sterilized control was added in order to be able to assess the effect of the non-specific soil community on biomass production. The sterilized control soil was discarded after harvest but the conditioned soil was retained to be used in the feedback phase of the experiment.

In the feedback phase the conditioned soils were split, half were used as a conspecific conditioned soil, the other half mixed with soils conditioned by the other species in this experiment in order to create a non-specific control. The difference in biomass production between plants growing in these two soils is a measure of plant–soil feedback. Simultaneously with these two treatments, the treatments from the conditioning phase were repeated using the same soil and inocula as used in the conditioning phase which had been stored at low temperature (4°C) during the conditioning phase. This allowed us to assess the effect of inoculation with non-conditioned soil. In order to test the effect of temperature on plant–soil feedback we performed this whole experiment in four greenhouses; two greenhouses for each temperature (see below).

Fig. 1 A graphic representation of the experimental setup consisting of a conditioning and a feedback phase. The feedback phase consists of two comparisons, one of biomass produced in conspecific conditioned soil versus a mixed, heterospecific soil and one of biomass produced in an inoculated versus sterilized soil, a repetition of the conditioning phase. This is done for 12 plant species (six pairs of a native and non-native plant species) and at two temperatures (within four greenhouses)
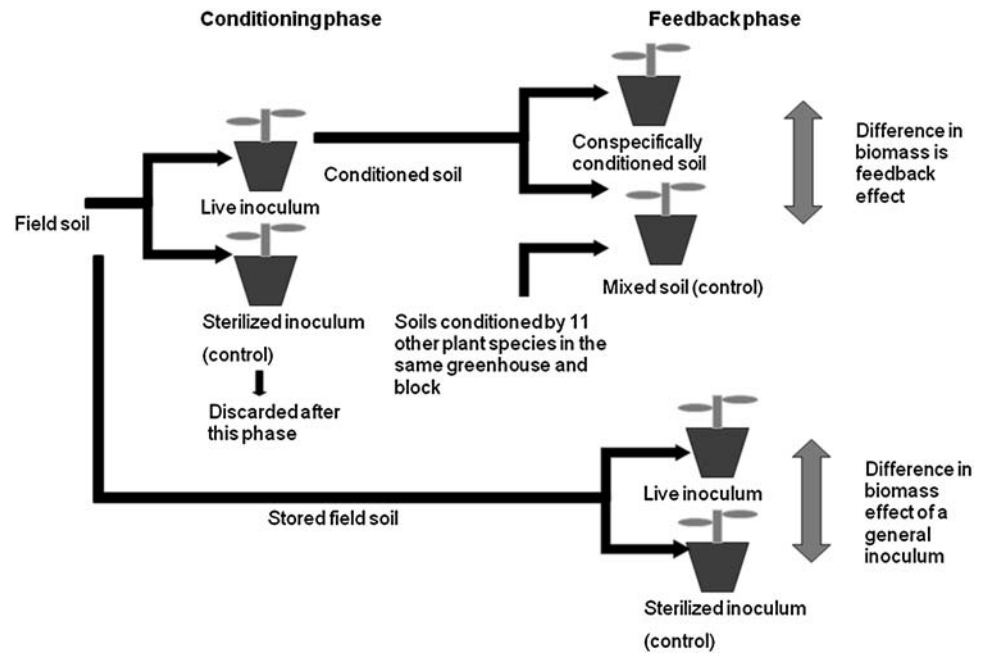

Table 1 Origin and seed source of the plant species used

Species	Pair	Invasive in other continents	Seed origin	First record	Native range
Poa annua	1	Yes	Collected in NL[a]	Indigenous	Europe
Eragrostis pilosa	1	Yes	Collected in NL[a]	1958	Southern Europe
Senecio vulgaris	2	Yes	B&T Worldseeds[b]	Indigenous	Eastern Europe
Senecio vernalis	2	Unknown	Cruydt-hoeck[c]	1915	Eastern Europe
Tragopogon pratensis	3	Yes	Cruydt-hoeck	Indigenous	Europe and Western Asia
Tragopogon dubius	3	Yes	Collected in Austria	1950s	Central Europe
Chenopodium album	4	Yes	Cruydt-hoeck	Indigenous	Holarctic
Corispermum intermedium	4	Yes	Collected in NL[d]	1900	Central Europe
Chenopodium polyspermum	5	Yes	B&T worldseeds	Archeophyte (before 1500)	Europe
Chenopodium botrys	5	Yes	Collected in NL[d]	1900–1924	Mediterranean
Geranium molle	6	Yes	B&T worldseeds	Indigenous	Europe
Geranium lucidum	6	Yes	B&T worldseeds	1975–1999	Central and Southern Europe

