



Competition and coexistence of rhizomatous perennial plants along a nutrient gradient

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Abstract

I studied competition and coexistence of three tall clonal perennial plant species, *Calamagrostis epigejos* (L.) Roth, *Solidago canadensis* L., and *Tanacetum vulgare* L. along a gradient of soil productivity over five years. A replacement series field experiment was conducted with high, moderate and low fertility levels in $1\text{ m} \times 1\text{ m}$ plots. There were significant effects of soil type on ramet density ($P < 0.001$), mean height ($P < 0.01$), and total biomass ($P < 0.01$). Ramet density, mean height, and total biomass increased with increasing soil fertility. There were also significant effects of mixture on ramet density ($P < 0.01$), but not on mean height and total biomass for all species. Significant neighbor effects on ramet density and total biomass ($P < 0.01$) were found for *Solidago*, showing that it is important whether *Tanacetum* or *Calamagrostis* is its neighbor within mixtures. During the five years there was only one case of competitive exclusion: *Calamagrostis* excluded *Solidago* on the most fertile substrate in the fifth growing season. In most cases species coexisted over the five years. Each of the three species was able to dominate in at least one combination of substrate type and mixture. The experiment showed that asymmetric competition for light on substrates of high fertility, symmetric competition for nutrients on nutrient-poor soil and positive interactions especially on substrates of intermediate fertility played a role. A founder effect was evident in aggregated mixtures of *Calamagrostis* and *Solidago* on the nutrient-rich substrate. A conceptual model of the relative importance of root competition for soil nutrients, shoot competition for light, and positive interactions along the fertility gradient is presented. The model emphasizes that positive interactions play an important role over a broad range of the productivity scale with a peak at intermediate levels of fertility. On the substrate of high productivity shoot competition for light is more important than positive interactions and root competition for soil nutrients as well. The competitive superiority of *Calamagrostis* on the most productive substrate was evident only in the long run. Rare events like extreme summer drought or selective herbivore pressure caused a switch in dominance in mixtures with *Solidago*, respectively *Tanacetum*. The guerrilla growth strategy of *Calamagrostis* and interference competition through a dense cover of aboveground biomass and litter could further cause competitive exclusion.

Introduction

For more than a century ecologists have focused on competition as a crucial process for community organization and for the distribution of organisms on a biogeographical scale (Darwin 1859, Cajander 1925, Ellenberg 1988). Gause (1934) formulated the ‘competitive exclusion principle’ that two species using

the same resources cannot coexist indefinitely in a limited environment. Considering the Gause Principle for plants, which all need nearly the same resources, it seemed surprising that so many species coexist within communities. This ‘paradox of the plankton’ (Hutchinson 1961) demanded an explanation (Grubb 1977; Braakhekke 1980; Shmida & Ellner 1984; Wilson 1990; Tilman & Pacala 1993). Among a dozen

explanations for this paradox, niche diversification is the oldest (Wilson 1990). Further hypotheses emphasize competitive equivalence and extremely long times to competitive exclusion or factors which interrupt the process of competitive exclusion in time or space (Reynolds et al. 1997).

Among community ecologists, there is still no doubt that competition plays an important role in structuring plant communities and experimental evidence supports this view (Connell 1983; Schoener 1983; Braakhekke 1985; Fowler 1986; Keddy 1989; Goldberg & Barton 1992; Gurevitch et al. 1992). Efforts have been made to develop predictive theories of plant competition, emphasizing mechanistic equilibrium models of competition along gradients of light and minerals (especially nitrogen) (Tilman 1982, 1985, 1988, 1990) or relating competitive success with individual plant traits, where certain individual plants or species are inherently better competitors than others (Grime 1979), forming competitive hierarchies and transitive networks (Keddy & Shipley 1989; Shipley & Keddy 1994).

