

Convergence patterns and multiple species interactions in a designed plant mixture of five species

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Received: 20 March 2006 / Accepted: 12 October 2006 / Published online: 16 January 2007
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Abstract It is known that convergence and divergence can occur in complex plant communities, but the relative importance of biotic and abiotic factors driving these processes is less clear. We addressed this issue in an experiment using a range of mixed stands of five species that are common in Swiss fens (*Carex elata*, *C. flava*, *Lycopus europaeus*, *Lysimachia vulgaris* and *Mentha aquatica*) and two levels of water and nutrients. One hundred and seventy-six experimental mixtures were maintained in large pots (75 l) for two consecutive growing seasons in an experimental garden. The stands varied systematically in the initial relative abundance of each of the five species and in overall initial stand abundance. The changes in biomass over 2 years were modelled as linear functions of treatments and the initial biomass of each species. The dynamics of the system were mainly driven by differences in the identity of species and by a negative feedback mechanism but also by different abiotic conditions. In all mixtures, *C. elata* became more dominant over time,

which caused an overall convergence of community composition. In addition, the rate of change of each species' biomass was negatively related to its own initial abundance. Thus, a negative feedback further contributed to the convergence of communities. Species responded differently to water level and nutrient supply, causing community dynamics to differ among treatments. However, the different abiotic conditions only slightly modified the overall convergence pattern. Competitive interactions between more than two species were weaker than the negative feedback but still significantly influenced the species' final relative abundance. The negative feedback suggests that there is niche partitioning between the species, which permits their coexistence.

Keywords Community change · Competition · Facilitation · Simplex design · Water nutrients

Introduction

Understanding the dynamic nature of complex plant communities is still a major challenge in ecology. Several literature surveys point to competition (Silvertown and Dale 1991; Goldberg and Barton 1992; Goldberg 1996) and site conditions (Callaway and Walker 1997; Aerts 1999; Fransen et al. 2001) as important factors influencing plant community change. The dynamics of assemblages with the same initial proportional composition may develop along different trajectories depending on abiotic conditions (Inouye and Tilman 1995; Fahey et al. 1998) or the identity of species initially present (Davis et al. 1987; Bakker and Wilson 2001). It is not clear, however, to what extent

Communicated by Bernhard Schmid.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-006-0594-x) contains supplementary material, which is available to authorized users.

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the initial proportions of species also influence community development.

Generally, two contrasting types of community development are possible, beginning from communities with different abundance of species. Convergence (Leps and Rejmanek 1991) occurs when contrasting communities become more similar over time, whereas divergence means that communities become more dissimilar with time. Convergence implies some form of negative feedback between the dominance of species and their performance. The niche theory (MacArthur and Levins 1967) suggests that stronger intraspecific than interspecific suppression can lead to convergence. Instead of competitive exclusion, the coexistence of different species is favoured, and we would expect communities to converge if such competitive interactions are of central importance. In comparison, divergence can result when positive feedback mechanisms that are strongest when species abundance is greatest occur in several species; the final community outcome depends on which of the species was dominant initially. Positive feedback can be mediated by local plant alterations of light, wind, temperature, water, pH, etc. (Wilson and Agnew 1992). Examples of both types of developments, convergence and divergence, have been observed repeatedly in natural plant communities (Nilsson and Wilson 1991; Inouye and Tilman 1995; Lichter 1998; Mann and Plug 1999). Overyielding detected in competition experiments has often been attributed to intraspecific competition being stronger than interspecific competition (Hill and Gleeson 1990; Piper 1998; Fridley 2003). Applied to plant community development, this suggests that these communities may converge.

A general convergence pattern can be modified by abiotic conditions. The degree of overyielding has been found to depend on resource supply (Inouye and Tilman 1988; Fridley 2002), suggesting that resource supply influences convergence. Recently, Liancourt et al. (2005) demonstrated that the competitive response of a species is modified by a changed water regime, leading to competitive exclusion of the less water stressed species under higher water availability. Such a mechanism is likely to influence the species' relative abundance in a community and thus produce a convergence pattern.

Most experimental studies to investigate the role of species effects in mixtures involve only two or three species (Goldberg and Barton 1992; Gibson et al. 1999), and much theoretical work has been done on the analysis and interpretation of such data (Freckleton and Watkinson 2000; Connolly et al. 2001; Inouye 2001). However, these experiments deal mostly with

pairwise comparisons, whereas in more complex mixtures, interactions affecting community composition may involve several neighbours (Ramseier et al. 2005). In examining species interactions and processes such as convergence/divergence, there is a need for multispecies experiments that will demonstrate the extent to which more complex interactions than pairwise affect community dynamics. The presence of a species being a strong competitor often negatively affects the performance (growth, seed production) of a target species; however, another strong competitor may further influence the competitive relationship between any other species. In the context of multiple species interactions, we distinguish between a species' competitive effect on the relationship between itself and another species, here defined as a *type A* influence. In comparison, a species effect on the relationship between two other species is defined as a *type B* influence.

The simplex design (Cornell 2002) enables us to quantify effects of many components on a target variable. It has been used by Ramseier et al. (2005) as the basis of an experimental design for five annual species in a short-term experiment. In the present study, we applied the simplex design and the modelling approach developed by Connolly and Wayne (2005) to address questions of convergence/divergence in multispecies communities of perennials. Mixtures composed of five wetland species were grown for 2 consecutive years under four environmental regimes produced by combining two levels of water availability and two nutrient levels. We will demonstrate to what extent the observed shifts in community composition can be explained by (a) species identity, (b) feedback in plant growth related to interaction between species and (c) abiotic conditions (water and nutrient levels). We hypothesise that competitive interaction between species can lead to convergence of different communities and that the modification of species performance by abiotic conditions will lead to a changed convergence pattern. We further hypothesise that multiple interactions between species can cause changes in final species proportions and that these multiple interactions are influenced by abiotic conditions.