[a] Seeds collected in the Netherlands by us at 51°59N, 4°39E

[b] B&T Worldseeds, Paguignan, 34210 Aigues-Vives, France. Seeds are collected in Southern France

[c] Cruydt-hoeck, P.O. Box 88, 9400 AB Assen, the Netherlands. Seeds are collected in the north of the Netherlands

[d] Seeds collected in the Netherlands by us at 51°53N, 5°39E

Non-native plant species with a first record in the Netherlands after 1900 and of European origin were selected from the standard list of the Dutch flora (Tamis et al. 2004). Each plant was paired with a native species (present before 1500 AD) that has a comparable ecology, life history, and morphology and is phylogenetically related (same genus or same family). Many selected species were rejected for practical reasons (seeds unavailable, parasitic or aquatic plants, poor germination, no similar native species available, etc.). We ended up with six plant pairs from

four different families. We selected two plant pairs from the families *Asteraceae* and *Chenopodiaceae*. These two families contain many neophytes in the Dutch flora (Tamis et al. 2004). The 12 selected species are (non-native/native): *Chenopodium botrys* L./*Chenopodium polyspermum* L.; *Corispermum intermedium* Schweigg./*Chenopodium album* L.; *Eragrostis pilosa* (L.) P. Beauv./*Poa annua* L.; *Geranium lucidum* L./*G. molle* L.; *Senecio vernalis* Waldst. & Kit./ *Senecio vulgaris* L. and *Tragopogon dubius* Scop./*T. pratensis* L. (Table 1).

Conditioning phase

Soils were conditioned by growing plants for 12 weeks in sterilized soil inoculated with a non-sterile or sterilized general soil inoculum. This period of 12 weeks is usually sufficient for the development of plant species-specific soil microbial communities (Bever et al. 1997; Klironomos and Hart 2002; Kardol et al. 2007). Seeds were collected or purchased from commercial suppliers that collect seeds from wild plant populations (Table 1). Soil (top layer, 25 cm deep) was collected from an ex-agricultural grassland in Wageningen, The Netherlands, where none of the species that were used in the experiment occurred. This grassland is relatively rich in plant species, so that it is expected to contain a large collection of soil biota. This soil is sandy with a clay fraction and relatively little organic matter and a neutral pH. The soil was homogenized and split in two, one half was sterilized by autoclaving at 121.5°C for 3 h to serve as a sterilized control, the other half was used as a non-sterile inoculum source. The mineral sub-soil from the same grassland was collected and autoclaved (121.5°C for 3 h) to form the bulk soil to which inocula were added before introducing the plants. This mineral soil was used to avoid artefacts of autoclaving of soil that is rich in organic matter. Half of the inocula and substrate was stored at 4°C for later use.

The sterilized bulk soil was inoculated with the non-sterilized or sterilized topsoil at a 5:1 (w/w) ratio. Pots of 19 cm diameter and 15 cm height were filled with 2,200 g of the resulting soil mixture (15% moisture w/w). These pots were planted with seedlings that were germinated in trays with autoclaved river sand. Each pot was planted with three similar-sized seedlings of the same species. The pots were equally distributed over four greenhouses, two with a 20/15°C (day–night) temperature regime and two with 25/20°C. The greenhouses had a day/night vapour pressure deficit of 0.70/0.51 kPa for both temperatures, resulting in similar evapotranspiration. Philips SOL-T armatures were used for additional light when natural light was lower than 800 µmol m^{-2} s^{-1} between 0600 and 2200 h. We used three randomized complete replicate blocks per greenhouse, so that the experimental design consisted of 12 species (six pairs), grown in two soil treatments in four greenhouses (two at low and two at high temperature) with three replicates per greenhouse and three plants per pot. This experimental design resulted in 288 pots.

Plants were watered every other day and harvested after 12 weeks of growth. Shoots were dried for 48 h at 70°C and weighed. In order to prepare the soil for the feedback phase, coarse roots were removed to prevent re-sprouting, but fine roots were left in the soil to serve as inoculum, as most microbial activity is situated in the rhizosphere. This proce-

dure, therefore, prohibited determination of root biomass. Soil that had been inoculated with sterilized inoculum was not used for the feedback phase, because of likely colonization by air-borne microorganisms during this growth period.

