Testing the plant growth-defense hypothesis belowground: Do faster-growing herbaceous plant species suffer more negative effects from soil biota than slower-growing ones?

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Table A1, Appendix B, Appendix C, Table D1, Table E1, Table F1, Table G1.

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Abstract

According to the growth-defense hypothesis in ecology, faster-growing plant species should suffer more from herbivores and pathogens than slower-growing species. Tests of this hypothesis have focused on aboveground plant tissues, herbivores and pathogens; however, it should also apply to root defense. To test whether faster-growing species suffer more negatively from soil biota than slower-growing species, we estimated first-season growth rates of 34 herbaceous plant species, and used weighted linear regressions to assess the relation between growth rates and responses to being grown in sterilized versus unsterilized soil (biotic soil effects), and to growing in soil previously occupied by conspecifics versus a mixture of species (conspecific soil effects). We found a negative relation between relative growth rate and biotic soil effects, with slower-growing species tending to suffer less or even benefit from the presence of soil biota, while faster-growing species were more negatively affected. Biotic soil effects were also negatively related to size-corrected growth rates. These relations remained negative after accounting for influential species, but a large amount of variation remained unexplained. Moreover, there was no clear relation between growth rates and conspecific soil effects. A simple relation between growth and defense aboveground may not be so clearly reflected belowground, due to the many interacting antagonistic and mutualistic organisms likely involved.

Introduction

The hypothesized relation between the ability of plants to grow fast and the ability to defend themselves against natural enemies is a fundamental concept in ecology (Coley 1988; Coley et al. 1985; Herms and Mattson 1992; Kempel et al. 2011; Van Zandt 2007). Recent global-scale (Lind et al. 2013) and meta-analytical studies (Endara and Coley 2011) suggest that a relation between the ability of plants to grow fast and the ability to defend themselves against natural enemies is the norm among multiple species in different communities. Faster-growing species occupy resource-rich environments, and invest resources into plant growth rather than defense against enemies. In contrast, slower-growing species, often from resource-poor environments, invest more in defenses, preventing losses of plant tissue at a cost to plant growth.

Although a growth-defense relation appears to be the norm, most work to date has been focused aboveground (Coley 1988; Coley et al. 1985; Herms and Mattson 1992; Kempel et al. 2011; Van Zandt 2007). The role of belowground natural enemies has received less attention (Rasmann et al. 2011), despite evidence that soil pathogens, particularly fungi, can cause high rates of root (Eissenstat & Yanai 1997) and seedling mortality (Jarosz and Davelos 1995; Packer and Clay 2000). There is growing interest in potential regulation of individual- and population-level plant performance by density-dependent effects of soil biota (Mangan et al. 2010; van der Putten et al. 2013). The concept of plant-soil feedback suggests that over time, species-specific pathogens accumulate in the soil occupied by individual plants, such that subsequent generations of individuals of the same species experience reduced growth and fitness (Bever 1994). The net soil biota effects are often negative, suggesting that species-specific fungal and bacterial pathogens outweigh more generalist mutualists (e.g. mycorrhizal fungi) in their effects on plant growth (Kulmatiski et al. 2008). Thus, plants should perform less well on soils previously occupied by conspecifics, compared to those previously occupied

by other species. However the strength and direction of net soil biota effects vary extensively among species and studies (Kulmatiski et al. 2008).

Susceptibility to belowground natural enemies could depend on successional stage and growth rates (Rasmann et al. 2011). If a relation between plant growth and defense occurs belowground, early successional and faster-growing plant species should be more susceptible to root herbivores and pathogens than slower-growing species. Faster-growing species are thought to produce thinner roots that are less well-defended physically or chemically than slower-growing species (Rasmann et al. 2011). However, a direct test of the association between growth rates or root traits and effects of soil microbial communities on plant growth is currently lacking. Specific root length (SRL) represents the length of root deployed for water and nutrient uptake per unit mass invested. High SRL has been linked to high rates of root proliferation (Eissenstat 1991), greater branching intensity and thinner roots (Comas and Eissenstat 2009). High root N-content of plant tissue correlates with less dense roots and shorter root lifespan, and these traits should characterise faster-growing but less well-defended species (Eissenstat and Yanai 1997; Tjoelker et al. 2005; Reich 2014). Slower-growing plant species are thought to better defend their roots with carbon-based lignins and phenolic compounds than faster-growing species (Eissenstat and Yanai 1997). We therefore expect SRL and C:N ratio to be correlated with species growth rates.

In this study, we assessed the relation between growth rates, and the net effects of soil biota (microbial fungi and bacteria) on plant growth. We estimated first-season growth rates for 34 herbaceous plant species in central Europe using non-linear growth curve models (Paine et al. 2012). We then measured the magnitude and direction of the effect of soil biota on these same species in a second experiment, by growing the plants on soil previously conditioned by the same species (conspecific, which was either sterilized or unsterilized to measure biotic soil effects) or a mixture of species (heterospecific). We also independently

measured SRL and root C:N ratio as root traits that could influence the vulnerability of plant roots to pathogens. We predicted that-

1) Plant species with faster growth experience more negative biotic soil effects; faster-growing species grow less well on conspecific unsterilized soil than sterilized soil. Slower-growing species, in contrast, are less negatively affected by unsterilized compared to sterilized soil.

2) Faster-growing species also suffer more negatively than slower-growing species when growing in conspecific soils compared to soils from a mixture of species if species-specific soil pathogens accumulate in conspecific soils.

3) Root traits are correlated with growth rates; specifically, faster-growing species have lower C:N ratios and higher SRL than slower-growing species.

4) Plants with a high SRL and a low C:N ratio suffer more negatively from soil biota than species with a lower SRL and a higher C:N ratio.

Materials and Methods

Study species

We collected seeds from wild populations of 34 herbaceous, mostly perennial plant species in southern Germany and Switzerland during 2012 (see Table A1). Species were selected to represent a broad range of growth rates based on Grime and Hunt (1975). If possible, we collected seeds from 10 parent plants per population; for two species we had six parent plants, and for one species three parent plants. The seeds were stored under cool, dry conditions until April 2013.

Growth-rate estimation

For full details of growth-rate estimation methods, see Appendix B. Briefly, we counted out 36 batches of 10 seeds per species, from a mixture of 1000 seeds with equal contributions

109 from each parent plant. We sowed each batch of ten seeds into 1.12-L pots, filled with a
110 mixture of topsoil, vermiculite and washed sand (ratio of 1:1:1 by volume), on 22 and 23
111 April 2013. The pots were checked every two days after sowing for germinated seeds until all
112 or most pots per species had emergent seedlings, and this date per species was designated
113 'week zero'. After removing all but one of the germinated seedlings per pot, up to three plants
114 (i.e. pots) were harvested weekly per species, from week one to week 12 (see Appendix B for
115 calculation of 'week zero' seedling biomass). This gave a total of 36 plants for most species
116 (See Appendix B for information on species with fewer plants harvested).

117 We estimated species growth rates in two ways. First, we calculated classical relative
118 growth rate (RGR) as the difference in ln(mean biomass) between week 10 and week zero,
119 divided by time (=70 days), giving an estimate of RGR in g g^{-1} day^{-1}. We chose 10 weeks
120 instead of 12, as plants were harvested only until week 10 for one of the species, *Lotus*
121 *corniculatus*. Because classical RGR inherently decreases with increasing plant size (Turnbull
122 et al. 2008), we also estimated size-corrected growth rate (SGR) at a common plant size for
123 all species, by fitting non-linear growth curve models for each species' biomass, over all
124 weeks with data available. We largely followed the protocol and used the R program scripts
125 provided by Paine et al. (2012). Four types of growth function were fitted: monomolecular,
126 three-parameter logistic, four-parameter logistic and Gompertz. SGR was then estimated
127 using the best-fitting model (identified as the model with the lowest Akaike's Information
128 Criterion, AIC), at the average biomass of plants (3.52 g) calculated across all species in week
129 6 (the midpoint of the total growth period for most species). When the lowest AIC model was
130 not distinguishable (i.e., within 2 AIC units' difference; Burnham and Anderson 2002) from
131 other models, an average SGR was calculated from the estimates of the models concerned
132 (Table A1). The SGR can be thought of as representing an average SGR equivalent to
133 conventional RGR, which is also an average (Turnbull et al. 2012). The estimated RGR and

SGR are shown in Table A1. Our growth rate estimates reflect first-season growth from seed of the species. This life stage is relevant to consider in our study, because seedlings and younger plants are likely to be susceptible to pathogen attack, while seedling growth and survival of mycorrhizal-dependent species would depend on successful mycorrhization of their roots (Kardol et al. 2013).

