Soil history affects plant growth and competitive ability in herbaceous species

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Abstract: Belowground soil characteristics are recognised as possible key factors in affecting plant species coexistence and community organisation. In this study, soil heterogeneity was generated by the growth of different herbaceous plants under controlled conditions, and thus related to growth and competitive ability of three naturally co-occurring species (Holcus lanatus, Inula viscosa and Pulicaria dysenterica). Soil changes induced by all species caused significant specific effects on the performance of these species and on their competitive hierarchies. Holcus lanatus was the strongest competitor on disturbed soil, but showed a dramatic negative feedback in monoculture. The experimental results are relevant for understanding community ecology and suggest that the investigation of species coexistence should take into account the possible role of plant-soil feedback processes.

Abbreviation: RCI – Relative Competition Index.

Introduction

Small-scale heterogeneity of belowground environment bears importance for community ecology because it can affect the performance of individual organisms and thus the species coexistence at the community level. Differences of plant responses to both spatial and temporal environmental heterogeneity have been reported in relation to nutrient distribution (Drew 1975, Crick and Grime 1987, Robinson 1994) and water availability (Novopansky and Goldberg 2001). Plants can induce belowground heterogeneity through several mechanisms: excretion of organic compounds from roots (Neumann and Martinia 2002), release of chemical compounds during organic matter decomposition (Rice 1984, Armstrong and Armstrong 2001), effects on soil microbial organisms and pathogens (Van der Putten et al. 1993, Bever 1994, Kliromos 2002), depletion of soil nutrients (Tilman 1988, Wedin and Tilman 1993) and water availability (James et al. 2003), changes of soil properties (Jackson and Caldwell 1993) which affect root penetration capability (Poot and Lambers 2003).

A specific case of plant-induced soil heterogeneity is the so called plant-soil "negative feedback" (Bever 1994), i.e., a relative negative condition for the establishment, growth and reproduction of individuals under their parent plants. Since ancient time this has been a well-known phenomenon in agriculture, often reported as 'soil sickness' (Singh et al. 1999). This negative feedback has been seldom considered in natural ecosystems (Van der Putten et al. 1988, Zucconi 1994) despite some early demonstrations of its existence (Florence 1965, McNaughton 1968). More recently, this type of plant-soil interaction has received greater scientific attention in relation to succession (Van der Putten et al. 1993, Packer and Clay 2000), coexistence (Bever 1994), and invasion processes (Kliromos 2002) in tropical and temperate forests (Stengel et al. 1989, Wills et al. 1997), coastal dunes (Van der Putten et al. 1993, Little and Maun 1996), old fields and grassland (Bever 1994, Holah and Alexander 1999, Blomqvist et al. 2000, Olff et al. 2000). Moreover, species coexistence and plant community structure can be affected both by the direct effect of soil feedback on species growth and the indirect effect on competition between species (Bever et al. 1997, Bever 2003, Van der Putten and Peters 1997). Examples of the consequences of soil heterogeneity generated by plants on species coexistence, succession and community structure have been reported for trees (Belsky 1994) and shrubs (Chapin et al. 1994, Vinton and Burke...
1995), but only in few cases for herbaceous plants with short life-span (Van der Putten et al. 1993).

This paper reports on an experimental study aimed to assess the induction of soil heterogeneity by plants and the related impacts on species interaction. The work was not aimed to unravel the mechanisms behind the build-up of plant-soil feedback conditions in the soil, but rather to understand how this process can affect the competitive ability of co-occurring species.

Two questions have been addressed by this work:

- Does plant growth build up a soil-related negative feedback in natural grasslands?
- Does different soil history affect species competitive ability and change the community competitive hierarchies?

**Methods**

Two perennial forbs (*Inula viscosa* (L.) Ait. and *Pulicaria dysenterica* (L.) Bernh.) and one grass (*Holcus lanatus* L.) were chosen for this study. The experimental plant and soil material was collected from a grazed grassland growing on alluvial soils along the Metauro River (Eastern Central Italy 43°51'46" - 13°00'22") where the three chosen species naturally coexist and are co-dominant with *Scirpus holoschoenus* L., *Festuca arundinacea* Schreb. and *Menha aquatica* L.

During winter (February 2000), after removal of surface undecomposed litter, about 100 kg of soil was sampled within the first 20 cm depth. The following day the soil was sieved in laboratory (mesh size < 2 mm). Large roots and rhizomes were chopped to reduce their size to 1 cm length and then reintroduced into the soil. Pots (12 cm diameter, 15 cm deep) were filled with 250 g of a mixture of dry soil and river sand (75/25).