Using data from competition experiments based on de Wit replacement series (de Wit 1960), Keddy & Shipley (1989) showed that pairwise interactions were predominantly asymmetric (non-reciprocal). Their definition of asymmetry is phenomenological and independent of hypothesized mechanisms. Asymmetric competition occurs when the dominant species experiences less interspecific than intraspecific interactions while the subordinate experiences more intense interspecific interactions (Shipley & Keddy 1994). Considering mechanism, Weiner (1986) provides evidence that when only roots compete, competition can be symmetric (reciprocal), but competition for light is asymmetric. Keddy et al. (1997) provided experimental evidence that interspecific competitive asymmetry increases with soil productivity.

Alternative to the traditional niche concept, where the differentiation of fundamental niches is assumed to be the result of past competition selection for specialization, Keddy (1989) proposed the competitive hierarchy model to explain the pattern of resource partitioning and the differential distribution along environmental gradients. The assumptions are (1) that the species in the community have inclusive niches, i.e. the gradient is a gradient of resource quantity, with all species having best performance at the same end of the gradient, that (2) species vary in competitive ability in a predictable manner and that competitive ability is an inherent characteristic of a species, and (3)

that competitive abilities are negatively correlated with fundamental niche width, perhaps because of inherent trade-off between ability for interference competition and the ability to tolerate low resource levels.

The concept of centrifugal organization of plant communities (Keddy 1989, 1990; Keddy & Wisheu 1992) is based on competitive hierarchies along environmental gradients. Gradients radiate outwards from a single core habitat to many different peripheral habitats. Interspecific competition is intense in the core habitat with light as a limiting resource. Weaker competitors are restricted to the peripheral end of the gradient as a result of a trade-off between competitive ability and tolerance limits. The peripheral habitats permit coexistence.

Welden & Slauson (1986) have pointed out that it is necessary to distinguish between the intensity of competition which qualifies the process of competition itself and the importance of competition which is related to the importance of other processes. Studying structuring mechanisms within communities, other kinds of interaction between plants like facilitation and mutualism should be taken into account. Whereas the role of competitive mechanisms in plant interactions may have been overemphasized in the past, positive interactions have been largely overlooked as important factors in community structure (but see Gigon & Ryser 1986). Recent research reveals that beneficial mutualistic effects or facilitation and competition may operate simultaneously and that the overall effects of one species on another may vary between different habitats as the relative importance of mechanisms shift (Bertness & Callaway 1994; Callaway 1995, 1997, 1998; Greenlee & Callaway 1996; Bertness & Leonard 1997; Callaway & Walker 1997).

Species known for their high 'competitiveness' or 'aggressivity' attract the attention of vegetation scientists and conservation biologists, and are suspected of ousting many other species. However, it seems astonishing that various species grow together and coexist within plant communities, even though they are all supposed to possess high competitive ability. In eastern Central Europe the most abundant communities of old-fields and derelict land are communities in which *Calamagrostis epigejos* (L.) Roth, a tall rhizomatous perennial grass and two rhizomatous perennial herbs, *Solidago canadensis* L. and *Tanacetum vulgare* L. are dominant, forming mono-, bi- or tridominant stands. Communities built up by those species represent the same successional stage of tall perennial herbs or grasses, and therefore dominance with respect to

these three species can hardly be interpreted as functional dominance within succession. Following Keddy (1990) these tall clonal perennials are all core species in the centrifugal organization model.

The species investigated are often clumped in natural communities. Silvertown et al. (1992) showed that the spatial pattern and configuration of competing species may be just as important as the density and frequency of competitors in determining the outcome. This study was designed to answer these questions:

- Does competitive exclusion of similar species occur under field conditions?
- Does the type of species aggregation influence the outcome?
- What kinds of biotic interactions occur and how important is competition in relation to other kinds of interaction?
- Does the importance of competition and positive interactions change across a productivity gradient?