Materials and methods

Plant material

Plant mixtures were established with five perennial species that are common in Swiss fens: *Carex elata* All. (tufted sedge), *C. flava* L. (yellow sedge), *Lycopus europaeus* L. s. str. (gypsywort), *Lysimachia vulgaris* L.

(yellow loosestrife) and *Mentha aquatica* L. (water mint) (Table S1, supplementary material). All plant material originated from the northern part of Switzerland.

Experimental design

Twenty-two mixtures were established in accordance with the simplex design (Cornell 2002) (Fig. 1), with all five species present in each mixture. Mixtures were equal stands (20% of each species), dominant stands (60% of one species, 10% of the four others) or codominant stands (35% of each of two species, 10% of the three others, Table 1). Equal and dominant stands were planted in two overall densities of 50 (high density) and 20 (low density) seedlings per pot; codominant stands were planted in an overall density of 20 seedlings per pot. Each mixture was established at two water and two nutrient levels and replicated twice. In total, 4,960 seedlings were transplanted into 176 pots, which were randomly distributed within two blocks.

Establishing the experiment

Based on results from earlier experiments, the species were sown at two different times so as to have seedlings of approximately the same size at the time of

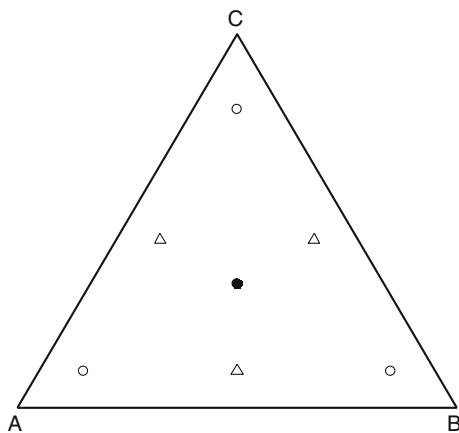


Fig. 1 Illustration of the simplex design for three species: A, B and C. The *triangle* represents schematically all possible mixtures of the three species. Each *vertex* represents 100% of a species; for example, *vertex A* is a monoculture of species A. *Interior points* represent three-species mixtures. The proportion of each species in the mixture is given by the distance of the point to each of the three sides. For example, the perpendicular distance of a point to the *A–B line* indicates the proportion of species C in the mixture. The design illustrated here consists of one equal stand (33-33-33% mixture, *black dot*), three stands with a dominant species (80-10-10% mixtures, *open dots*), and three stands with two codominant species (45-45-10% mixtures, *triangles*). The principles of the simplex design have been extended to five species in this study (see Table 1)

transplantation (Table S1). Sowing trays (soil: 70% peat, 25% compost, 5% quartz sand) were placed in a transparent, unheated, plastic tunnel. When seedlings were 1.5- to 2-cm tall, they were transplanted to new trays with a spacing of 5 cm. In total, twice as many seedlings were grown than were required. The seedlings were planted on 7 and 8 May 2001 in plastic pots with 75 l volume (50-cm diameter, 45-cm tall). The pots were filled with quartz sand (1- to 1.7-mm grain diameter) and were placed on concrete slabs at an experimental site of the Swiss Federal Institute of Technology (520-m asl, Hoenggerberg, Zurich, Switzerland). Before transplanting, the soil was carefully washed from the seedlings' roots. Within each pot, individuals were placed in a hexagonal array, with a spacing of either 6 cm (high density) or 10 cm (low density). The spatial arrangement of species in the pots was determined by a restricted randomisation to ensure that an equal number of seedlings per species were neighbouring seedlings of all other species and the border as far as possible. Individuals that died in the first 3 weeks of the experiment were replaced.

Two water levels were established. Initially, all pots were maintained with standing water at the sand surface (at a 42-cm height in the pot) to ensure seedling establishment. After 7 weeks, six holes were drilled along the sides of the pots 21 cm from the bottom, resulting in a dry zone above (low water treatment). By contrast, the high water treatment was created by leaving standing water at the sand surface. During the growing season, this level was adjusted every second day with tap water, unless there had been sufficient rain.

Two nutrient levels were used with three times the amount of all nutrients in the high level compared with the low level. In the first year, 2 gm⁻² nitrogen (N) and 0.5 gm⁻² phosphorus (P) were applied for the low, and 6 gm⁻² N and 1.5 gm⁻² P for the high nutrient condition. To account for the higher plant biomass in the second year, N and P application was increased by a factor of 1.5. A common complete fertiliser was applied (including C–NH₂, NH₄, NO₃, P₂O₅, K₂O, B, Cu, Fe, Mn, Mo, Zn; Wuxal, Maag, Switzerland), and the N/P ratio (N/P = 4) was adjusted with KNO₃. Nutrients were supplied weekly from May to October in 2001 and every second week from March to August in 2002.

Maintenance and measurements

Plants were checked weekly for pest infestation. Due to an aphid attack, mainly on *L. vulgaris*, an insecticide (Pirimicarb, Maag, Switzerland) was sprayed on 5 and 20 May 2001 and on 21 May and 5 June 2002.