Feedback phase

Plant–soil feedback was examined by comparing biomass production of plants grown in conspecific conditioned soil with plants grown in a mixture of soils conditioned by all the different species, the latter forming a heterospecific control. The conspecific and heterospecific soils were prepared as follows: conditioned soil that originated from non-sterilized inocula was collected from each individual pot, homogenized and split into two parts of 1,000 g. One part was placed in a new pot serving as conditioned conspecific soil. The other part was mixed with all other conditioned soils from the same block and then subdivided over individual pots, serving as heterospecific soil. Since there were 12 plant species the specific soil community was diluted 12-fold. Effects of the specific soil community on plant performance are not detectable if the soil community is diluted to this degree (van der Putten et al. 1988). Factors such as decomposition, nutrient uptake and mineralization are averaged by mixing.

Both the conspecific and heterospecific soils have been used in the previous growth phase and nutrients have been taken up by the plants growing in these soils. To correct for this, nutrients were added to both soils during this growth phase. From the fourth week until harvest, 25 ml of a nutrient solution (12.5 mmol KNO$_3$ l^{-1}, 6.50 mmol Ca(NO$_3$)$_2$ l^{-1}, 3.75 mmol MgSO$_4$ l^{-1}, 7.50 mmol NH$_4$H$_2$PO$_4$ l^{-1}, 0.21 mmol FeEDTA l^{-1}) was added weekly; this is the amount expected to be taken up by the plants in the conditioning phase.

Additionally, the soil that had been stored in cold storage during the conditioning phase was used to create inoculated and sterilized treatments in the same manner as in the conditioning experiment. This allows us to assess the effect of inoculation with unconditioned soil simultaneously.

Pots with a diameter of 14 and 13 cm height were filled with 1,000 g of soil. The seeds were treated in the same manner as in the conditioning phase, with the distinction that one seedling was planted per pot instead of three. Pots were placed in randomized complete blocks in the same greenhouses. As there are 12 plant species, four soil treatments (conspecific, heterospecific, unconditioned and sterilized), four greenhouses over two temperatures, and three replicates per greenhouse this resulted in 576 plants. After 12 weeks all plants were harvested, roots were washed to remove the soil and both root and shoot biomass was dried at 70°C for 48 h and weighed.

Data analyses

The conditioning and feedback phases of the experiment were analysed separately as they were not performed simultaneously. For the feedback phase the non-conditioned and sterilized soils were analysed separately from the conspecific and heterospecific soil treatment; these treatments test different hypotheses (effect of inoculation and plant–soil feedback, respectively) and both have their own control. For all three analyses a mixed model was used with biomass as dependent factor (only aboveground for the conditioning phase as roots were not harvested). The effect of temperature was tested with greenhouse as a random factor. In this way the effect of temperature is tested with greenhouses and not pots as replicates (resulting in two replicates per temperature). The effect of plant origin (native or non-native) was tested with species as error term; species was entered as a random factor nested within origin. Normality and homogeneity of variance were assessed by visual inspection of the residuals, and assumptions for ANOVA analyses were met. For the interaction between soil inoculation and temperature and the interaction between soil conditioning and temperature, the effect size (η^2) is calculated as the factor SS/error SS. Root/shoot ratio was calculated and analysed using the same model as mentioned above.

Additionally, soil feedback was analysed based on total biomass by calculating the ratio (conspecific soil − heterospecific soil)/heterospecific soil. This resulted in a proportional reduction (indicating negative feedback) or increase (indicating positive feedback) in biomass in conspecific soil compared to the heterospecific control. Replicates were obtained by pairing plant biomass originating from the conspecific and heterospecific soil from the same block. As the residuals were not normally distributed in this analysis, Mann–Whitney U tests were used to test if the effect of feedback was affected by temperature and/or nativeness.

Pearson correlation coefficients were used to test for a relation between biomass production in a pot in the conditioning phase and in the same soil in the feedback phase.

Because this experiment was not designed to test for effects within species, we chose to use more species pairs and less replicates per species. However, we present the results within species as this allows us to assess which species are in line with the general pattern.

Data was analysed using Statistica 7.0 (Statsoft Inc.) and SPSS 12.03 (SPSS Inc.).