Effects of soil biota

For full details on how effects of soil biota were measured, see Appendix C. During May 2013, we filled 170 4.5-L pots with a substrate consisting of a mixture of sand, vermiculite and topsoil (as used previously, with a ratio of 1:1:1) to 4 L, and then added an extra 200 ml of sieved, homogenized soil collected from the field to each pot, which was thoroughly mixed with the other substrate. The field-collected soil was obtained from seven meadow/grassland areas in the vicinity of the University of Konstanz. (See Appendix C and Table D1 for collection details). Field-collected soil was used to inoculate the substrate with a larger range of soil biota for the conditioning phase. For each species, we then sowed 100 seeds (from the same source as the seeds used in growth rate estimation) into each of five replicate pots on 22 and 23 May 2013 (the pots were placed outside). Once the seeds had germinated, we removed excess seedlings until five remained (evenly spaced) in each pot. These plants were then grown for 14 weeks until 17 - 18 September 2013. After this soil-conditioning phase, the aboveground biomass per pot was removed, and the soil per individual pot was sieved to remove the majority of roots.

We then filled 510 1.2-L pots with 1 L of 1:1 washed sand and vermiculite, and 100 ml of soil from the conditioning phase that represented one of the following three treatments:
1) Unsterilized soil from a replicate conditioning pot of one species (conspecific soil)
2) Sterilized soil from a replicate conditioning pot of one species (conspecific, sterilized). Soil was sterilized at 121°C for 40 minutes in an autoclave

160 3) Unsterilized soil from a mixture of soils made from one replicate conditioning pot of every
161 species (heterospecific soil). This mixture included soil occupied by every species in equal
162 measure, including the planted target, and so represents a dilution of accumulated conspecific
163 soil biota. This treatment is realistic, as microbes that affect plants and accumulate in their
164 soils in a plant species-specific manner may not be completely absent from soil unoccupied
165 by the host species (Maron et al. 2014).

166 Conspecific and heterospecific soil treatments were always paired according to the
167 replicate conditioning pot used for the soil inocula. Because we had five replicate
168 conditioning pots for each of the 34 species, we then had a maximum of five replicate 1.2-L
169 pots per species for each of the above soil inoculum treatments. This gave a total of 15 pots
170 per species. Into each pot per species, we planted a single seedling, grown from seeds
171 representing the same parent plants as those used during the conditioning phase and for
172 growth rate estimation. The plants were then grown in a greenhouse for 12 weeks, watered
173 weekly, and fertilized every two weeks with 100% Hoagland solution (see Appendix B for
174 details of growing conditions and Table E1 for the Hoagland solution recipe). After 12 weeks
175 of growth, the aboveground biomass was harvested, and dried at 70°C for 72 h. The
176 belowground biomass was washed carefully to remove the substrate before drying. Both
177 belowground and aboveground biomasses were then weighed, and total biomass was
178 calculated.

179

180 *Specific root length and root C:N ratio*

181 Five replicate plants of each species were grown simultaneously with the plants used to
182 measure soil biota effects for 10 weeks to estimate specific root length (SRL) and root C:N
183 ratio (see Appendix B for details). After 10 weeks, and immediately after washing, the plant
184 root systems were stored in water for a maximum of 24 h. Two subsamples were taken
185 (blindly) from each replicate root system and stained using Neutral Red root staining solution.

186 An 8-bit greyscale image of each subsample was taken at 600 dpi with a flatbed scanner
187 (Regent Instruments, Epson Expression 10000 XL). Total root length per subsample was then
188 measured using the WinRhizo program (WinRHIZO^{TM} 2012, © Regent Instruments Canada
189 Inc.). Specific root length (SRL) was then calculated per subsample by dividing root length
190 (cm) by root dry mass (after drying for 72 h at 70°C). An average SRL from the two
191 subsamples per plant was calculated, and average SRL for the species was calculated from the
192 replicate plants.
193 To estimate root C:N ratio, approximately 3 mg of dried (unstained) root biomass per
194 plant was ground into a powder using a milling machine (MM 300, Retsch GmbH, Haan
195 Germany). The C and N content of 0.3-0.9 mg of powdered root per plant was then measured
196 using a CHNSO combustion analyzer 'Euro EA' (HEKAtech GmbH, Wegberg Germany).
197 The mean root C:N ratio was then calculated per species. *Lathyrus pratensis* was excluded
198 from the SRL and C:N ratio analysis, and *Hypericum perforatum* and *Geum urbanum* from
199 the C:N analysis, due to measurement problems and limited root material.
200
201 *Analysis*
202 We calculated the biotic soil effect as the mean difference in biomass between plants growing
203 in unsterilized *versus* sterilized conspecific soil, from the replicate pairs of plants grown. We
204 also calculated the conspecific soil effect as the mean difference in biomass between plants
205 grown in conspecific and heterospecific soil. The sterilization approach has been advocated
206 for determining the strength and sign of general soil feedback effects, while the conspecific-
207 heterospecific approach has the advantage of avoiding unwanted effects of sterilization
208 procedures (Brinkman et al. 2010). Because some plants died, soil effects were occasionally
209 measured for fewer than five replicates per species (See Table A1). We also calculated the
210 variance of biotic soil effects and conspecific soil effects per species. *Origanum vulgare* was

excluded from analyses of conspecific soil effects, due to insufficient numbers of surviving plants.

In order to assess the relations between species mean growth rates (RGR or SGR) or root traits and biotic or conspecific soil effects, we fitted weighted linear regression models using the function lm() in the program R. Each species' mean biotic or conspecific soil effect was weighted in the model by the reciprocal of the species' variance of the effect (added to the model using 'weights='). To account for variation in plant size among species, the mean summed biomass of plants in the replicate pairs used to calculate soil effects was included as a covariate (centered on the overall mean and scaled by the standard deviation) in analyses with RGR and root traits. This covariate was excluded from models considering SGR because SGR is already size-corrected and there was co-linearity between the two variables (r=0.62). We then compared the fit of the models including RGR to models including only the biomass covariate, and the models including SGR to intercept models, using the Akaike Information Criterion (AIC). If AICs for models including growth rates were >2 units smaller than AICs for the simpler comparator models, then the growth rates model was considered a better fit. When a model including growth rates or root traits gave a better fit than the simpler model, we inspected the model estimates. A relation between SGR, RGR, SRL or root C:N and soil effects could be driven by influential species in the data set. To address this, we removed each species, one at a time, and inspected changes in the parameter estimates (plus their direction) as a measure of each species' influence.

Because plant species have varying degrees of phylogenetic relatedness among them (Felsenstein 1985), we reran the regressions described above incorporating phylogenetic information using phylogenetic generalized least squares models with the R package 'nlme' (Pinheiro et al. 2014). Trait-growth rate correlations were redone using phylogenetic independent contrasts (Felsenstein 1985). We used a phylogenetic tree of the 34 species constructed using the online program PHYLOMATIC version 3 (Webb and Donoghue 2005)

(http://phylodiversity.net/phylomatic/) and the Angiosperm Phylogeny Website (Chase and Reveal 2009) (http://www.mobot.org/mobot/research/apweb/). Approximate branch lengths were added to the tree using the *bladj* function of PHYLOCOM (Webb et al. 2008) and fixed node and tree root ages from Wikstrom et al. (2001). Analyses were conducted using the R program version 3.1.0 (R Core Team 2014). In addition, we tested the significance of correlations between growth rates and the two root traits (we used Spearman's' rank correlation, to account for outliers and non-normal distributions).