Table 1 Number of planted individuals per pot for the experimental plant mixtures following the simplex design. Every mixture was established in two water and nutrient levels and replicated twice

	<i>Carex elata</i>	<i>Carex flava</i>	<i>Lycopus europaeus</i>	<i>Lysimachia vulgaris</i>	<i>Mentha aquatica</i>	Total
High density						
Equal stand	10	10	10	10	10	50
Dominant stands	30	5	5	5	5	50
	5	30	5	5	5	50
	5	5	30	5	5	50
	5	5	5	30	5	50
	5	5	5	5	30	50
Low density						
Equal stand	4	4	4	4	4	20
Dominant stands	12	2	2	2	2	20
	2	12	2	2	2	20
	2	2	12	2	2	20
	2	2	2	12	2	20
	2	2	2	2	12	20
Codominant stands	7	7	2	2	2	20
	7	2	7	2	2	20
	7	2	2	7	2	20
	7	2	2	2	7	20
	2	7	7	2	2	20
	2	7	2	7	2	20
	2	7	2	2	7	20
	2	2	7	7	2	20
	2	2	7	2	7	20
	2	2	2	7	7	20

L. europaeus and *M. aquatica* stolons that grew beyond the pot were cut fortnightly; this biomass was added to the yield of the two autumn harvests. Extraneous plants that germinated from seeds in the second year were removed entirely.

Initial shoot biomass was estimated by drying and weighing 20 seedlings per species, which were randomly selected from among those remaining after planting. From 9 to 12 October 2001, living biomass per species was cut 4 cm above the sand surface to obtain an estimate of biomass production in the first year. The cutting was not made at the sand surface because the disturbance would have been too large. Finally, after two growing seasons, all plants were harvested from 19 to 29 August 2002 by cutting all above-ground living biomass. All samples were dried (75°C) to constant weight, and dry mass per species and pot was determined.

Data analysis

Initial summary analyses were performed. The net relative growth rate between planting and harvesting (RGR, defined as in Connolly and Wayne 1996) was analysed separately for each species using multiple regression. We applied the following notation to define mixtures with s species. For the i th species, it is

w_i : the initial biomass per individual, that is, the mean biomass of the selected seedlings after planting (Table S1)
 d_i : the number of planted individuals per pot (Table 1)

y_i : the initial biomass per mixture at the start of the experiment, where $y_i = d_i w_i$

Y_i : the final biomass per mixture at the end of the experimental period. Y is the total biomass of the mixture = $\sum_i Y_i$

x_i : the species biomass proportion in the mixture at the end = $\frac{Y_i}{Y}$

For the i th species (*with* $i = 1, \dots, s$), the model for RGR_i was

$$\text{RGR}_i = \alpha_i^* + \sum_{j=1}^s \beta_{ij}^* y_j + \gamma_i^* \text{Water} + \delta_i^* \text{Nutrient} + \varepsilon_i^* \quad (1)$$

β_{ij}^* is a measure of intraspecific competition if $i = j$, and of interspecific competition if $i \neq j$. The coefficients γ_i^* and δ_i^* measure the effects of changing water and nutrient levels, respectively, from low to high (for further details see supplementary material).

Because in this paper we are focusing on the influences of species and abiotic conditions on community shift, we analysed the change of species proportions. Species proportions in a mixture change when their RGRs differ. Therefore, the RGR difference (RGRD) method was applied (Connolly and Wayne 2005), which models the relationships between the difference in RGRs (each species compared with one of the species chosen as reference) and the initial biomass of species and the abiotic variables, as

$$Z_i = \text{RGR}_i - \text{RGR}_s = \alpha_i + \sum_{j=1}^s \beta_{ij}y_j + \gamma_i \text{Water} + \delta_i \text{Nutrient} + \varepsilon_i \tag{2}$$

for $i = 1, \dots, s-1$, with s as the reference species, in this case *C. elata*. The regression coefficients of the RGRD models are related in a simple way to those of the RGRs: $\alpha_i = \alpha_i^* - \alpha_s^*$; $\beta_{ij} = \beta_{ij}^* - \beta_{sj}^*$ with a similar relationship for the abiotic and error terms (Ramseier et al. 2005). A positive value of β_{ij} (called an influence coefficient in Ramseier et al. 2005) indicates that an increase in y_j , the initial biomass of the j th species, leads to an increase in the final proportion of the i th species relative to that of the reference species s . The converse is true for a negative coefficient. Applying the above-mentioned definition for multiple species interactions to the RGRD models, a *type A* influence is the effect of a species on the RGRD between itself and another species. By contrast, a *type B* influence is the effect of a species on the RGRD between two other species.

Although four RGRD regressions are sufficient to describe the relationships among species in our case ($i = 1, \dots, s-1$) (Ramseier et al. 2005), ten pairwise comparisons are possible between five species. For convenience, all ten RGRD regressions were calculated. The values of initial biomass were centred for the RGRD (and RGR) models. Thus, the intercept is interpreted as the mean RGRD (RGR) at mean initial species' biomass under low water with low nutrient conditions. Zero values of one species' final biomass (*M. aquatica*) were replaced by an estimated value following the recommendation of Stahel (2002, p. 30). The inclusion of quadratic species terms and the two-way interactions was determined by the BIC criterion (Schwarz 1978) (for details on the model selection, see supplementary material).

The shift of a species' proportion was displayed by plotting the fitted, final proportion at mean density in relation to the initial species proportion. Fitted proportions (\hat{x}) were calculated using a generalisation of the method in Connolly and Wayne (2005). Approximate standard errors of difference between fitted proportions were calculated using a Taylor series approximation method. The range of values for which differences between the starting and the fitted proportions were significant was computed using the Johnson Neyman technique (Johnson and Neyman 1936).