Results

Comparing sterilized soil and non-conditioned inoculum

As the comparison between unconditioned soil and the sterilized control has been performed in the conditioning phase as well as in the feedback phase, we present the statistics of both results. There was a significant effect of inoculation in the conditioning phase and a similar trend was observed in the feedback phase (Table 2) However, there was no interaction between the effect of inoculation on biomass production and origin or temperature ($\eta^2 = 0.002$, $\eta^2 = 0.004$ in the conditioning and feedback phase, respectively). Despite differences in setup (e.g. pot size), as described in "Materials and methods", the results of both conditioning experiments were remarkably similar (Table 2). Individual species

Table 2 Nested mixed model ANOVA results for the effect of soil inoculation (*inoc.*) with an unconditioned inoculum on aboveground (*Conditioning phase*) or total biomass (*Feedback phase*) and the effect of conspecific conditioned soil and a heterospecific control (a mix of 12 conditioned soils) on total biomass

Factor	Type	df	Conditioning phase			Feedback phase			df	Conditioned versus mixed		
			Error df	F	Sign	Error df	F	Sign		Error df	F	Sign
Temperature	Fixed	1	3.8	6.1	†	2.8	1.4	n.s.	1	3.1	7.872	†
Greenhouse (temp.)	Random	2	242	1.1	n.s.	240	4.1	*	2	238	3.376	*
Origin	Fixed	1	10	0.1	n.s.	10	0	n.s.	1	10	0.017	n.s.
Spec. (orig.)	Random	10	11.7	12.1	***	12	9.3	***	10	7.1	29.563	***
Inoculation	Fixed	1	10	7.9	*	10.1	3.5	†	1	10.3	1.499	n.s.
Temp. × spec. (orig.)	Random	10	242	1.8	†	240	1.8	†	10	238	1.975	*
Temp. × inoc.	Fixed	1	242	0.6	n.s.	240	0.9	n.s.	1	238	0.001	n.s.
Temp. × orig.	Fixed	1	10.1	0.2	n.s.	10.2	0.2	n.s.	1	10.1	0.026	n.s.
Orig. × inoc.	Fixed	1	10	1.5	n.s.	10.1	0.6	n.s.	1	10.3	14.157	***
Spec. (orig.) × inoc.	Random	10	242	5	***	240	3.5	***	10	238	0.852	n.s.
Temp. × orig. × inoc.	Fixed	1	242	0.009	n.s.	240	0.04	n.s.	1	238	0.084	n.s.

Temperature (*temp.*) is tested over greenhouses, and origin (*orig.*; native or non-native) is tested over species (*spec.*)