Results

Growth rates

Both RGR and SGR varied among the 34 species. RGR after 10 weeks of growth ranged from 0.094 g g^{-1} day^{-1} (*Knautia arvensis*) to 0.143 g g^{-1} day^{-1} (*Agrostis capillaris*) (Table A1). SGR values calculated for the average plant size at week 6, ranged from 0.0004 g g^{-1} day^{-1} (*Hypericum perforatum*) to 0.0750 g g^{-1} day^{-1} (*Rumex maritimus* and *Plantago major*) (Table A1).

Effects of soil treatments

We expected species with faster growth to suffer more negative soil effects than slower growing species. Linear regression models of biotic soil effects including RGR or SGR were generally a better fit compared to simpler models (Table 1). Both RGR and SGR varied negatively with biotic soil effects, with slower-growing species tending to be less negatively or even positively affected by the presence of soil biota (Table 1; Fig. 1). Removal of each species in turn revealed that parameter estimates for both RGR and SGR remained negative in all cases (Table F1). A less steep relation between RGR and biotic soil effects occurred in only 9 cases when a species was removed compared to the model estimate including all species (Table F1). The most influential species were *Brachypodium sylvaticum* (also an

outlier, identified from a quantile-quantile normality plot), *Hypericum perforatum*, *Knautia arvensis* and *Lathyrus pratensis*; the latter two species showed net positive biotic soil effects (1.30 and 0.12), and their removal reduced the slope of the relation (Table F1). Removal of species led to a shallower relation between SGR and biotic soil effects in 14 cases, and the most influential species were again *Brachypodium sylvaticum*, *Knautia arvensis* and *Lathyrus pratensis*, but also *Plantago lanceolata* (Table F1). For conspecific soil effects, neither of the linear models including RGR or SGR was distinguishable from simpler models according to AIC, with no clear relation between the growth rates and conspecific soil effects (Table 1). The estimates for models explaining biotic and conspecific soil effects qualitatively differed little when phylogenetic information was included (Table G1).

Specific root length and root C:N

We expected species' root traits to correlate with growth rates, and in turn, to be related to soil effects. Specific root length correlated positively with RGR, as predicted, but not with SGR (Table 3). Root C:N correlated positively with RGR and SGR, but only significantly so for RGR (Table 3). Phylogenetically independent contrasts revealed a significant positive correlation between SRL and RGR, but not between SRL and SGR (Table 3). Contrasts of root C:N were not significantly correlated with RGR or SGR (Table 2). Neither biotic nor conspecific soil effects showed a clear relation with mean species' SRL, but biotic soil effects became more negative with increasing root C:N (Table H1), which also represented a better fit (AIC: 113.33) than the simpler model including only the biomass covariate (AIC: 118.97). However, this relation was no longer negative after removal of the outlying and most influential species, *Brachypodium sylvaticum* (Table F1).

Discussion

We expected faster-growing plant species to suffer more negatively from soil biota than slower-growing species, and found some evidence in support of this expectation. Biotic soil effects varied negatively with relative growth rate, switching from net beneficial to net deleterious effects of soil biota (Fig. 1A). Similarly, biotic soil effects varied negatively with SGR, indicating that faster-growing species suffered more strongly from soil biota than slower-growing species (Fig. 1B). For both measures of growth rate, the negative relation was reduced when some of the most influential species were removed, suggesting that it may be driven by a subset of the species studied. Conspecific soil effects did not vary clearly with either RGR or SGR, whereas the effect of growing in conspecific soils relative to heterospecific soils on total biomass was significantly negative across all species (mean effect = -0.275 g; Table 1, intercept model). Therefore some species-specific differences in soils must have been present.

Two caveats are warranted for the approaches used in our study. First, the soil sterilization approach used in plant-soil feedback studies can have unintended side effects, such as increasing nutrient availability (Trevors 1996), which may give the impression of greater plant biomass without soil biota. However, the volume of soil used to inoculate plants was less than 10% of the total volume of substrate, and the subsequent regular fertilization of plants would likely have overwhelmed any differences in nutrient availability caused by sterilization. Second, our estimates of RGR/SGR and soil effects may not be entirely representative of the species in general, due to the relatively few genotypes sampled, and extra variation contributing to differences among species, that is derived from sampling error. We cannot rule out that changes in sampling regime of source material might result in a differently-shaped relation. However, the same genotypes were used to estimate growth rates and soil effects, which should reduce the likelihood that a relation of soil effects to growth rates is confounded by genotype differences.

What explains the relations between effects of soil biota on plant growth and species growth rates? Plants engage in complex interactions with soil microbes via their roots, ranging from pathogenic (deleterious) through neutral to mutualistic (beneficial). Plant species differ in their associations with mycorrhizal fungi (Reinhart et al. 2012) and the direction of effect of these associations (Klironomos 2003). Moreover, mycorrhization varies with successional stage (Rasmann et al. 2011), and slower-growing species may depend more on mycorrhizal fungi than faster-growing species (Reich 2014). Our results suggest some slower-growing species benefitted more from soil biota than faster-growing species (Fig.1). Such species (lower RGR) may benefit relatively more from soil mutualists than they suffer from pathogens, leading to net beneficial effects of soil biota, but this net benefit declines for species with faster growth rates until the effects of pathogens outweigh those of mutualists (net deleterious effects of soil biota). Interestingly, performance of the slower-growing *Knautia arvensis* is known to benefit consistently from association with arbuscular mycorrhizal fungi (Doubková et al. 2013). However, care is warranted in interpreting these linear relations as general patterns, as they reflect responses by specific species, such as *Knautia arvensis* and *Lathyrus pratensis*, which grew slowly and benefitted from the presence of soil biota. Although models including growth rates explained sufficiently more variation than simple intercept and covariate models, much variation remain unexplained, and we cannot rule out the possibility that relations could in fact be non-linear. Determination of how generalizable the direction and shape of the relation are among angiosperms will require assessment of more species.

If slower-growing species have a net benefit from soil mutualists, and faster-growing species suffer a net deleterious effect from pathogens, then a key question is whether and how this difference is driven by differences in the roots of faster- and slower-growing species. We hypothesized that faster-growing species would have lower root C:N and greater SRL

compared to slower-growing species. We found that SRL varied positively with RGR, indicating longer roots per unit mass for faster-growing species. However, C:N ratio correlated positively with RGR (contrary to our hypothesis), and not with SGR. Root C:N varied negatively with biotic soil effects, which was also contrary to our prediction, but in line with its weak but positive correlation with growth rates (Table 2). However, this significant relation disappeared after accounting for the most influential species. Thus, the relation of growth rates to soil biota effects may be linked to factors other than simple root traits.

Plant defense against soil pathogens will involve production of constitutive and induced defense compounds. Biochemical pathways involving salicylic acid are involved in plant defense against microbes (Vlot et al. 2009), but also appear to play a role in plant growth and development, as illustrated by transgenic salicylic-acid-depleted *Arabidopsis* plants exhibiting higher growth rates (Rivas-San Vicente and Piasencia 2011). Compounds such as salicylic acid could offer a direct mechanism for observed relations between growth and defense both within and among species, but whether species with differing growth rates vary in expression of these compounds remains to be tested. Other attributes of roots and defense compounds could be linked to both plant growth rate and soil biota effects, but expression of these traits themselves can be mediated by soil organisms such as mycorrhizal fungi (Rasmann et al. 2011). As soil microbial communities are hyperdiverse, with many directly and indirectly interacting groups of species (Wardle et al. 2004), the relation between belowground plant traits and the net effects of soil biota on plant growth is likely to be more complex than for aboveground traits and natural enemies (Endara and Coley 2011).