To answer these questions a substitutive experiment with two-species replacement series, in which the species are grown in mixtures and in monocultures, keeping the total density the same (de Wit 1960; de Wit & van den Bergh 1965; van den Bergh 1968) was carried out on three substrates of different nutrient status. A replacement design was chosen because it is valuable for comparing the outcome of competition between plant species under different environmental conditions, but reveals non-competitive and positive effects of mixtures as well (Hall 1974; Trenbath 1974; Goldberg & Barton 1992).

To show the effect of the aggregation type of clonal plants regular and aggregated mixtures of *Tanacetum* and *Solidago* (which represent both the phalanx growth strategy type) were planted in combinations with *Calamagrostis* (which represents the guerrilla type).

Methods

Description of species

Calamagrostis epigejos L. (Roth), Wood Small-reed or Bush grass is a tall perennial rhizomatous grass with natural habitats on sand-dunes, river banks, mires, montaine steppes and subalpine grassland in Eurasia. In eastern Central Europe *C. epigejos* is synanthropic and one of the most abundant grass species in forests, along railway-lines and roadsides and on any urban and industrial wasteland (Rebele 1996a). It has been

introduced to North America both accidentally and deliberately and grows there along roadsides and on wasteland (Aiken et al. 1989).

Tanacetum vulgare L., Common tansy is a tall perennial herb from Eurasia and has been introduced to America and Australia. Natural habitats can be found in subalpine mountain river valleys in Siberia, whereas most occurrence in Europe is synanthropic. In the 18th and 19th centuries, *T. vulgare* was cultivated for medical purposes and dispersed by man. Today, tansy is common in rural and urban-industrial areas, occurring in similar habitats to *C. epigejos*, with the exception of forests.

Solidago canadensis L., Canada goldenrod is also a tall rhizomatous perennial herb which is native to North America with natural habitats in tall-grass prairies. *S. canadensis* L. sensu lato includes several taxa which are frequently granted species status (Werner et al. 1980; Weber 1997). The Canada goldenrod was introduced to Europe and had been cultivated since the 17th century and is now one of the most abundant perennial herbs in Central Europe on old-fields, and on urban and industrial wasteland. The Central European taxa are supposed to be identical with *S. altissima* L. (Weber & Schmid 1993) or closely related to it (Weber 1997), but in German floras different taxa of *S. canadensis* L. are not distinguished.

C. epigejos, *T. vulgare* and *S. canadensis* co-occur in old-field and wasteland communities in eastern Central Europe. Each of the three species is able to colonize disturbed sites and to dominate in early and mid-successional stages as well. The three clonal species are similar in size, but differ in dispersal characteristics and growth type. *S. canadensis* and *T. vulgare* represent the phalanx and *C. epigejos* the guerrilla growth strategy within the phalanx-guerrilla growth type continuum. The three species also show different germination characteristics and different seasonal patterns of growth (Lehmann & Rebele 1994; Rebele 1996b).

Study site and climatic data

I conducted my study from 1987 to 1991 at the Kehler Weg garden of the Institute of Ecology, Technical University of Berlin. The garden is located in the SW of Berlin (52°27' N, 13°17' E) at 50 m above sea level on a glacial till plateau within a residential area. Mean annual temperature at Berlin-Dahlem, the next weather station about 2 km from the study location, is 8.8 °C, and long-term mean annual precipitation is 595 mm.

Relative to the annual mean, 1987 was cooler, the years 1988 to 1990 were much warmer (up to an annual mean of 10.4 °C), and precipitation fluctuated with a minimum of 449 mm in 1989 to a maximum of 692 in 1987.

Mean annual deposition (1987–1991) of nitrogen ($\text{NH}_4\text{N} + \text{NO}_3\text{N}$) at an open oldfield about 3 km from the study location was 11.2 kg ha⁻¹, mean annual deposition of Ca was 11.3 kg ha⁻¹ (Cornelius et al. 1997). Mean annual deposition (May 1988–April 1989) of K amounted 1.9 kg ha⁻¹, and of Mg 1.1 kg ha⁻¹ (U. Fischer 1989 in report). Data for the deposition of P was not available.