Four different soil treatments were settled by growing the three species as monocultures and using the bare soil as control. Seeds of all species were collected in the field and sowed in the pots (30 seeds/pot during spring 2000). After 7 and 21 days, germinated seedlings were thinned at a density of 15 plants/pot. Plants were daily watered with distilled water at field capacity without addition of nutrient solution at any time. Control pots were watered at field capacity as in the other treatments. Pots were weeded weekly to avoid the emergence of seedlings of other species from the soil seedbank. Irrigation was maintained for 90 days and then stopped to dry the soil until plant death which occurred within 15 days. Dry above-ground biomass was removed by cutting at the soil surface without any soil disturbance.

The same pots, with the soil containing the residual dead roots of the different species from the previous growth period, were used to establish the growth and competition experiments. The four soil "histories" (Kliromnos 2002) were named Control, *Holcus, Inula* and *Pulicaria* according to the species grown in the pots in the first experimental period as described above (Fig. 1). The following treatments were established in the second experimental phase in all soil types (soil histories): (a) isolated individual plants (b) three plants/pot of the same species and (c) three plants/pot of different species (Fig. 1).

The experiment was organised according to a completely randomised factorial design with seven species combinations, four soil histories and 10 replicates for a total of 280 pots (4 × 7 × 10). The pots were rearranged at random every three days to avoid effects of eventual environmental heterogeneity. Seedlings were obtained from germinated seeds in 9-cm petri dishes with wet filter paper in growth chamber at 25°C. Forty-eight hours old seedlings were transplanted into 1 cm deep holes in the pot soils. Isolated plants were placed in the pot centre, while in the three plants/pot treatments they were located according to a triangular design. Withered seedlings were replaced within the first 48 hours. Plants were irrigated daily with distilled water without any nutritive solution for 60 days. All the experiments were conducted in a growth chamber with temperature of 22-24°C for 18 hours and 16-18°C for 6 hours during day and night, respectively. Light intensity during day cycle was maintained at 220 μmoles m⁻² s⁻¹ PAR at plant level.

Before the start of the growth and competition experiment, 5 g of soil was taken from 25 pots selected at random for each soil history and grouped into 5 pooled samples for colorimeteric measures of NO₃⁻ and NH₄⁺ extractable with KCl 1 N (Wedin and Tilman 1993). Measurements were made by spectrophotometer (NANO-COLOR 400D).

At the end of the experiments, after 60 growing days, above and below ground dry biomass of all plants was measured after desiccation at 80°C for 72 hours. Separation of roots of different individual plants and their cleaning from soil were obtained by careful washing with tap water.

Intraspecific and interspecific interactions were assessed by the relative competition index (RCI index, Grace 1995). This index standardises competition intensity thus allowing the comparison of species with different growth rates in absence of interaction:


\[ RCI = \frac{(B_w - B_{wa} \text{ or } B_{wi})}{B_w} \]

where \( B_w \) is the biomass of individual plants in isolated growth, \( B_{wa} \) is the average biomass of the three plants growing in the same pot in intraspecific interaction and \( B_{wi} \) is the biomass of single plants in the mixture treatments with interspecific interaction. RCI may vary between +1 and -\( \infty \); with positive and negative values reflecting competitive and facilitative interactions, respectively. Zero RCI indicates null interaction effect.

Statistical analysis was done by one-way ANOVA. Values were log-transformed when required for normalization.

**Results**

In absence of interactions plant growth of all species was significantly affected by the soil history (ANOVA Holcus \( F=12.4 \) p<0.01; Pulicaria \( F=3.16 \) p<0.01; Inula \( F=10.2 \) p<0.01) (Fig. 2). The growth of Inula and Pulicaria was higher in control substrate condition. Holcus growth was highest in control, intermediate on Inula and Pulicaria soils and reduced in monoculture.

**Figure 1.** Schematic representation of experimental design. In the growth experiment, seven different assemblages of individual plant (no species interaction, intraspecific and interspecific interaction) were planted on four different soil “histories”. 

- **Control**
- **Holcus**
- **Inula**
- **Pulicaria**

**SOIL "HISTORY" GENERATION**

**Growth experiment (60 days)**

**PLANT AND SOIL INTERACTION (PSI)**

**INTRASPECIFIC COMPETITION + PSI**

**INTERSPECIFIC COMPETITION + PSI**
Competitive species interaction was observed in all the species combinations and soil histories (Fig. 3). Intraspecific competition intensity was significantly affected by soil history only for *Inula* (*F* = 6.83 *p* < 0.01; *Holcus* *F* = 2.14 *p* = 0.09; *Pulicaria* *F* = 2.71 *p* = 0.07). On the other hand, the intensity of interspecific competition was significantly affected by soil history for *Holcus* (*F* = 8.01 *p* < 0.01) and *Pulicaria* (*F* = 2.69 *p* < 0.05), but not for *Inula* (*F* = 1.07 *p* = 0.17). Intraspecific competition of *Inula* was higher in all the soil history compared to control soil. For *Holcus*, interspecific competition was higher in monoculture (*Holcus* soil history) and reduced in *Inula, Pulicaria* and control substrates. For *Pulicaria*, interspecific competition was higher in all soil types compared to *Holcus* soil history.