To conclude, evidence partially supports a negative association of soil biota with plant growth rates. However, the considerable unexplained variation indicates that relations may be more complex. Moreover, effects of soil biota appeared to be largely unrelated to the simple root traits specific root length and root C:N ratio, despite evidence that these traits were

363 correlated with growth rates. Strong relations between plant growth rates and defense from
364 aboveground enemies may not be clearly reflected belowground, due to the diversity and
365 complexity of soil microbial communities, involving multiple mutualistic and antagonistic
366 interactions with plants. Further work could focus on disentangling the relations of growth
367 rates to effects of soil mutualists from those of pathogens, to understand how these two
368 groups might contribute to the relations observed.

369

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376 **Online Table A1.** The 34 plant species used in the study, the locations of the populations where seeds were sample from (Lat./Long. when
377 available), the number of parent plants, and the date when all pots contained seedlings ('week zero') for growth rate estimation. Also shown are the
378 AICs for growth curve model fits. The lowest AIC model was used to estimate size-corrected growth rate (SGR); where growth models were
379 indistinguishable (< 2 AIC units' difference), an average SGR was calculated from the estimates of the respective models (underlined). Relative and
380 size-corrected growth rate (RGR, SGR) estimates (g g^{-1} day^{-1}) are also shown. * Biennial species; †Annual species. ‡ Species were not covered with
381 substrate for germination. Numbers in bold refer to the number of replicate values for 1- effects of unsterilized *versus* sterilized soil, 2- the effects of
382 conspecific *versus* heterospecific soil, 3- specific root length and 4- root C:N ratio per species.

Species	Family	Population location	# parent plants	Week 0	Mono-molecular AIC	3-parameter logistic AIC	4-parameter logistic AIC	Gompertz AIC	RGR	SGR	**1**	**2**	**3**	**4**
Daucus carota	Apiaceae	47°41'32"N, 9°10'39" E	10	6.5.2013	111.66	-42.97	-45.06	-53.60	0.112	0.027	5	5	5	4
Centaurea jacea	Asteraceae	47°41'21"N, 9°11'02" E	10	2.5.2013	91.04	<u>-3.78</u>	<u>-3.16</u>	<u>-3.74</u>	0.106	0.034	5	5	5	5
Cirsium arvense‡	Asteraceae	47°41'19"N, 9°11'33" E	10	10.5.2013	73.73	<u>35.46</u>	36.28	<u>33.61</u>	0.133	0.048	3	5	3	3
Cirsium oleraceum	Asteraceae	47°41'21"N, 9°11'02" E	10	8.5.2013	70.57	<u>11.57</u>	<u>13.39</u>	13.94	0.09	0.050	5	5	5	5
Pulicaria dysenterica‡	Asteraceae	47°41'13" N, 9°7'29" E	10	7.5.2013	65.16	2.86	0.36	-8.84	0.138	0.053	5	5	3	3
Senecio jacobaea	Asteraceae	47°42'27" N, 9°5'58" E	10	8.5.2013	86.14	<u>4.51</u>	6.45	<u>3.70</u>	0.112	0.049	5	5	5	5
Taraxacum officinale‡	Asteraceae	47°40'33" N, 9°10'05" E	10	3.5.2013	30.95	-19.58	-19.41	-31.04	0.123	0.057	5	5	5	5
*Echium vulgare**	Boraginaceae	47°42'40" N, 9°5'06" E	10	2.5.2013	34.05	-0.91	-0.20	-13.01	0.104	0.067	5	5	5	5
Diplotaxis tenuifolia	Brassicaceae	47°41'13" N, 9°7'29" E	10	10.5.2013	12.18	1.23	-1.43	-5.47	0.110	0.043	4	5	5	5

Campanula glomerata	Campanulaceae	47°41’24” N, 9°10’28” E	10	9 5.2013	45.62	-78.10	-75.93	-65.72	0.126	0.013	3	4	5	2
Rumex maritimus†	Caryophyllaceae	Faverois, CH	10	9.5.2013	83.97	3.65	-0.053	-13.66	0.129	0.075	5	5	5	5
Rumex obtusifolius	Caryophyllaceae	Colisses, CH	10	3.5.2013	20.22	-4.69	-10.64	-17.08	0.122	0.053	5	5	5	5
Silene alba‡	Caryophyllaceae	47°42’27” N, 9°5’58” E	10	7.5.2013	50.83	-0.82	0.90	-1.104	0.106	0.069	5	5	5	5
Silene vulgaris‡	Caryophyllaceae	47°40’33” N, 9°10’05” E	10	6.5.2013	24.07	-15.58	-13.73	-16.60	0.105	0.050	5	5	5	5
Knautia arvensis	Dipsaceae	47°41’15”N, 9°11’27” E	10	7.5.2013	94.41	-28.61	-28.02	-31.98	0.094	0.037	5	5	5	5
Lathyrus pratensis	Fabaceae	47°41’29”N, 9°11’08” E	10	9.5.2013	60.79	-64.83	-64.33	-68.43	0.104	0.010	3	3	_	_
Lotus corniculatus	Fabaceae	47°41’21”N, 9°11’02” E	10	10.5.2013	66.57	16.42	17.92	15.44	0.123	0.036	5	5	5	4
Trifolium pratense	Fabaceae	47°41’21”N, 9°11’02” E	10	9.5.2013	72.26	4.70	5.37	3.45	0.102	0.041	5	5	5	4
Hypericum perforatum	Hypericaceae	47°41’13” N, 9°7’29” E	10	8.5.2013	_	-53.42	-51.26	-54.78	0.116	0.0004	4	4	4	_
Origanum vulgare‡	Lamiaceae	47°45’13” N, 9°3’13” E	6	6.5.2013	_	-27.17	-31.75	-18.34	0.126	0.014	3	_	5	3
Salvia pratensis	Lamiaceae	47°41’32”N, 9°10’39” E	10	3.5.2013	106.12	-3.41	-2.69	-4.35	0.108	0.060	5	5	5	4
Lythrum salicaria‡	Lythraceae	47°41’13”N, 9°11’21” E	10	10.5.2013	68.83	-30.55	-29.48	-33.73	0.141	0.0530	5	5	4	5
Epilobium hirsutum	Onagraceae	47°45’9” N, 9°2’39” E	10	3.5.2013	49.53	-39.28	-43.08	-55.45	0.144	0.067	5	5	5	5
*Oenothera biennis**	Onagraceae	47°40’18” N, 9°12’31” E	10	7.5.2013	72.49	-25.27	-26.85	-32.54	0.124	0.055	5	5	5	5
Plantago lanceolata	Plantaginaceae	47°41’16”N, 9°11’24” E	10	6.5.2013	66.42	-14.05	-13.71	-18.61	0.101	0.047	5	5	5	5
Plantago major‡	Plantaginaceae	47°45’9” N, 9°2’50” E	6	10.5.2013	74.87	-8.49	-6.77	-5.29	0.108	0.075	5	5	4	4
Agrostis capillaris	Poaceae	47°41’28”N, 9°11’13” E	10	8. 5.2013	73.12	43.77	45.70	45.89	0.143	0.044	5	5	5	5
Brachypodium sylvaticum	Poaceae	Bern, CH	10	7 5.2013	110.45	-63.17	-63.95	39.35	0.111	0.053	3	3	5	4