Experimental plots and substrates

66 experimental plots (1 m × 1 m) were established in concrete basins in the experimental garden in October 1986 and filled blockwise with three substrates, a nutrient-rich topsoil, a ruderal landfill soil of moderate nutrient status and a nutrient-poor sand (Figure 1). The squares were separated by concrete partitions 80 cm deep. The fill depth was 80 cm with a 20 cm gravel layer underneath for drainage.

The topsoil was a silty sand mixed with litter compost and dung. It contained 2% organic C, 0.102% total N, and had a pH of 7.6 in 1986. The ruderal soil was also a silty sand with 23.1% coarse soil. It had 0.94% C, 0.027% N, and a pH of 7.5. The sand was fine sand with a pH of 7.5 and contained only 0.12% C and 0.008% N (for details see Table 1 and Rebele 1996b).

Experimental design

A standard replacement design was used with monocultures and three 50%–50% species mixtures. For mixtures with *Calamagrostis*, two different types of planting were performed: regular mixed and aggregated pattern (Figure 2). The plots were planted with 2-month-old seedlings of *T. vulgare* and *S. canadensis* grown in the greenhouse, and with ramet transplants of *C. epigejos* in total densities of 25 plants per plot in monocultures and regular mixtures and 24 plants in aggregated patterns. Planting took place in May 1987 and the experiment proceeded for five growing seasons until September 1991. Species other than those planted were allowed to grow from the second growing season until plots were harvested. There were three replications of each of the substrate types in monocultures and mixtures, with the exception of *Solidago/Calamagrostis* mixtures in aggregated plantings

with two replicates. All treatments were performed on all three soil types. The cultures were placed randomly within the substrate blocks. Herben & Krahulec (1990) criticized that the de Wit approach tends to produce artificially deterministic interactions, since the standardization of the design excludes many of the processes which produce variability in the competition outcome. To overcome the limitation of ex situ experiments, the replacement experiment was carried out in the garden for a period of five years with fluctuating environmental conditions and without manipulation of the species composition after the initial phase. Though herbivory was not included in the experimental design, it was part of the fluctuating environment, with the exception of large herbivores which were excluded by the garden fence. A period of five years was thought to be a minimum for an experiment with the perennial plants used, bearing in mind that stands of *Calamagrostis epigejos*, *Solidago canadensis* and *Tanacetum vulgare* often persist for ten to twenty years before they are replaced by woody stages during succession. All species are of similar size, therefore an inherent size bias was thought not to be relevant in the replacement series experiment. Similarity in size is an important assumption of the replacement series design (de Wit 1960; Harper 1977; Keddy 1989).

Soil sampling

I took 5 five samples of each substrate in October 1986. These were pooled, dried at air temperature, and sieved through a 2 mm mesh. A subsample was ground with an agate ball mill. The soil samples were analyzed for grain size, pH, total organic C and N, total and plant available P, K, Ca, and Mg. During the harvest of plant material from September 1 to October 2 1991, soil samples of each plot were collected from the main rooting zone of the plants approx 10 to 20 cm deep. The samples were treated as above and analyzed for the same physicochemical parameters except grain size. Each sample was analyzed in duplicate. For data analysis means of the duplicate samples were used.

Grain size of fine soil was determined in accordance with German standard (DIN 19683, Sheet 2, 1973); pH was measured in 0.01 M CaCl_2 suspension with a glass electrode according to DIN 19684, Part 1 (1977). Total organic C and N of soil samples were measured by means of an automatic LECO CHN-932 analyzer. Total P, K, Ca, and Mg contents of the substrates were analyzed after extraction with concentrated nitric acid. Plant available P, K, Ca, and