Convergence patterns and their visualisation

Convergence or divergence of mixtures was evaluated with a new measure, the convergence index (CI), which

is based on percent similarity (PS) (Inouye and Tilman 1995). We define the CI as

$$\text{CI} = \frac{\left\{ \frac{1}{n} \sum_{j < k} \text{PS}_{jk} \right\}_{\text{End}}}{\left\{ \frac{1}{n} \sum_{j < k} \text{PS}_{jk} \right\}_{\text{Start}}} \tag{3}$$

with n = number of mixture pairs and $\text{PS}_{jk} = \sum_i \min(x_{ij}, x_{ik})$, where x_{ij} and x_{ik} are the observed proportion of species i in mixture j and k , respectively, and $\min(x_{ij}, x_{ik})$ is the smaller of x_{ij} and x_{ik} . CI values greater than 1 indicate convergence; values smaller than 1 indicate divergence. The CI was calculated with all the possible pairs of the 44 mixtures per abiotic condition. Bootstrapping was applied to estimate the 95% confidence interval of the CI (Davison and Hinkley 1999).

The convergence pattern was displayed by plotting predicted species proportions at mean density to the triangular plots (Fig. 1). Thus, one triangle reveals the changes of a three-species mixture. If three more triangles are added to Fig. 1, the resulting four triangles illustrate an unfolded tetrahedron. Folding the corners of such a figure together results in the tetrahedron with a fourth species at the top. By calculating the predicted proportions for each of the triangles, the change of four species in a mixture are simultaneously illustrated. Because the component proportions for every triangle have to add up to 1, the predicted proportions of the three species in each triangle were transformed with $\hat{x}_i^* = \frac{\hat{x}_i}{\hat{x}_1 + \hat{x}_2 + \hat{x}_3}$ (for $i = 1, \dots, 3$), and the \hat{x}_i^* were plotted. All analyses were performed using the statistical software R (R Development Core Team 2005).

Results

Biomass production and effects on RGR

The total biomass per pot (mean of all conditions) was six times greater in the second than in the first year (Fig. S1, supplementary material). Total biomass per pot was slightly increased by the higher-water level, whereas it was raised threefold by the higher nutrient level in both years. After 2 years, *C. elata* had by far the largest biomass production, being three times that of the second strongest species, *L. europaeus*.

The mean RGR across all growth conditions at final harvest was largest for *C. elata* (fitted RGR = 4.75), followed by *L. europaeus* (4.28), *L. vulgaris* (3.93), *C. flava* (2.70) and *M. aquatica* (0.290). Intraspecific competition, i.e. the effect of a species' initial biomass on its own RGR, was stronger than interspecific effects

in all but two cases (the effect of *C. elata* on RGR_{Le} and RGR_{Lv} was stronger than on RGR_{Ce} , Table S2, supplementary material). Generally, higher nutrient application had a stronger effect on RGR than did higher-water level, except for the RGR of *M. aquatica*, which depended mostly on the water level (Table S2). Higher water level interacted considerably with nutrients and species competition. For example, the negative effects of *C. elata* on the RGR_{Lv} and of *M. aquatica* on the RGR_{Ma} were less pronounced with higher water level (positive water \times species competition interactions).

Changes in species proportions and negative feedback

The fitted proportions of the five species, which were calculated based on the RGRD analysis (Eq. 2), correlated well with the observed proportions. The explained variance r^2 varied between 0.838 for *C. elata* and *L. europaeus* to 0.734 for *L. vulgaris* (Fig. S2, supplementary material). This suggests that the predicted values (Fig. 2, 3) calculated from the model allow reliable inference on species behaviour in the present model community.

The role of species identity and species influences on their own proportions

As mentioned above, the intercept indicates the RGRD at equal species proportions (= 0.2 with five species) and mean density and reflects differences in species identity. Following this approach, *C. elata* has been favoured over the remaining species just due to its identity, revealed by the significant, positive intercepts for the RGRDs between *C. elata* and the remaining species (Table 2). These positive values, in turn, were reflected by a significant increase in *C. elata*'s final proportion relative to its starting proportions (Fig. 2a). By contrast, *C. flava* and *M. aquatica* lost in relation to the remaining species due to their identity, indicated by their significant, negative intercepts (Table 2). As a consequence, the final proportions of *C. flava* and *M. aquatica* generally decreased (Fig. 2d, e). The proportions of *L. europaeus* and *L. vulgaris* did not change due to their identity. Though their intercepts were significant in three out of four cases (Table 2), they were both positive and negative, which did not result in a significant difference of their final proportion relative to the starting proportion of 0.2 (Fig. 2b, c).

Increased initial biomass of a species caused a relative decrease of its own final proportions, which

was indicated by the negative species coefficients on the RGRD between itself and all other species (*type A* influences, Table 2). This proportional decrease at high initial biomass resulted in a negative feedback for all species except *C. elata*, for which this effect was less pronounced (Fig. 2). For example, the proportions of *L. europaeus* remained constant or increased at low starting values but fell significantly under the starting proportion, when its initial biomass was raised (Fig. 2b, low water conditions). The negative feedback resulted from the generally stronger intra- than interspecific competition on the species' RGRs (Table S2).