Dactylis glomerata	Poaceae	47°41’7”N, 9°11’22” E	10	10.5.2013	40.56	-13.43	-13.09	-13.17	0.111	0.067	5	5	5	5
Deschampsia cespitosa‡	Poaceae	47°41’36” N, 9°10’42” E	10	7.5.2013	_	-38.98	-37.09	-37.63	0.123	0.056	5	5	5	5
Phleum pratense‡	Poaceae	47°41’16”N, 9°11’16” E	10	3.5.2013	94.70	3.70	3.75	-4.600	0.128	0.042	5	5	4	5
Geum urbanum	Rosaceae	47°41’29” N, 9°10’56” E	10	6.5.2013	154.24	-26.22	-25.18	-27.50	0.100	0.035	5	5	3	_
Sanguisorba minor	Rosaceae	47°41’22”N, 9°11’14” E	10	3.5.2013	84.53	-44.87	-47.08	-51.55	0.100	0.042	5	5	5	5
*Verbascum thapsus**	Scrophulariaceae	47°41’13” N, 9°7’29” E	3	3.5.2013	89.90	-31.42	-31.50	-55.93	0.136	0.060	5	5	5	5

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Online Appendix B. Methods for growth rate estimation

In April 2013, we sowed out the seeds of all 34 species and destructively harvested the biomass of resulting plants over a 12-week growth period, in order to estimate species-specific growth rates. The aim was to harvest three plants per species once every week, from soon after germination (referred to as 'week zero'), to 12 weeks later. To this end, we filled 1224 pots (1.12 L in volume) with a mixture of topsoil ('Rasenerde', Ökohum GmbH), vermiculite and washed sand (ratio of 1:1:1 by volume). This gave a total of 36 pots per species. The seeds were stratified at -18°C for one week, prior to sowing. The seeds were removed from stratification on 19 April 2013, and on 22 and 23 April, they were sown into individual pots (one batch of 10 seeds per pot per species). Thus a total of 12240 seeds were sown. The ten seeds were sown in the center of the pot, and 24 of the species were covered with a thin layer of the substrate, approximately as thick as the breadth of the seeds. The ten remaining species (indicated in Table A1) were not covered with substrate, as they required high-light conditions for germination. The pots were evenly distributed across three tables in a greenhouse, so that there were 12 pots per species on each table (giving a total of 408 pots per table). The pot positions on each table were randomized on 24 and 25 April 2013. Pots were placed on top of an absorbent fleece lining in order to maintain water availability throughout the growth period (see below).

In order to optimise germination, the greenhouse temperature regime during the germination phase was set so that heating turned on automatically if the temperature was below 5°C, and ventilation turned on automatically if 20°C was reached between 6 am and 8 pm, and if 10°C was reached between 8 pm to 6 am. Between these values, the temperature fluctuated according to conditions outside the greenhouse. Shortly after sowing, the pots were watered evenly from above; subsequently, the tables were flooded with water once a week (and were drained of excess water after 20 minutes) to ensure non-limiting water availability,

and in order to avoid disturbing the seedlings and therefore affecting their growth. The pots were checked regularly after sowing (29 April, 1 May, 5 May, 8 May and 10 May), for germinated seeds until all or most pots per species had emergent seedlings.

When all pots of one species contained emergent seedlings, all seedlings except one per pot were carefully removed, counted, washed clean of substrate, and were dried for 72 hours at 70°C. The total biomass of these seedlings per pot per species was weighed, and an average biomass per seedling calculated. We then calculated the mean biomass of a seedling in a pot, for the 12 pots of a species per table. This gave three replicate seedling biomass values per species soon after germination ('week zero'). The exact date of week-zero biomass varied per species with a range of eight days (Shown in Table A1), as did subsequent weekly harvests. This approach ensured that growth was estimated from biomass of plants harvested precisely x weeks from week zero for every species. For two species- *Diplotaxis tenuifolia* and *Dactylis glomerata*- only 24 pots contained germinated seeds: therefore pots were redistributed so that two pots per week could be harvested weekly for each of these species, from 1 week to 11 weeks after week 0.

After the last week-zero seedlings were harvested, the temperature settings were changed on 13 May to a minimum temperature 15°C and a maximum temperature of 24°C (from 6 am – 8 pm) and 20°C (from 8 pm – 6 am). To ensure non-limiting light conditions, additional lighting automatically switched on if the natural irradiation was below 100 µmol/(m^2*s) during daytime (6 am – 8 pm). To make sure the plants had a non-limiting supply of nutrients, they were fertilized weekly with a 1‰ solution of Universol Blue (Everris GmbH), starting on the 16th of May (250 ml per plant). The fertilizer contained 18% nitrogen, 11% phosphate, 18% potassium oxide, 2.5% magnesium oxide and other trace nutrients. Every week until 12 weeks after week zero, three plants (one per table) per species for most species were destructively harvested; aboveground biomass was cut, and belowground biomass was washed to remove substrate. Both components of biomass were dried at 70°C for

72 hours, weighed, and total biomass was calculated. These biomass values were then used to estimate species growth rates. For some species, some plants died, and when this occurred, we reassigned harvesting dates so that three plants for that species could be harvested every week up until at least week 8. All species had plants harvested up to week 10.

We estimated species growth rates in two ways. First, we calculated classical relative growth rate (RGR) as the difference in mean biomass between week 10 and week zero, divided by time (=70 days), giving an estimate of RGR in g g^{-1} day^{-1} (Grime and Hunt 1975). We chose 10 weeks instead of 12, as one species (*Lotus corniculatus*) only had plants harvested up until week 10. Classical RGR has received some criticism as a measure of plant growth rates, because it inherently decreases with increasing plant size, which makes comparisons of growth rates among species with differing plant sizes difficult (Turnbull et al. 2008). Therefore, we estimated size-corrected growth rate (SGR) at a common plant size (biomass) for all species. We achieved this by fitting non-linear growth curve models to the biomass (ln-transformed+1) of each species individually (using biomass data for all weeks with data available), following the protocol and using the R program scripts provided by Paine et al. (2012). Briefly, four types of growth function were fitted to the biomass data: monomolecular, three-parameter logistic, four-parameter logistic and Gompertz. The models were fitted using the function 'gnls' in the R package 'nlme' (Pinheiro et al. 2013). In each model, variance heterogeneity was accounted for by allowing the variance to increase exponentially with fitted mean biomass values (using the 'varExp' function in nlme). Once all four models were fitted per species, Akaike's Information Criterion (AIC) for the four models were compared to assess which model best fit the biomass data (the model with the lowest AIC). Then, using the best-fitting models for each species, SGR was estimated at the average biomass of plants (3.52 g) calculated across all species in week 6 (the midpoint of the total growth period for most species). When AICs of the lowest AIC model and at least one other model were indistinguishable (with <2 AIC units difference), we calculated an average SGR

value from the estimates of the respective models. Our approach ensured that all species had actually attained biomasses predicted by the best-fitting models at this time point, and the estimate can be thought of as representing an average SGR equivalent to conventional RGR, which also represents an average (Turnbull et al. 2012). The estimated RGR and SGR are shown in Table A1.

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Online Appendix C. Methods for measuring effects of soil biota and root traits

Effects of soil biota

Seeds collected from the same plants as the seeds used for growth-rate estimation were used in order to condition soils with monocultures for all 34 plant species. In May 2013, we filled 170 4.5-L pots with a substrate consisting of a mixture of sand, vermiculite and topsoil (as used previously, with a ratio of 1:1:1) to 4 L, and then added an extra 200 ml of sieved, homogenized soil collected from the field to each pot, which was thoroughly mixed with the other substrate. The field-collected soil was obtained from seven meadow/grassland areas in the vicinity of the University of Konstanz. The GPS co-ordinates and the common plant species for these areas are shown in Table D1.

Approximately 0-10 cm depth of soil was obtained from 12-20 systematically located points in each area. This yielded a total of ~40 L of soil, which was bulked, sieved using a 5 mm mesh, and mixed thoroughly. For each species, we then sowed 100 seeds into each of five replicate pots on 22 and 23 May 2013 (the pots were placed outside), and once the seeds had germinated, we removed excess seedlings until five remained (evenly spaced) in each pot. These plants were then grown for 14 weeks until 17-18 September 2013. After this period, the aboveground biomass per pot was removed, and the soil per individual pot was sieved to remove the majority of roots, and then stored at 4°C for a short period before initiating the soil feedback experiment.