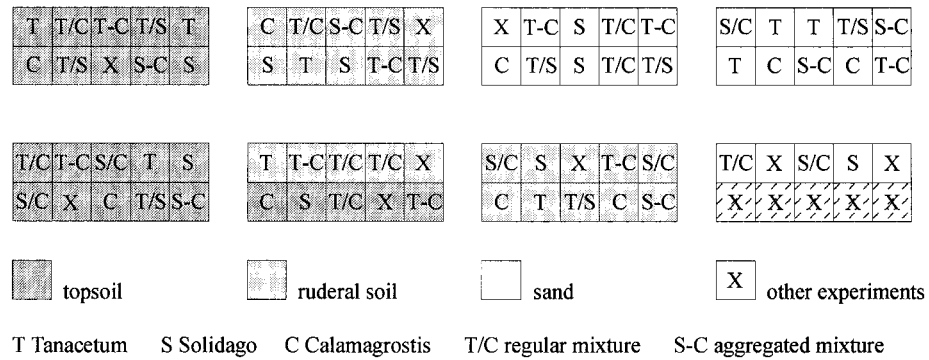


Figure 1. Experimental design of the replacement experiment.

Table 1. Physicochemical characteristics of substrates at the beginning and the end of the experiment. For the data of 1991 means of all plots of a substrate type ($n = 22$) and standard deviations are presented

	Topsoil		Ruderal soil		Sand	
	1986	1991	1986	1991	1986	1991
Coarse soil (>2mm)%	14.9		23.1		1.0	
Sand%	84.2		88.2		96.3	
Silt%	13.1		11.4		2.5	
Clay%	2.7		0.4		1.2	
pH CaCl ₂	7.6	7.1 ± 0.0	7.5	7.4 ± 0.1	7.5	7.0 ± 0.2
C org.%	2.00	2.54 ± 0.13	0.94	1.13 ± 0.07	0.12	0.24 ± 0.05
N total%	0.102	0.161 ± 0.013	0.027	0.047 ± 0.008	0.008	0.016 ± 0.003
P total ppm	775	675 ± 100	149	215 ± 77	99	105 ± 36
P available ppm	184	249 ± 14	85	90 ± 16	36	23 ± 4
K total ppm	2496	2216 ± 154	1032	1255 ± 74	637	691 ± 61
K available ppm	621	318 ± 44	104	120 ± 16	58	71 ± 17
Ca total ppm	11220	10175 ± 660	11340	8368 ± 1096	960	836 ± 187
Ca available ppm	9400	9360 ± 114	8800	8220 ± 1158	500	425 ± 50
Mg total ppm	1550	1636 ± 90	1031	1168 ± 210	408	405 ± 21
Mg available ppm	228	199 ± 15	146	138 ± 12	21	33 ± 16

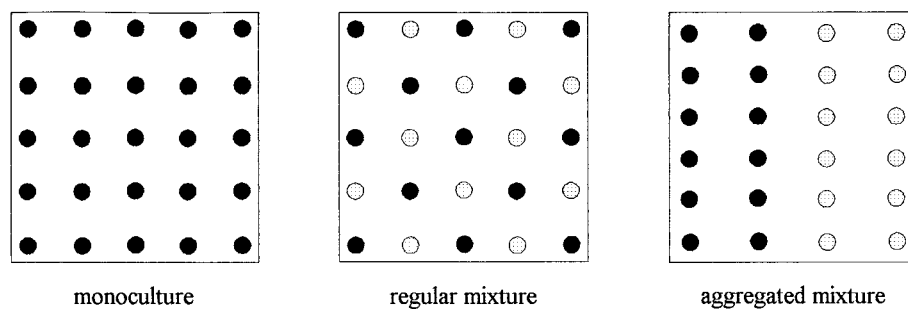


Figure 2. Planting design of monocultures and mixtures.

Mg were determined after extraction with ammonium lactate acetic acid (lactate method after Egner/Riehm; Schlichting et al. 1995). P was measured colorimetrically; K, Ca, and mg were measured by flame atomic absorption spectrometry (Perkin Elmer 3100).