† $0.1 > P > 0.05$, * $P < 0.05$, *** $P < 0.001$; not significant (*n.s.*) $P > 0.05$
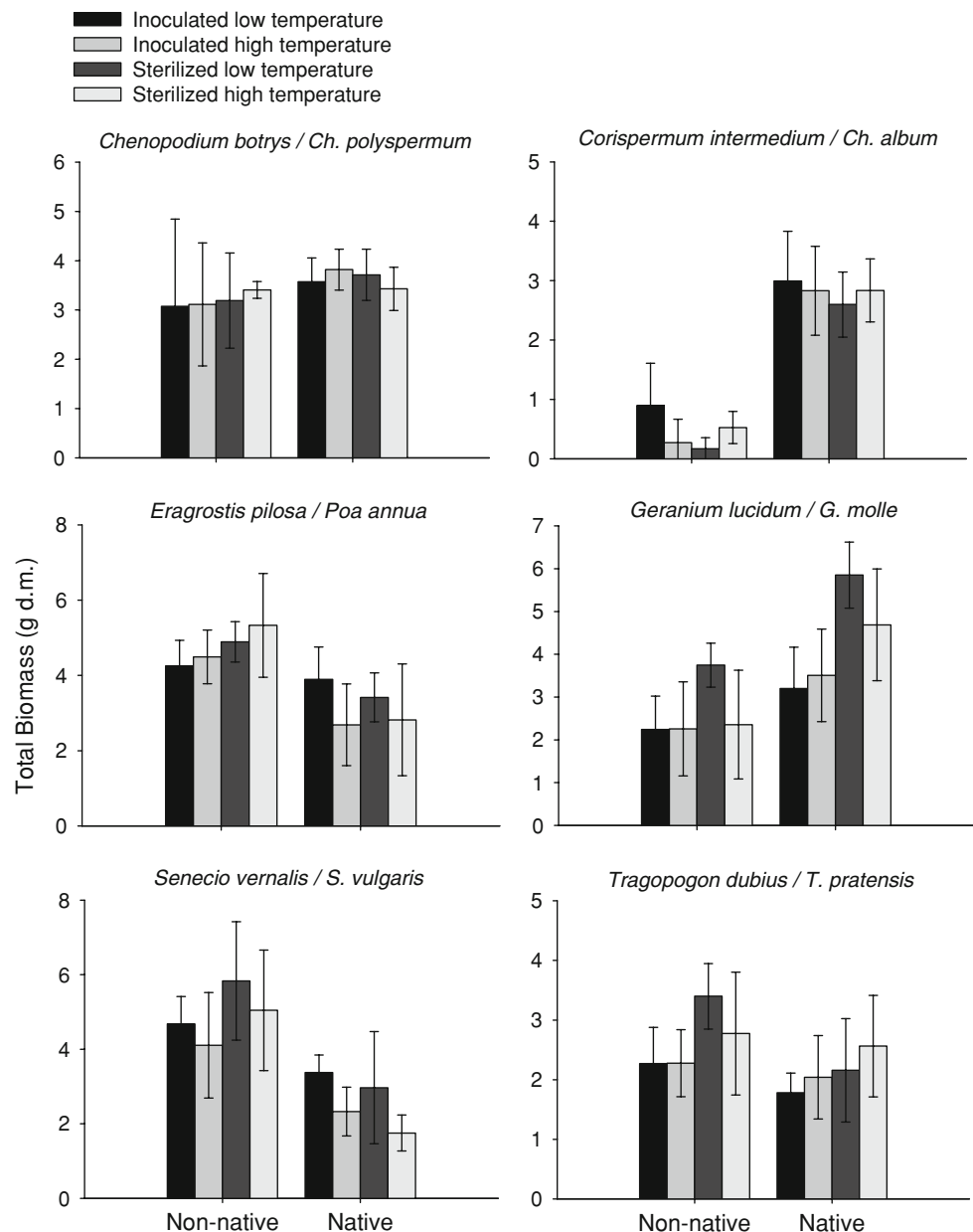
responded differently to soil inoculation resulting in a highly significant interaction between species (origin) and inoculation in both runs (Fig. 2; Table 2). Some plant species produced more biomass in inoculated soils (e.g. *Poa annua* in run 1: $F_{1,20} = 11.6$, $P < 0.001$) while other species produced less biomass in inoculated soil (e.g. *Tragopogon dubius* in run 1: $F_{1,20} = 16.4$, $P = 0.001$). Root/shoot ratio only depended on plant species and was neither affected by temperature nor by inoculation (Table 3).

Comparing conspecific and heterospecific conditioned soil

Temperature had a nearly significant effect on biomass production in the feedback experiment with conspecific and

heterospecific soil. The effect of temperature depended on plant species resulting in a significant temperature × species(origin) interaction (Table 2; Fig. 3). However, the effect of temperature did not differ significantly between native and non-native plant species (Table 2). The effect of soil conditioning on plant biomass depended on the origin of the plant species (origin × inoculation effect), but the effect of soil conditioning did not depend on temperature ($\eta^2 < 0.0001$). The native species produced, on average, 10% less biomass in conspecific than in heterospecific soil ($F_{1,3.01} = 51.8$, $P = 0.005$). The non-native species, on the other hand, produced on average 10% more biomass in conspecific than in heterospecific conditioned soil ($F_{1,3.00} = 9.6$, $P = 0.05$). Therefore, native plants experienced growth

Table 3 Root/shoot ratio

Factor	Type	df	Error df	F	Sign
Unconditioned soil					
Temperature	Fixed	1	3.3	0.1	n.s.
Greenhouse (temp.)	Random	2	233	2.1	n.s.
Origin	Fixed	1	15.9	0.06	n.s.
Spec. (orig.)	Random	10	13.1	31.4	***
Inoculation	Fixed	1	10.1	0.5	n.s.
Temp. × spec. (orig.)	Random	10	233	1.8	†
Temp. × inoc.	Fixed	1	233	0.1	n.s.
Temp. × orig.	Fixed	1	10.0	2.1	n.s.
Orig. × inoc.	Fixed	1	10.1	2.1	n.s.
Spec. (orig.) × inoc.	Random	10	233	1.4	n.s.
Temp. × orig. × inoc.	Fixed	1	233	1.174	n.s.
Conditioned soil					
Temperature	Fixed	1	2.6	0.8	n.s.
Greenhouse (temp.)	Random	2	235	1.4	n.s.
Origin	Fixed	1	10.0	0.3	n.s.
Spec. (orig.)	Random	10	3.5	71.0	**
Conditioning	Fixed	1	10.3	0.3	n.s.
Temp. × spec. (orig.)	Random	10	235	1.3	n.s.
Temp. × cond.	Fixed	1	235	0.0	n.s.
Temp. × orig.	Fixed	1	10.1	0.0	n.s.
Orig. × cond.	Fixed	1	10.2	2.0	n.s.
Spec. (orig.) × cond.	Random	10	235	0.6	n.s.
Temp. × orig. × cond.	Fixed	1	235	0.8	n.s.