Role of water and nutrients and interactions

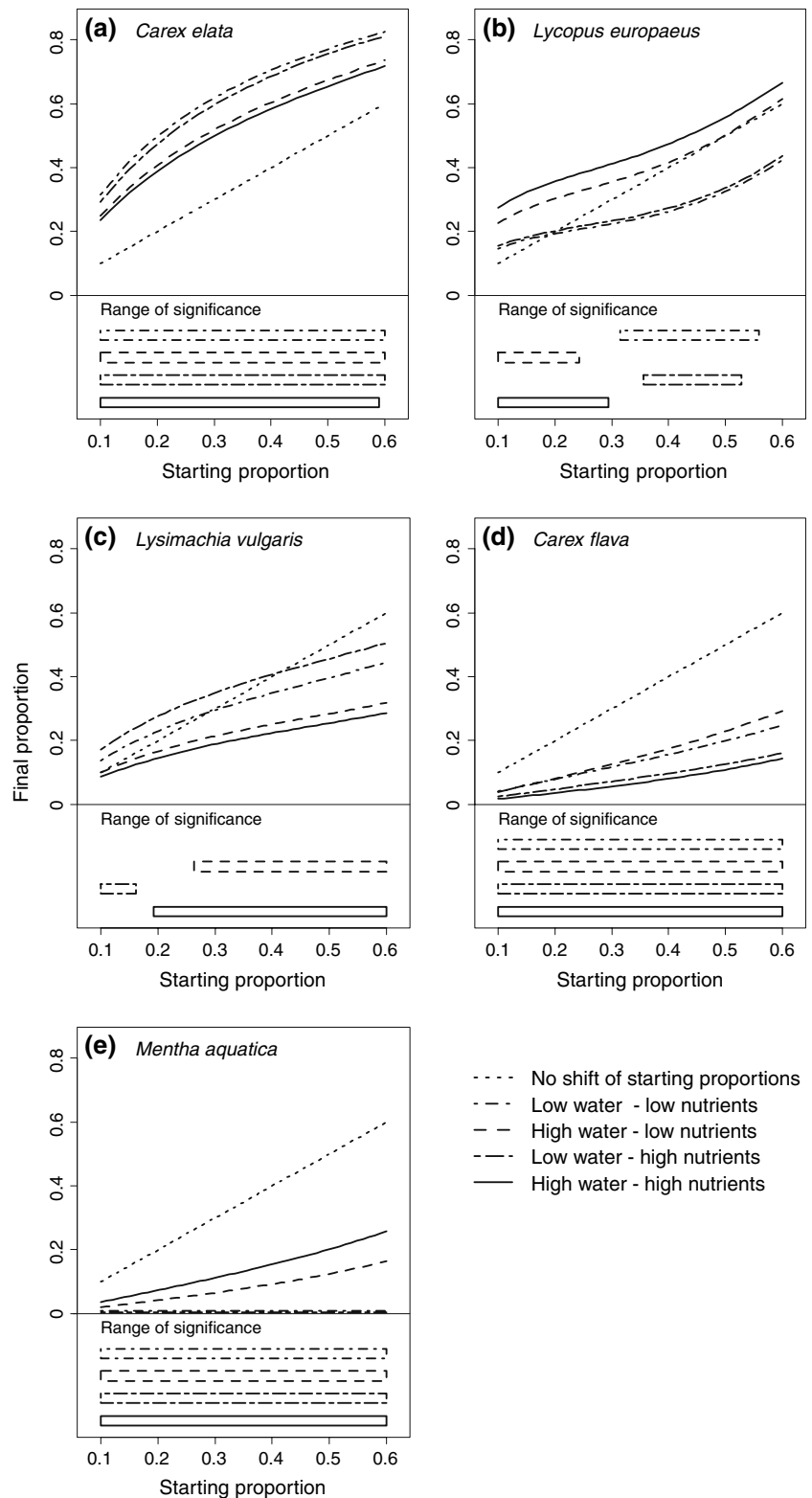
Generally, water affected the final species proportions more than did nutrients, which was revealed by comparing the range of absolute values of RGRD coefficients for water (0.120–4.427) and nutrients (0.095–0.977) (Table 3). This strong effect was mainly caused by the reaction of *M. aquatica* to the different water conditions. Higher water level significantly promoted both *L. europaeus* and *M. aquatica* over *C. elata* (Table 3a), which resulted in a general decrease in the final proportions of *C. elata* (Fig. 2a). Higher water level also reduced the final proportions of *L. vulgaris*, whereas an increase in the proportions of *L. europaeus* and *M. aquatica* was observed (Table 3a; Fig. 2). Higher nutrient application significantly favoured *L. europaeus* over *C. flava* and *M. aquatica* (Table 3b), thus increasing the final proportions of *L. europaeus* (Fig. 2b), whereas proportions of *C. flava* were always lower with the high nutrient treatment (Table 3b; Fig. 2d).

The species' reactions to the higher nutrient level also depended on the water level. For example, the high nutrient application promoted *L. vulgaris* over the remaining species at the low water level (Table 3b) and thus increased its final proportions, whereas the opposite result was obtained with the high water level (Table 3c: negative water \times nutrient interaction; Fig. 2c). These results show that species interactions were strongly altered by abiotic conditions, leading to changed final species proportions.

Influence of species biomass on two other species

There were various influences of one species on the relationship between two other species, revealed by the *type B* influences (= influence of initial species biomass on the RGRD between two other species). For example, higher initial biomass of *C. elata* favoured *L. europaeus*, *C. flava* and *M. aquatica* over *L. vulgaris*

Fig. 2 Effects of increasing initial proportions of a species on its own final proportions at different water–nutrient conditions in experimental plant mixtures after 2 years. The lines are fitted proportions (\hat{x}), which were calculated following Connolly and Wayne (2005). Horizontal bars indicate the range of values for which vertical differences between the no-shift line and the fitted proportions are significant ($P \leq 0.05$). Missing bars indicate no significance over the whole range



(Table 4). By contrast, both higher initial biomass of *C. elata* and *C. flava* promoted *M. aquatica* over the three remaining species under consideration. These multiple interactions were partly modified by changed water

conditions: With the higher water level, increasing initial biomass of *C. elata* mitigated the negative effects of the remaining three species over *L. vulgaris*. Furthermore, only with the higher water level did higher