Cover and plant material

Cover of green phytomass was recorded nearly monthly during the growing seasons from 1987 to 1991 as percentage cover of *Tanacetum*, *Solidago*, and *Calamagrostis*. All plants were harvested at the end of the fifth growing season and separated into species and above and below ground parts. I determined aerial shoot density and shoot height. Plants other than the study species were separated into grasses, herbs and woody plants and divided into material above and below ground. The species composition at the end of the fifth growing season is described in Rebele (1996b). The importance of other species increased with decreasing soil fertility, but the study species were dominant throughout in all substrates (median: 88% of total dry matter). An exception were 'monocultures' of *Tanacetum* on topsoil plots, where *Tanacetum* was replaced by *Arrhenatherum elatius*, after nearly all green leaves of *Tanacetum* were eaten by slugs in the fifth growing season. Total litter was harvested separately. All below-ground material was washed and all plant material was dried at 80 °C for 48 h and then weighed.

Data analysis

A three-level nested analysis of variance (Sokal & Rohlf 1981) was used to determine the effects of the three different substrates (fixed treatment effects), the planting design within substrate blocks, and different neighbor species on ramet density, mean height, and total biomass for each species. A two-level nested ANOVA was performed for soil data of 1991 to test the influence of soil type and culture within substrates on total nutrient contents after five years. Statistical procedures were carried out using SPSS/PC+, version 3.0.

For the calculation of Relative Yields (RY) of biomass total dry matter of the other 'weed' species was taken into account. Biomass of other species in 'monocultures' was added to the yield of the study species. Biomass of other species in mixtures was added to the dry matter of the study species with the lower yield. So relative yields of the lower yielding species a were calculated as the quotient of dry matter yield in mixture (including other species) and dry matter yield

in monoculture (including other species) and relative yields of the higher yielding species b were calculated as the quotient of dry matter yield in mixture and dry matter yield of monoculture (including other species), respectively. This procedure weights the lower yielding species more, but it was used to obtain correct Relative Yield Totals (RYT), which were calculated as the sum of relative yields $RY_a + RY_b$ (de Wit & van den Bergh 1965).

(1) calculation for the lower yielding species a:

$$RY_{tdm,a} = (dm_{a,mix} + dm_{o,mix}) / (dm_{a,mono} + dm_{o,mono a})$$

(2) calculation for the higher yielding species b:

$$RY_{tdm,b} = dm_{b,mix} / (dm_{b,mono} + dm_{o,mono b})$$

(3) calculation for Relative Yield Total:

$$RYT = RY_a + RY_b$$

(tdm: total dry matter; dm: dry mass per plot; mix: mixture; mono: monoculture; a: species a; b: species b; o: other species)

In replacement diagrams (Figure 4) mean total dry matter of the study species and mean total dry matter of all plants in monocultures and mixtures are shown; the relative importance of other spontaneously growing species can be seen when dry matter of the study species is subtracted from total dry matter.

Results

Soil characteristics

Soil data are presented to show whether resource depletion or nutrient accumulation had occurred during the five years of the experiment. Because of different sampling methods, the soil data of 1986 and 1991 cannot be compared statistically.

Organic matter increased in the plots of all substrate types and therefore total organic C and N increased (Table 1). In topsoil plots C_{org} increased from 2.00% in 1986 up to a mean of 2.54% in 1991; mean C_{org} of ruderal soil were 0.94 in 1986 and 1.13% in 1991 and of sand 0.12% and 0.24%, respectively. Accordingly, total N contents increased from 0.102% up to 0.161% in topsoil, from 0.027% to 0.047% in ruderal soil, and from 0.008% to 0.016% in sand.