Nested mixed model ANOVA results for unconditioned soil (sterilized orinoculated) and conditioned soil (con- or heterospecific)

Dependent variable is root/shoot ratio (ln transformed). For abbreviations, see Table 2

Temperature is analysed over greenhouses, and origin (native or non-native) over species to prevent pseudoreplication

† $0.1 > P > 0.05$, ** $P < 0.01$, *** $P < 0.001$; n.s. $P > 0.05$

reduction and non-native plants growth enhancement in their own soil, independent of the ambient temperature. The soil feedback effect, analysed as the relative difference between biomass produced in conspecific and heterospecific soil, showed similar results. Soil feedback depended on species origin (Mann–Whitney $U = 1731$, $P = 0.003$), with a more positive effect for non-native than for native species. This was not influenced by ambient temperature [Mann–Whitney $U = 2091$, not significant (n.s.)]. Root/shoot ratio was again only dependent upon plant-species and did not depend on temperature or conditioning (Table 3). In order to check if the effect of conditioning may have been due to nutrient depletion, we correlated biomass production in the conditioning phase with biomass production in the feedback phase in the same soil. There was no correlation (Pearson $R = -0.03$, n.s.).

The effects of temperature and soil inoculation per species are represented in Table 4. There were few significant effects as a result of low power. However, the direction of the response was similar across species. Increased temperature had a negative effect on all species except *C. intermedium*, although this effect was only significant for *T. dubius*. The effect of the soil inoculation was more variable, positive in some (higher production in conspecific than in heterospecific soil) and negative in other species. All native species showed negative plant soil feedback effects while all but one non-native species (*E. pilosa*) showed positive effects.

Discussion

Temperature influences virtually all ecosystem processes (e.g. Bakkenes et al. 2002; Hickling et al. 2006; Brooker et al. 2007); however, in our study a temperature difference of 5°C did not influence net plant–soil feedback. Temperature did not influence plants native to the Netherlands differently from plants originating from a warmer climate region. Temperature also did not change the effect of inoculation or conditioning on plant growth. Therefore, we conclude that enhancement of atmospheric temperature does not have a direct effect on plant–soil feedback patterns. We are confident that this is not a result of lack of power, as the effect sizes (as represented by η^2) are very small. Growth of native and non-native species did not differ during the soil conditioning phase; only in the feedback phase of the experiment differences in plant biomass were observed. These results suggest that these two groups of species have different effects on the soil community in the conditioning phase.

In the present study we focused on the temperature as one aspect of climate change. We did not include changes in water availability, length of growing season, frequency of extreme events and direct effects of increased CO_2. These can all affect plant–soil interaction (van der Putten and Peters 1997; Chakraborty and Datta 2003; Ainsworth and Long 2005; Suttle et al. 2007; Kreyling et al. 2008) and these effects may co-vary with increased temperatures. Therefore, these factors need to be investigated in future studies for a more complete understanding of the effects of climate change.

As micro-organisms tend to be more active at higher temperatures, their impact on plant performance could increase with temperature (e.g. Bekal and Becker 2000; Allen et al. 2005) as has been found for aboveground pathogens and herbivores (Roy et al. 2004). Opposite results, i.e. a decreased pathogenic effect with increased temperature, have also been reported (Smiley and Uddin 1993; Allen et al. 2005; Matheron and Porchas 2005). It is important to re-emphasize that plant–soil feedback effects are net effects of many different plant–soil interactions.