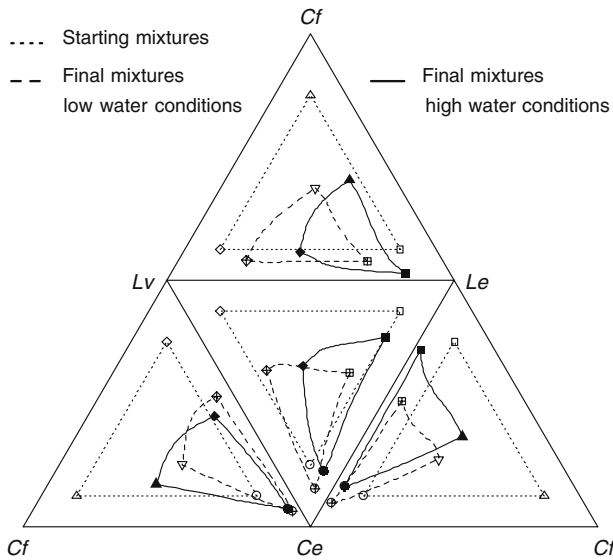


Fig. 3 Change of mixtures after 2 years. The *hatched and continuous lines* are predicted mixtures, the *same symbols* indicate the same stands, and the water effects shown are for low nutrient conditions. If no shift occurred, the final mixtures would lie on the *dotted line*. The *four triangles* illustrate an unfolded tetrahedron; folding the corners together results in the tetrahedron with *Carex flava* at the *top*. The species with the least biomass production was omitted (*Mentha aquatica*). *Ce*: *C. elata*, *Le*: *Lycopus europaeus*, *Lv*: *Lysimachia vulgaris*, *Cf*: *C. flava*

biomass of *L. europaeus* favour *C. elata*, *L. vulgaris* and *M. aquatica* over *C. flava* (Table 4, Water × species interactions).

Convergence patterns

The mixtures converged after 2 years: the CI was significantly greater than 1 under all four abiotic conditions (Table 5), indicating that mixtures with different proportions became more similar over time. The degree of convergence differed little between the four conditions. Only at high water with low nutrient level was the CI smaller. Figure 3 illustrates the convergence of mixtures at low nutrients. The resulting tetrahedron-like figure formed by the fitted lines (Fig. 3: hatched lines for low water conditions) was clearly smaller than the tetrahedron of the starting mixtures (dotted lines). All the mixtures shifted towards *C. elata*; that is, the final proportion of *C. elata* always increased. The shift was largest when the remaining species were initially present in high proportions. Changed abiotic conditions varied the convergence pattern. With the high water level, the mixtures also shifted towards *L. europaeus* (Fig. 3: continuous lines), and the degree of convergence was slightly less pronounced, in agreement with the CI (Table 5). This less pronounced

Table 2 Intercepts and regression coefficients for *type A* influences, that is, the influences of increased initial biomass of a species on the relative growth rate difference (RGRD) between itself and another species: the species in the column minus the species in the row [for example $RGRD_{Ce-Le} = RGR_{Ce} - RGR_{Le}$ for the cell in the second column and fourth row (bold)]

RGRD _{Col-row}	Intercept		Lycopas europaeus		Lycopas europaeus		Lycopas europaeus		Lycopas europaeus		Lycopas europaeus		Lycopas europaeus		Lycopas europaeus		Lycopas europaeus		
	Ce	Le	Le	Le	Le	Le	Le	Le	Le	Le	Le	Le	Le	Le	Le	Le	Le	Le	
<i>Ce</i>	-	-	-0.944***	-2.763***	2.932**	-0.775***	-1.408***	-1.840***	-0.271**	-6.583***	-1.219***	1.259**	-	-	-	-	-	-	-
<i>Le</i>	0.944***	-0.164	-	-	-	0.169	-1.043***	-0.896***	-0.411***	-5.638***	-1.560***	1.542***	-	-	-	-	-	-	-
<i>Lv</i>	0.775***	0.438*	-0.169	-2.716***	3.484**	-	-	-1.065***	-0.297*	-5.808***	-1.382***	1.511***	-	-	-	-	-	-	-
<i>Cf</i>	1.840***	-0.295	0.896***	-2.875***	3.372**	1.065***	-1.436***	-	-	-4.743***	-1.391***	1.629***	-	-	-	-	-	-	-
<i>Ma</i>	6.583***	-1.238***	5.638***	-1.448	2.700	5.808***	-1.092	4.743***	-0.858***	-	-	-	-	-	-	-	-	-	-

A positive coefficient indicates that the species in the column will be favoured over the species in the row. The coefficients are rearranged from Table S3 to allow a clear interpretation of *type A* influences and species-specific RGRDs (Intercepts)
Ce *C. elata*, *Le* *L. europaeus*, *Lv* *L. vulgaris*, *Cf* *C. flava*, *Ma* *M. aquatica*

**P* ≤ 0.05
 ***P* ≤ 0.01
 ****P* ≤ 0.001

Table 3 Regression coefficients for the influences of increased water and nutrient levels on the relative growth rate difference (RGRD) between the species in the column minus the species in

the row [for example, $RGRD_{Ce-Le}$ for the cell in the second column and fourth row (bold)]