We filled 510 1.2-L pots with 1 L of 1:1 washed sand and vermiculite, and 100 ml of soil from the conditioning phase that represented one of the following treatments:

1) Unsterilized soil from a replicate conditioning pot of the same species (conspecific soil)

2) Sterilized soil from a replicate conditioning pot of the same species (conspecific, sterilized). Soil was sterilized at 121°C for 40 minutes in an autoclave

3) Unsterilized soil from a mixture of soils made from one replicate conditioning pot of every species (heterospecific soil)

Note that conspecific and heterospecific soil treatments were always paired according to the replicate conditioning pot used for the soil inocula. Because we had five replicate conditioning pots for each of the 34 species, we then had a maximum of five replicate 1.2-L pots per species for each of the above soil-inoculum treatments. This gave a total of 15 pots per species. Into each pot per species, we planted a single seedling, grown from seeds representing the same parent plants as those used in the conditioning phase and in the growth-rates estimation. The seeds had been germinated two weeks earlier in a growth chamber on sterile sand (temperature = 15°C/20°C 12h/12h darkness/light, light level = 150µmol $m^{-2}s^{-1}$, relative humidity = 90%). The plants were then grown in a greenhouse for a period of 12 weeks. The temperature was kept below 24°C from 6 am to 8 pm, and 16°C between 8 pm and 6 am. Additional light exposure (125 µmol m^{-2} s^{-1}) was given from 6-9 am and 5.30-8 pm. Five tables were used, each for one replicate of all three soil treatments (conspecific, heterospecific, conspecific and sterilized) of a species. At the start and every second week of the experiment, the plants were randomized within tables. As fertilizer, a 100% Hoagland's solution was used (The recipe is shown in Table E1).

Watering was done once a week with 200 ml given to every plant, and Hoagland's solution formed the watering treatment once every two weeks with the same volume. After 8 weeks, the plants were watered twice a week (a total of 400 ml). After 12 weeks of growth, the aboveground biomass was dried at 70°C for 72 hours, and the belowground biomass was washed carefully to remove the substrate before drying. Both belowground and aboveground biomasses were then weighed, and total biomass was calculated.

Measuring root traits

Five replicate plants per species were grown simultaneously with plants used for measuring soil biota effects (and using the same batch of seedlings), to estimate specific root length (SRL) and root C:N ratio. Plants were grown in 0.5 L pots in a mixture of sand and

vermiculite (ratio 1:1) for 10 weeks (16th of September to 26th of November), under the same conditions as the soil-biota-effects plants, except that they were watered and fertilized with 150 ml of 100% Hoagland's solution once a week. After 10 weeks, the plants were harvested, and roots were washed carefully to remove substrate. Immediately after washing, roots were stored in water for no more than 24 hours. Then the root systems were cut up into approximately 3 cm long fragments and two subsamples were taken blindly from each replicate and stained for one hour in Neutral Red staining solution. The staining solution was prepared using 65 ml of 1M NaOH and 5.25 g citric acid ($C_8H_8O_7H_2O$, final concentration 25 mM), added to 800 ml tap water and mixed carefully. The solution was filled up to 1 L and then the pH was adjusted to a value of 6, before adding and dissolving 0.35g Neutral Red dye.

For scanning, root material was washed again to remove excess staining solution and then arranged carefully in a square petri-dish containing water. An 8-bit greyscale image of each subsample was taken at 600 dpi, with a flatbed scanner (Regent Instruments, Epson Expression 10000 XL). Total root length per subsample was then measured using the WinRhizo program (WinRHIZOTM 2012, © Regent Instruments Canada Inc.). Specific root length (SRL) was calculated per subsample as the root length (cm) divided by the root dry mass (after drying for 72 hours at 70°C). An average SRL from the two subsamples was calculated, and average SRL for the species was calculated from the five replicate plants.

To estimate root C:N ratios, dry root biomass per plant was placed into 2 ml Eppendorf tubes containing two ceramic balls with an average diameter of 2.8 mm. The tubes were loaded onto a milling machine (MM 300, Retsch GmbH, Haan Germany). The material was ground for 15-30 min with 20 shakes per second. The powdered samples were placed into small tin cups (using 0.3-0.9 mg). The tin cups were rolled into small balls and C and N content were measured by combustion, after drying in an incubator for at least 24 hours. The combustion was done with a CHNSO analyzer 'Euro EA' (HEKAtech GmbH, Wegberg Germany). A mean root C:N ratio was then calculated per species.

Online Table D1. GPS locations of soil collection from fields containing grassland and meadow species (common species listed).

GPS co-ordinates (Latitude, Longitude)	Common plant species
47°41’26” N, 9°11’27” E	*Achillea millefolium, Ajuga reptans,*
47°41’18” N, 9°11’28” E	*Alopecurus pratensis, Anthoxanthum odoratum,*
47°41’16” N, 9°11’34” E	*Arrhenatherum elatium, Brachypodium sylvaticum,*
47°41’13” N, 9°11’18” E	*Cardamine pratensis, Centaurea jacea,*
47°41’10” N, 9°11’26” E	*Cynosurus cristatus, Dactylis glomerata,*
47°40’59” N, 9°11’25” E	*Daucus carota, Geum rivale,*
47°40’39” N, 9°11’46” E	*Glechoma hederacea, Heracleum sphondylium,*
	Knautia arvensis, Lathyrus pratensis,
	Lotus corniculatus, Phleum pratense,
	Pimpinella major, Plantago lanceolata,
	Ranunculus acris, Rhinanthus alectorolophus,
	Rumex acetosa, Sanguisorba minor,
	Senecio jacobaea, Silene vulgaris,
	Taraxacum officinale, Trifolium pratense,
	Trisetum flavescens, Veronica chamaedrys

Online Table E1. The recipe used for creating the 100% Hoagland's solution, applied as fertilizer every two weeks (as 200 ml per plant) to the plants grown under different soil treatments.

Component	**Stock solution concentration (in water)**	**Volume used in final solution (L^{-1}, in water)**
2M KNO_3	202g L^{-1}	2.5 ml L^{-1}
2M $Ca(NO_3)_2$ x 4 H_2O	118 L^{-1}	2.5 ml L^{-1}
Iron (Sprint 138 iron chelate)	15g L^{-1}	1.5 ml L^{-1}
2M $MgSO_4$ x7 H_2O	493g L^{-1}	1 ml L^{-1}
1M NH_4NO_3	80g L^{-1}	1 ml L^{-1}
Micronutrients:		
H_3BO_3	2.86g L^{-1}	1 ml L^{-1}
$MnCl_2$ x $4H_2O$	1.81g L^{-1}	
$ZnSO_4$ x $7H_2O$	0.22g L^{-1}	
$CuSO_4$	0.051g L^{-1}	
Na_2MoO_4 x $2H_2O$	0.12g L^{-1}	
1M KH_2PO_4 (pH to 6.0 with 3M KOH)	136g L^{-1}	0.5 ml L^{-1}

Online Table F1. Changes in model parameter estimates for linear models explaining biotic soil effects with omission of each species (estimate with all species – estimate with 1 species omitted). The slope estimates for the four most influential species are in bold.