Fig. 3 Mean (±SD) biomass of plants grown in conditioned conspecific soil or a heterospecific control at low (20/15°C) or high (25/20°C) temperatures. Each *panel* represents a pair consisting of a non-native and a native plant species
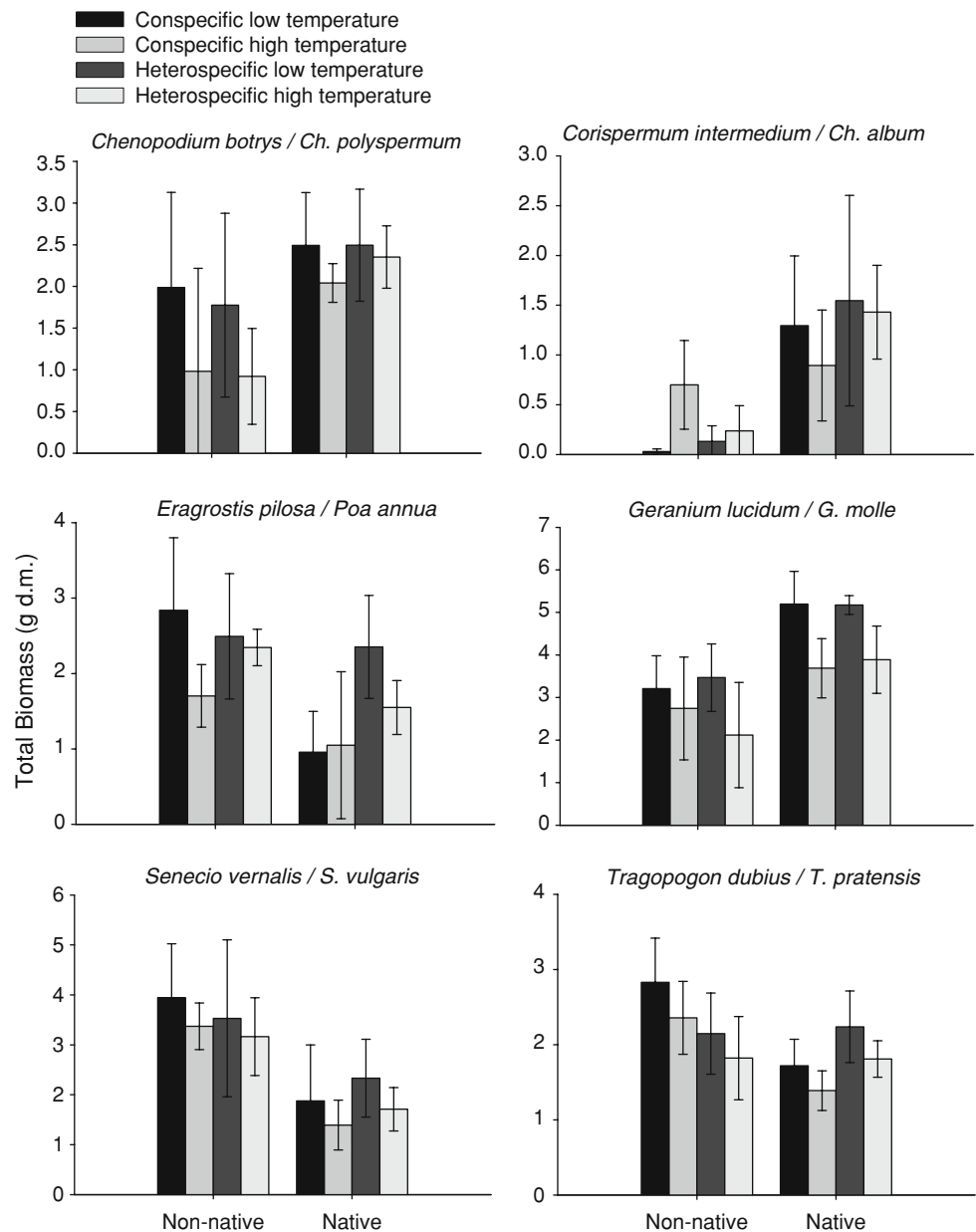
Interactions between different components in the rhizosphere community might compensate for the direct effect of temperature (e.g. Gavito et al. 2003; Piśkiewicz et al. 2007). We did not measure soil temperature during this experiment but soil temperatures in greenhouses tend to follow those of the air, with some time delay, depending on pot size (S. R. Troelstra and R. Wagenaar, unpublished results). Considering the volume of the pots used in our experiment, the air-moisture deficit and the evaporation, we expect the difference between the two treatments to have been close to 5°C.