RGRD _{Col-row}	<i>Ce</i>	<i>Le</i>	<i>Lv</i>	<i>Cf</i>	<i>Ma</i>
a) Water					
<i>Ce</i>	–	0.648***	–0.120	0.228	4.306***
<i>Le</i>	–0.648***	–	–0.768***	–0.420**	3.658***
<i>Lv</i>	0.120	0.768***	–	0.349*	4.427***
<i>Cf</i>	–0.228	0.420**	–0.349*	–	4.078***
<i>Ma</i>	–4.306***	–3.658***	–4.427***	–4.078***	–
b) Nutrient					
<i>Ce</i>	–	0.095	0.236	–0.452***	–0.741**
<i>Le</i>	–0.095	–	0.141	–0.548***	–0.836***
<i>Lv</i>	–0.236	–0.141	–	–0.689***	–0.977***
<i>Cf</i>	0.452***	0.548***	0.689***	–	–0.289
<i>Ma</i>	0.741**	0.836***	0.977***	0.289	–
c) Water × nutrient					
<i>Ce</i>	–	0.116	–0.327	–0.325	1.349***
<i>Le</i>	–0.116	–	–0.442**	–0.441*	1.233***
<i>Lv</i>	0.327	0.442**	–	0.001	1.675***
<i>Cf</i>	0.325	0.441*	–0.001	–	1.674***
<i>Ma</i>	–1.349***	–1.233***	–1.675***	–1.674***	–

A positive coefficient indicates that the species in the column will be favoured over the species in the row. The coefficients are rearranged from Table S3 to allow a clear interpretation

Ce *Carex elata*, *Le* *Lycopus europaeus*, *Lv* *Lysimachia vulgaris*, *Cf* *C. flava*, *Ma* *Mentha aquatica*

* $P \leq 0.05$

** $P \leq 0.01$

*** $P \leq 0.001$

Table 4 Regression coefficients for relevant *type B* influences, that is, the influences of increased initial species biomass on the relative growth rate difference (RGRD) between two other

species: the species in the column minus the species in the row [= for example $RGRD_{Lv-Le}$ for the cell in the second column and fourth row (bold)]

RGRD _{Col-Row}	<i>Carex elata</i> <i>Lv</i>	<i>Carex elata</i> <i>Ma</i>	<i>Carex flava</i> <i>Ma</i>	Water × <i>Ce</i> <i>Lv</i>	Water × <i>Le</i> <i>Cf</i>
<i>Ce</i>	–	–	0.587**	–	–1.194*
<i>Le</i>	–0.602***	1.074**	0.417*	0.612*	–
<i>Lv</i>	–	1.677***	0.561**	–	–1.681*
<i>Cf</i>	–0.734**	0.943**	–	0.713*	–
<i>Ma</i>	–1.677***	–	–	1.321*	–2.688**

A positive coefficient indicates that the species in the column will be favoured over the species in the row. The coefficients are rearranged from Table S3 to highlight the relevant *type B* influences

Ce *C. elata*, *Le* *Lycopus europaeus*, *Lv* *Lysimachia vulgaris*, *Cf* *C. flava*, *Ma* *Mentha aquatica*

* $P \leq 0.05$

** $P \leq 0.01$

*** $P \leq 0.001$

convergence pattern was mainly caused by the strong increase in final proportions of *L. europaeus* and *M. aquatica* with the higher water level.

Discussion

Change in species relative abundance in a community depends on the relative performances of all species

(Suding et al. 2003; Connolly and Wayne 2005; Ramseier et al. 2005); yet few studies have explicitly investigated the link between the competitive ability of individual species and the changing proportions of species in a mixture. The partitioning facilitated by the RGRD method shows how the relative sizes of the RGRs for species and the various strengths of intra- and interspecific competition on species’ RGRs can be interpreted as determinants of proportional changes in

Table 5 Convergence index (CI) calculated for the final mixtures and the four water–nutrient combinations. CI values significantly greater than 1 indicate convergence. Bootstrapping was applied to estimate the 95% confidence intervals. For calculation details of the CI, see text

Abiotic condition	Convergence index CI (95% confidence interval)
Low water–low nutrient	1.162 (1.125, 1.191)
High water–low nutrient	1.059 (1.025, 1.085)
Low water–high nutrient	1.160 (1.121, 1.193)
High water–high nutrient	1.141 (1.110, 1.164)

community. Our results reveal that strong effects of species identity and a negative feedback mechanism, due to the interplay of intra- and interspecific competition among the five species, led to a convergence pattern after 2 years. This pattern was modulated by abiotic environment.

Feedback and convergence

The convergence in our experiment was partly caused by negative feedback (Fig. 2). The convergence pattern was less clear when *C. elata*, the species with the largest RGR, was omitted in a further analysis. In this case, only two out of the four CI values were significantly greater than 1, which indicates that the identity of *C. elata* was also important for the convergence pattern through the large difference in relative growth rates between *C. elata* and the remaining species. *C. elata* took up much of the resources and dominated the mixtures, a pattern also shown by Edelkraut and Guesewell (2006). Thus, we found a convergence pattern following an abundance distribution with a clearly dominant species. This is in agreement with many studies demonstrating convergence for a small set of species, which dominate a mixture and produce much of the biomass (Inouye and Tilman 1995; Prach and Pysek 1999). By contrast, the subdominant species varied strongly in presence and abundance and showed less clear patterns. The chance of subdominant species to establish and persist depends on gaps in the vegetation, where competition of the dominants is reduced (Silvertown and Smith 1989; Suding and Goldberg 2001).

Convergence has repeatedly been deduced from a chronosequence of habitats (Grau et al. 1997; Lichter 1998) or by recording vegetation succession over time (Arevalo et al. 2000). In these studies, late-successional stages of forests showed a generally higher similarity in species composition than did early successional stages. There is also evidence of convergence in conjunction with dominance of a few species, as found in the

present experiment: Prach and Pysek (1999) evaluated 223 species for dominance in succession and found only nine species that covered up to 80% in some habitats. Environmental conditions, such as nutrient availability (Inouye and Tilman 1995), light availability (Lichter 1998) or soil pH (Christensen and Peet 1984), have been suggested as determinants for convergence patterns.