	RGR model				**SGR model**			**Root C:N model**			
Omitted species	**Δ Intercept**	**Δ Biomass**	**Δ RGR**	**RGR estimate**	**Δ Intercept**	**Δ SGR**	**SGR estimate**	**Δ Intercept**	**Δ Biomass**	**Δ C:N**	**C:N estimate**
Agrostis capillaris	-0.025	0.006	0.283	-18.672	<0.001	-0.110	-13.797	<-0.001	0.002	<0.001	-0.083
Brachypodium sylvaticum	-0.425	-0.123	**2.099**	**-20.488**	0.017	**-7.074**	**-6.832**	1.948	0.343	**-0.100**	**0.017**
Dactylis glomerata	-0.031	-0.025	-0.004	-18.384	0.001	-0.384	-13.523	0.063	-0.010	-0.004	-0.079
Deschampsia cespitosa	-0.075	0.019	0.897	-19.285	-0.002	0.803	-14.710	-0.032	-0.002	0.003	-0.086
Phleum pratense	-0.008	0.003	0.110	-18.498	<-0.001	0.005	-13.912	-0.021	0.003	0.001	-0.084
Campanula glomerata	-0.072	0.003	0.687	-19.075	-0.004	-0.136	-13.771	-0.566	0.049	**0.023**	**-0.106**
Knautia arvensis	0.472	0.047	**-3.602**	**-14.786**	<-0.001	**1.281**	**-15.188**	0.074	0.023	0.002	-0.085
Centaurea jacea	0.015	0.005	-0.073	-18.315	<0.001	0.055	-13.962	0.028	0.006	<-0.001	-0.082
Cirsium arvense	-0.015	0.005	0.191	-18.579	<-0.001	0.037	-13.943	0.005	0.004	<0.001	-0.083
Cirsium oleraceum	0.099	0.022	-0.631	-17.758	<-0.001	0.341	-14.248	0.094	0.033	-0.002	-0.081
Pulicaria dysenterica	-0.137	0.012	1.361	-19.750	<-0.001	0.383	-14.290	0.037	0.002	-0.001	-0.082
Senecio jacobaea	-0.061	-0.050	-0.040	-18.348	0.002	-1.018	-12.889	-0.529	-0.085	**0.019**	**-0.102**
Taraxacum officinale	-0.006	0.008	0.136	-18.524	<-0.001	0.083	-13.990	0.027	0.007	<-0.001	-0.082
Daucus carota	0.004	0.002	-0.018	-18.370	<0.001	0.072	-13.979	0.026	-0.001	<-0.001	-0.082
Echium vulgare	-0.007	-0.004	0.024	-18.412	<0.001	-0.068	-13.839	-0.014	-0.008	<0.001	-0.083
Plantago lanceolata	-0.005	-0.001	0.032	-18.420	<0.001	-0.001	-13.906	<0.001	0.003	0.002	-0.083
Plantago major	-0.049	-0.001	0.395	-18.784	-0.012	**3.047**	**-16.954**	0.018	-0.012	<-0.001	-0.082
Verbascum thapsus	-0.052	0.025	0.734	-19.122	<-0.001	0.149	-14.056	-0.005	0.027	0.002	-0.085
Salvia pratensis	0.008	0.003	-0.034	-18.355	<-0.001	0.085	-13.992	0.018	0.004	<-0.001	-0.082
Origanum vulgare	-0.037	0.002	0.348	-18.737	<0.001	0.021	-13.928	-0.210	-0.039	**0.010**	**-0.093**
Rumex maritimus	-0.002	0.004	0.059	-18.447	<0.001	-0.254	-13.653	-0.038	-0.025	<0.001	-0.084
Rumex obtusifolius	0.015	0.092	0.875	-19.263	0.002	-0.691	-13.215	-0.093	-0.066	0.001	-0.084
Silene alba	0.015	0.009	-0.029	-18.359	<-0.001	0.026	-13.933	0.003	0.014	<0.001	-0.084
Silene vulgaris	-0.012	-0.004	0.052	-18.440	<0.001	-0.066	-13.841	<0.001	-0.003	<-0.001	-0.083
Diplotaxis tenuifolia	-0.007	-0.004	0.012	-18.400	<0.001	-0.067	-13.840	-0.027	-0.008	<0.001	-0.084
Epilobium hirsutum	0.068	-0.012	-0.727	-17.662	0.002	-0.569	-13.338	0.021	-0.005	-0.002	-0.081
Oenothera biennis	0.035	-0.034	-0.683	-17.705	0.018	-0.669	-13.238	-0.059	-0.044	<0.001	-0.083
Lythrum salicaria	-0.007	0.001	0.081	-18.470	<0.001	-0.055	-13.852	-0.002	-0.001	<-0.001	-0.083

Geum urbanum	0.096	0.004	-0.786	-17.602	<0.001	0.724	-14.631				
Sanguisorba minor	0.078	0.014	-0.524	-17.864	<-0.001	0.328	-14.235	0.079	0.016	-0.002	-0.081
Lathyrus pratensis	0.825	0.019	**-6.840**	**-11.548**	0.047	0.698	-14.605				
Trifolium pratense	0.022	0.001	-0.175	-18.214	<-0.001	0.167	-14.073	0.039	<0.001	-0.002	-0.081
Lotus corniculatus	-0.063	0.006	0.650	-19.038	<0.001	0.370	-14.277	0.067	-0.001	-0.003	-0.080
Hypericum perforatum	-0.596	-0.094	**5.028**	**-23.416**	-0.233	**5.941**	**-19.848**				

Online Table G1. Parameter estimates (± standard error) from phylogenetic generalised least squares models of the relationship between classical relative growth rates (RGR), size-corrected growth rates (SGR), root C:N or Specific root length and i) biotic soil effects; ii) conspecific soil effects. Pagel's lambda (λ) is shown, which indicates the strength of phylogenetic correlation in the relationship between independent and dependent variables.

	Biotic soil effect	Conspecific soil effect
Intercept	**2.047 (0.804)**	-0.752 (0.736)
Biomass (sum, g)	**-0.132 (0.056)**	**-0.049 (0.018)**
RGR	**-18.019 (7.293)**	5.603 (6.497)
λ	1.081	-0.167
Intercept	0.029 (0.059)	-0.223 (0.124)
SGR	**-15.191 (4.108)**	-1.860 (2.482)
λ	0.627	-0.173
Intercept	0.356 (0.657)	0.115 (0.375)
Biomass (sum, g)	-0.081 (0.057)	-0.038 (0.021)
Root C:N ratio	-0.052 (0.032)	-0.015 (0.021)
λ	0.846	-0.167
Intercept	0.592 (0.453)	-0.130 (0.375)
Biomass (sum, g)	**-0.181 (0.059)**	-0.039 (0.027)
SRL	-0.026 (0.017)	-0.001 (0.012)
λ	1.031	-0.166

Online Table H1. Parameter estimates (± standard error) of the relationships between classical relative growth rates (RGR), size-corrected growth rates (SGR) root C:N or specific root length (SRL) and i) biotic soil effects; ii) conspecific soil effects, for 34 herbaceous plant species.

	Biotic soil effect	Conspecific soil effect
Intercept	1.218 (0.606)	0.370 (0.414)
Biomass (sum, g)	-0.050 (0.049)	-0.047 (0.027)
Root C:N ratio	-0.083 (0.030)	-0.028 (0.023)
Intercept	0.580 (0.441)	0.150 (0.322)
Biomass (sum, g)	-0.156 (0.041)	-0.073 (0.028)
SRL (cm g^{-1})	-0.023 (0.017)	-0.010 (0.011)

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Figure 1. Relations between biotic soil effects on plant biomass and a) classical relative growth rate (RGR), and b) size-corrected growth rate (SGR). Negative soil effects indicate plants had reduced biomass in unsterilized soils; positive soil effects indicate greater biomass in unsterilized soils. Error bars represent 95% confidence intervals. The species with the largest weighting was *Hypericum perforatum*. Solid lines show fitted values from the models, and dashed lines are 95% confidence intervals about the fitted lines. Horizontal line at y=0 represents a biotic soil effect of zero (i.e. plant biomass in sterilized and unsterilized soil is equal).