Plants introduced into foreign areas, for instance on other continents, are known to experience less negative plant–soil feedback than native species (Klironomos 2002;

Knevel et al. 2004; Reinhart et al. 2005; Reinhart and Callaway 2006; van Grunsven et al. 2009). The fact that the same effect can also occur in plant species that expanded their range within a continent, e.g. as a result of climate change, has been acknowledged only recently (van Grunsven et al. 2007; Engelkes et al. 2008; van Grunsven et al. 2010). Both inter- and intracontinental range expanders showed less negative plant–soil feedback than native plant species in these studies.

The results in our study are in concordance with this; the native plant species experienced a net negative effect of conditioning on biomass production while the non-native species experienced a (marginally significant) positive effect. The non-native plant species have colonized the

Table 4 Effect of temperature and soil conditioning on total biomass of all species separate

	Chenopodium botrys	Chenopodium polyspermum	Corispermum intermedium	Chenopodium album	E. pilosa	P. annua	G. lucidum	G. molle	S. vernalis	S. vulgaris	T. dubius	T. pratensis
Temperature												
Fixed	−0.49	−0.12	4.9	−0.18	−0.24	−0.21	−0.27	−0.27	−0.13	−0.27	−0.16	−0.18
	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	***	n.s.
Greenhouse (temp.)												
Random	n.s.	n.s.	n.s.	**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Soil conditioning												
Fixed	0.1	−0.06	0.52	−0.26	−0.06	−0.49	0.07	−0.02	0.09	−0.20	0.31	−0.22
	n.s.	n.s.	n.s.	n.s.	n.s.	***	n.s.	n.s.	n.s.	n.s.	***	***
Soil × temp.												
Fixed	n.s.	n.s.	*	n.s.	*	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

Temperature is analysed over greenhouses. Effects of temperature and conditioning are fraction changes

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, n.s. $P > 0.05$

Netherlands relatively recently (Table 1). A release from their specific pathogens during the range expansion can explain the difference between native and non-native species. Local soil communities have not yet developed pathogenicity to these exotic plants. The plant–soil feedback pattern observed in our general analysis (including all plant species) is reflected by almost all plant species, when tested separately (Tables 3, 4). Although the trends within the separate species are rarely significant as a result of low power and high intraspecific variation, the observed trends are in agreement with the general pattern.

In theory, effects such as those found in this study could have been due to changes in abiotic conditions, such as nutrient depletion in the conditioning phase or increased nutrient availability in the sterilized control as a result of autoclaving (Troelstra et al. 2001). Because we used relatively small amounts of sterilized inocula it is unlikely that this effect has played a role in the present experiment. Nutrients were added in order to compensate for possible species-specific differences in nutrient uptake during the conditioning part of the experiment. Biomass production in the conditioning part, which is strongly correlated with nutrient uptake, was compared between native and exotic plant species and did not differ. A lack of correlation between the biomass in the first and second phase (e.g. Kardol et al. 2006), ruled out the possibility that the differences in feedback effects were due to nutrient depletion. Moreover, adding soil fauna (De Deyn et al. 2003) or microbial components (Kardol et al. 2007; van der Putten et al. 2007) as an inoculum to sterilized soil has confirmed the biotic origin of these soil conditioning effects in comparable experiments.

In the feedback phase of our experiment we did not use inoculation but whole conditioned soils. This is in contrast to a number of other feedback studies (e.g. Bever 1994; Reinhart et al. 2003). As a control, we used a mixture of soils conditioned by all plant species in the experiment. The main advantage of this method is that the disturbance of the conditioned soil is minimized and it prevents differences in average nutrient content between the two treatments while creating a non-species-specific plant community. We used soil from a single site, instead of a range of sites, to produce the soil inocula for the conditioning experiment. Thereby, we excluded site differences in soil community composition. It is unknown to what extent the selection of this site has affected the outcome.

We conclude that the net effect of plant–soil interactions appears to be insensitive to increases in ambient temperature. Reduced negative soil feedbacks of the non-native species affect plant performance more than different temperature effects on the outcome of plant–soil feedback between native and non-native plant species. As a result of climate change many plant species will expand their range into new, previously colder areas (Bakkenes et al. 2002). This can result in a large number of non-native plant species that have a reduced plant–soil feedback compared to native plants. Future studies should consider how these predicted changes in plant species composition will influence the functioning of invaded ecosystems. Furthermore, both the role of specific soil organisms in plant–soil interactions and aspects of global climate change, besides temperature, should be explored.

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