Connolly and Wayne (2005) have focused attention on the potential importance of species identity in changing plant communities, apart from intra- and interspecific competitive effects. This is confirmed by our results. The large differences in average RGR between species identity would by themselves lead to considerable change in species' relative abundance. For example, *C. elata* always increased its final proportions irrespective of its relative abundance at the start, whereas the proportions of *C. flava* and *M. aquatica* were always reduced (Fig. 2). Such relevance of species identity and specific traits for community dynamics has also been proposed by Grime et al. (1997) and Craine et al. (2002).

Change of species proportions have many times been attributed to interspecific competition (e.g. Reader et al. 1994; Peltzer and Köchy 2001). In the present experiment, the shift was also induced by a negative feedback, caused by stronger intra- than interspecific competition. Being present in high initial abundance, each species' own performance was more reduced than that of others, which resulted in a relative decrease in final proportions of the dominants. The same result occurred when the harvested biomass of the first year was used as predictor of the values for RGRD in the second year (results not shown). In this analysis, the influence of species on final proportions was weaker, but the relationship between species influences on itself and other species remained the same. The strong negative feedback suggests that the species occupy different niches. Thus, our results agree with recent studies focusing on the importance of different niche use for species coexistence in plant communities (Loreau and Hector 2001; Jumpponen et al. 2002; McKane et al. 2002; Wright 2002; Weigelt et al. 2005). The generally stronger intra- than interspecific competition in our study has been found by many authors (e.g. Johansson and Keddy 1991). Other studies, however, found the reverse pattern (Huckle et al. 2002), or equal strength of intra- and interspecific competition (Aguilar et al. 2001). The relationship between intra- and interspecific competition can change with time (Mal et al. 1997), may rely on environmental conditions (Schenk et al. 1997) and can also be confounded with measurement scales (Connolly et al. 2001).

Species' influences on the relationship between two other species (*type B* influences) were generally weaker than the influences on itself; yet these three-species effects suggest that change in species' relative abundance may involve more complex relationships between species. A facilitation effect was detected between the two *Carex* species and *M. aquatica*: higher initial biomass of *C. elata* and *C. flava* favoured *M. aquatica* relative to the other species (Table 4). In this case, *M. aquatica*, which prefers wet conditions, may have profited from higher moisture level in the dense swards of *Carex*; and the facilitation effect is likely to promote the coexistence between the two species. Our data provide support to the increasing evidence that facilitation may have an important role in plant coexistence (Bellingham et al. 2001; Kikvidze et al. 2001; Callaway et al. 2002; Franks 2003).

Effects of environment

In a discussion of the role of abiotic conditions in modifying competitive ability, Goldberg (1996) concluded that competitive hierarchies will not a priori be similar under different abiotic conditions. In our experiment, both abiotic factors had effects on plant species' abundance, comparable with those due to species identity and negative feedback. For example, the convergence pattern was further varied by changed water conditions, the mixtures also shifting towards *L. europaeus* under high water level. The higher water level not only favoured the performance of *L. europaeus* and *M. aquatica* (Fig. 2), but also changed their competitive behaviour to their own advantage (e.g. interactions in Table 2). This pattern reduced the strong dominance of *C. elata* and, in turn, diminished the degree of convergence with the high water with low nutrient condition. Higher water level also affected the competitive interactions between *C. flava* and the other species: Varied water level had no direct effect on *C. flava*'s RGR, suggesting that the species was not stressed with the dryer conditions. Yet, the higher water level significantly favoured all other species over *C. flava* with increasing *L. europaeus* biomass, indicating a reduced competitive response of *C. flava* with high water level. This behaviour can be explained by a trade-off between the ability to tolerate stress and the competitive response of a species, as proposed by Liancourt et al. (2005). Our 2-year data suggest that such modifications of species interactions by abiotic conditions are also relevant for plant community change.

In evaluating changes in community structure, the results of experiments lasting for one or two growing

seasons should be interpreted with some caution. The long-term outcome of species interactions may differ from results observed in the first 2 years (Weiher et al. 1996; Mal et al. 1997). In our case, even small influences on other species proportions may induce a high change in species composition in the long run. The dynamics are further complicated in the presence of recruitment from seeds, whereas during the germination phase, interspecific competition also plays a crucial role (Chapin et al. 1994). Competition for light may prevent seedling establishment and reduce recruitment by inhibiting both germination and survival (Foster and Gross 1998).

Conclusions

We conclude that the main causes for a shift in species proportions were the identity of species, a negative feedback mechanism due to stronger intra- than interspecific competition and the availability of water and nutrients. The first two factors led to a significant convergence of the mixtures, initially set up in a high range of proportions. The negative feedback mechanism suggests that there is niche differentiation between species that promotes their coexistence. We showed that multiple interactions between species are relevant for changes in plant relative abundance and that such interactions are modified by different abiotic conditions. We demonstrated also that the simplex design and the models for RGR and RGRD are useful tools in understanding plant community dynamics. The design allows us to link the direct effects on a species performance with changes in species proportions and more general patterns, such as convergence.

Acknowledgments We thank J. Burri for support in seedling establishment and U. Somalvico and the gardeners of the Botanical Garden Zurich for planting. We also thank M. Fotsch for assistance in the maintenance of the experiment, P. Borer, P. Kadelbach, T. Steffen and K. Wartenweiler for help during harvest, and C. Palmer for linguistic corrections. P. Edwards, R. Mack, and two anonymous reviewers provided helpful comments on the manuscript. The project was funded by the ETH Zurich (Grant No. 0-20891-01). The performed experiment does completely comply with the current Swiss law.

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