The intensity of competition was higher in intraspecific than in interspecific interaction in *Inula* (RCI = 0.55 and 0.34, respectively), *t*-test with *p* < 0.01. In contrast, *Pulicaria* and *Holcus* showed a reversed effect with lower intraspecific than interspecific competition (corresponding values of RCI = 0.54 vs. 0.7, *t*-test with *p* < 0.05; 0.52

**Figure 2.** Plant growth of three herbaceous species according to four soil histories without interspecific and intraspecific interactions. Isolated plants were grown for 60 days on soil which, before the experiment, was either maintained bare (control) or used to grow plants of the same three different species for 90 days. Different letters indicate significant differences (Newman-Keuls test *P* < 0.05), bars indicate SE (*n* = 10).

**Figure 3.** Intraspecific (left) and interspecific (right) interaction intensity (RCI, see text for details) according to four different soil histories for three herbaceous species. Different letters indicate significant differences (Newman-Keuls test *P* < 0.05), bars indicate SE (*n* = 10). Losses of some pots in a *Pulicaria* treatment (*) did not allow statistical analysis.
Soil history, plant growth and competitive ability

Figure 4. Effect of soil history on soil nitrate concentration immediately before the growth experiment. Different letters indicate significant differences (Newman-Keuls test P<0.01), bars indicate SE (n=5).

vs. 0.64, t test with p<0.05 for the former and latter species, respectively.

Soil history did not affect the soil ammonium concentration (ANOVA F=1.73 p=0.18 data not shown) while nitrate concentration was significantly higher in control compared to all other soil histories (ANOVA F=92.7 p<0.01; Fig. 4).

Discussion

Although the paper reports on short-term experiments carried out in small pots, whose extrapolation to field conditions might be difficult, the results showed that the induction of soil heterogeneity by plants does affect the growth and competitive ability of plant species in species-specific way.

Isolated plants of all species showed reduced growth on “used” soils compared to control conditions. The most affected species was *Holcus lanatus* which showed the lowest growth and competitive ability when grown on its own substrate, which is an evidence of negative plant-soil feedback. The better performance of all plants on control soil could likely be related to nitrate availability, which was significantly affected by plant growth during the soil history pre-treatments (Fig. 4). The high nitrate levels in control soils were probably created by the organic matter mineralization and the absence of uptake by plants. This result supports the hypothesis that a positive growth response in soil disturbance and vegetation removal experiments (Connell 1983, Diaz et al. 2003) might not be only the effect of competition release, but also dependent on mineral nutrient flushes due to organic matter decompo-

sition processes. The effects of different soil histories on plant growth are difficult to generalise because they seemed strictly species-specific and not imputable to nitrogen availability. The only general trend was the better plant performance for all species on control soils in absence of competition.

All the observed intraspecific and interspecific interactions were competitive (Fig. 3) and this effect was dependent only on root interaction, since no significant shading was present. Soil histories affected competition intensity for *Imula viscosa* more in interspecific than in intraspecific interactions. This species was the only one which showed a reduction of intraspecific competition intensity on control compared to other soil histories. Interspecific competition effects were very strong in *Holcus lanatus*. This species showed low suppression levels on control soil (RCI=0.25), but major growth reduction in monoculture (RCI=0.82) and on *Imula* and *Pulicaria* soil histories (RCI=0.84 and 0.79, respectively). These results clearly indicate that *Holcus* has better performance on nutrient rich soils, but it can be strongly suppressed by interspecific competition on different soil histories and in continuous monoculture. This observed negative plant-soil feedback on growth and competitive ability could explain why *Holcus lanatus* populations decline in absence of frequent disturbance, while this species has been reported as a good competitor in rich mineral soils of disturbed environments (Buckland et al. 2001). Also, *Pulicaria* showed differences of interspecific competition intensity, with a minor effect on *Holcus* soils (RCI=0.47), but strong suppression on other soil types. Surprisingly, *Pulicaria* evidenced a heavy growth reduction in competition treatments on control soils (RCI=0.87) despite the fact that the same soils produced the best performance of isolated plants of the same species. This is interesting because it shows that the net effect of soil history on plants is the combined output of species affinity to the soil substrate with the intensity of interspecific competition. In other words, the competitive outcome of interspecific interactions can be affected by both the direct and indirect species interactions (Miller 1994, Levine 2000) and by the soil history of different soil patches.

In conclusion, in this study soil heterogeneity generated by plants affects plants growth and competitive ability of species in special manner. These results indicate that soil history could change the competitive hierarchies in this plant community at a scale of local patches, i.e., of individual plants. Consequently, soil heterogeneity induced by plants seems to be one of the mechanisms involved in the high spatio-temporal turnover of herbaceous communities (Van der Maarel 1996), and this subject cer-
tainly deserves further experimental tests in different plant communities.

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