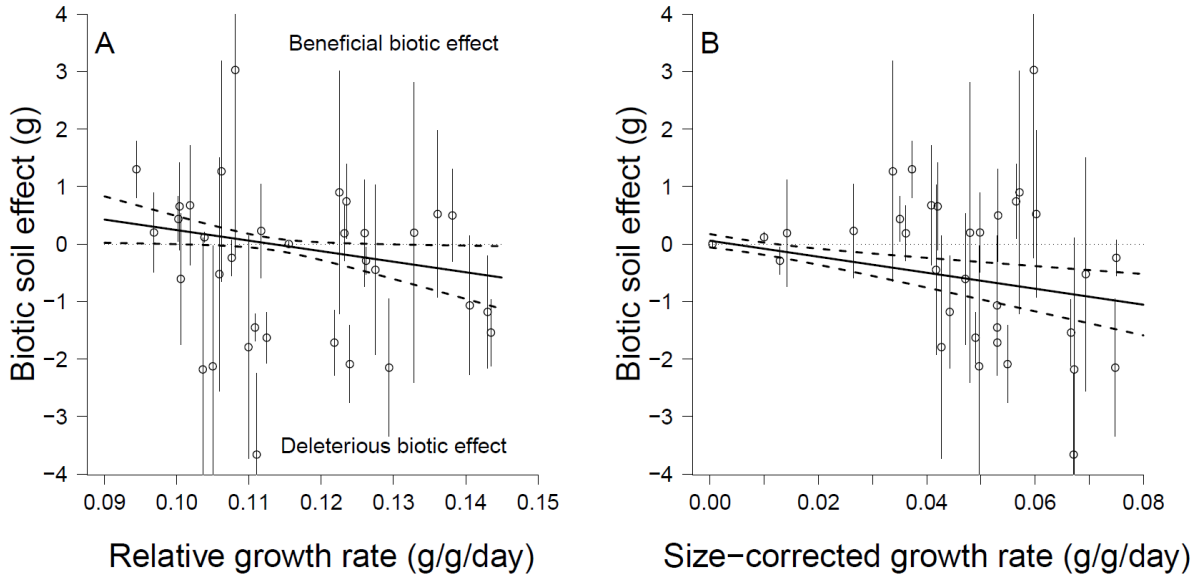


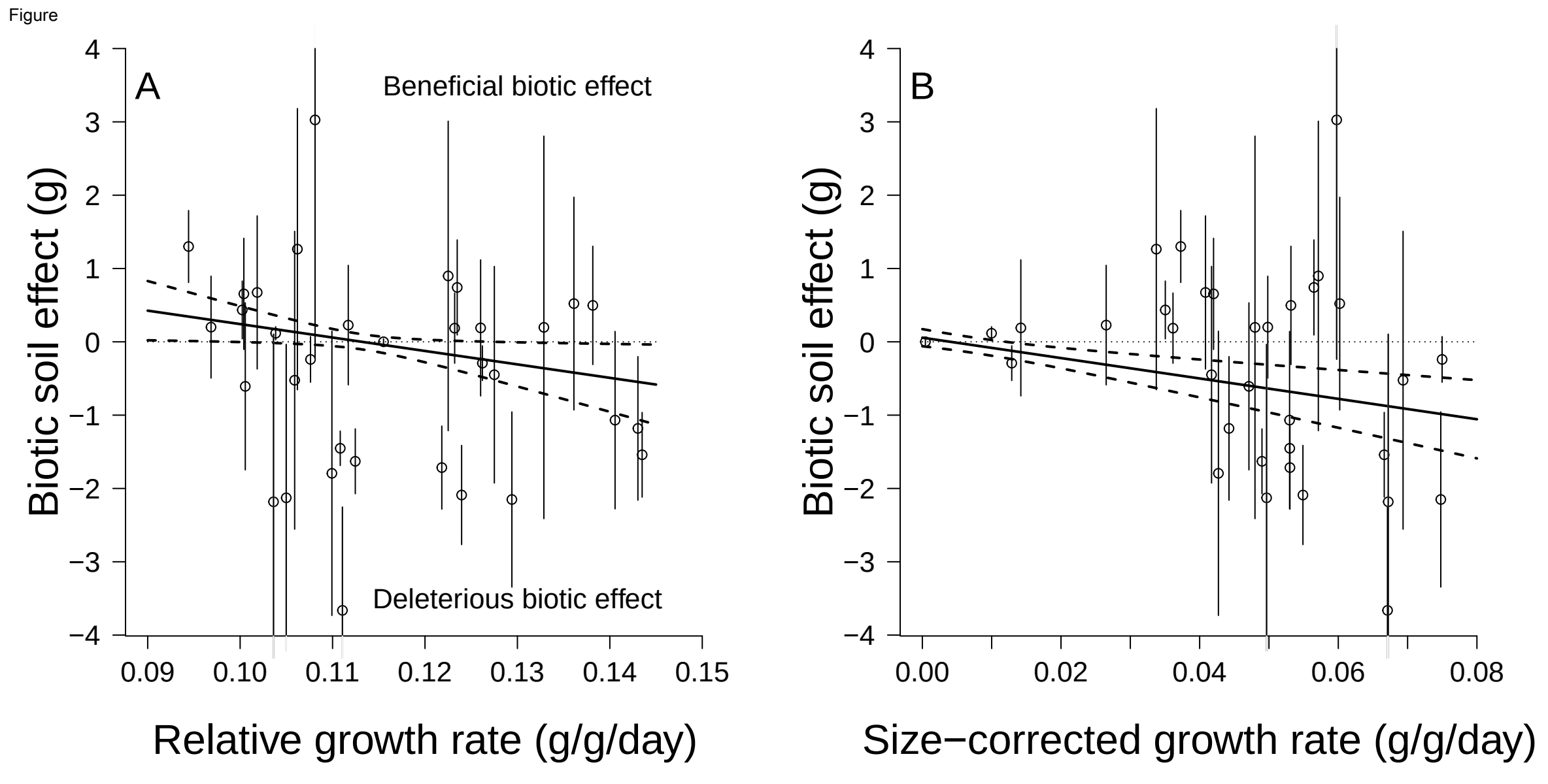
Table 1. Parameter estimates (± standard error) and AICs of intercept models, intercept and biomass covariate models, and linear models including relative growth rates (RGR) or size-corrected growth rates (SGR) that explain i) biotic soil effects; ii) conspecific soil effects, for 34 herbaceous plant species.

	Biotic soil effect		Conspecific soil effect	
	Estimates	AIC	Estimates	AIC
Intercept	-0.042 (0.04)	129.21	-0.275 (0.089)	73.43
Intercept	-0.701 (0.219)	122.19	-0.458 (0.100)	69.75
Biomass (sum, g)	-0.546 (0.175)		-0.216 (0.089)	
Intercept	2.117 (0.992)	119.65	-0.868 (0.734)	70.68
Biomass (sum, g)	-0.139 (0.041)		-0.056 (0.024)	
RGR	-18.388 (8.738)		6.484 (6.517)	
Intercept	0.057 (0.060)	118.56	-0.253 (0.152)	75.40
SGR	-13.907 (3.661)		-0.466 (2.805)	

Table 2. Spearman's rho correlation coefficients and p-values (in parentheses) testing the correlations between relative growth rate (RGR) and size-corrected growth rate (SGR), and root C:N ratio and specific root length (SRL). Correlations were done using raw root traits and growth rates per species, and also using phylogenetically independent contrasts. The number of species (n) considered in each correlation is also shown.

		n	RGR	SGR
Root C:N	Raw	31	0.360 (0.047)	0.301 (0.099)
	Contrasts	31	0.284 (0.129)	0.223 (0.235)
SRL (cm g^{-1})	Raw	33	0.382 (0.029)	-0.195 (0.276)
	Contrasts	33	0.499 (0.004)	-0.308 (0.087)

Figure


A
Beneficial biotic effect
Deleterious biotic effect
Biotic soil effect (g)
Relative growth rate (g/g/day)
B
Biotic soil effect (g)
Size−corrected growth rate (g/g/day)