For other nutrients the situation varied. Total and plant available Ca levels decreased in plots of all three substrates. Total and available K contents increased in

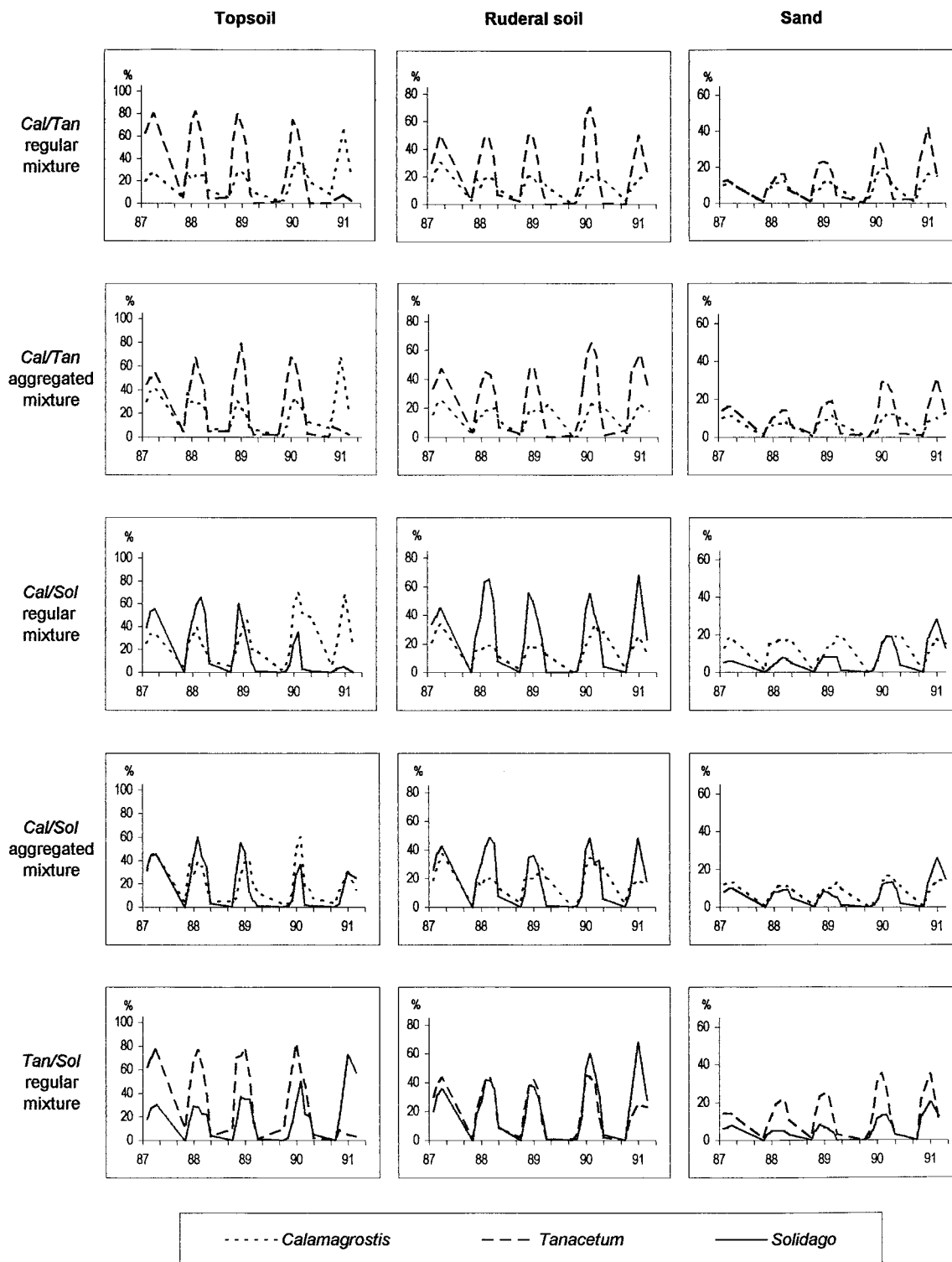


Figure 3. Mean plant cover of study species growing in mixtures during five years of investigation.

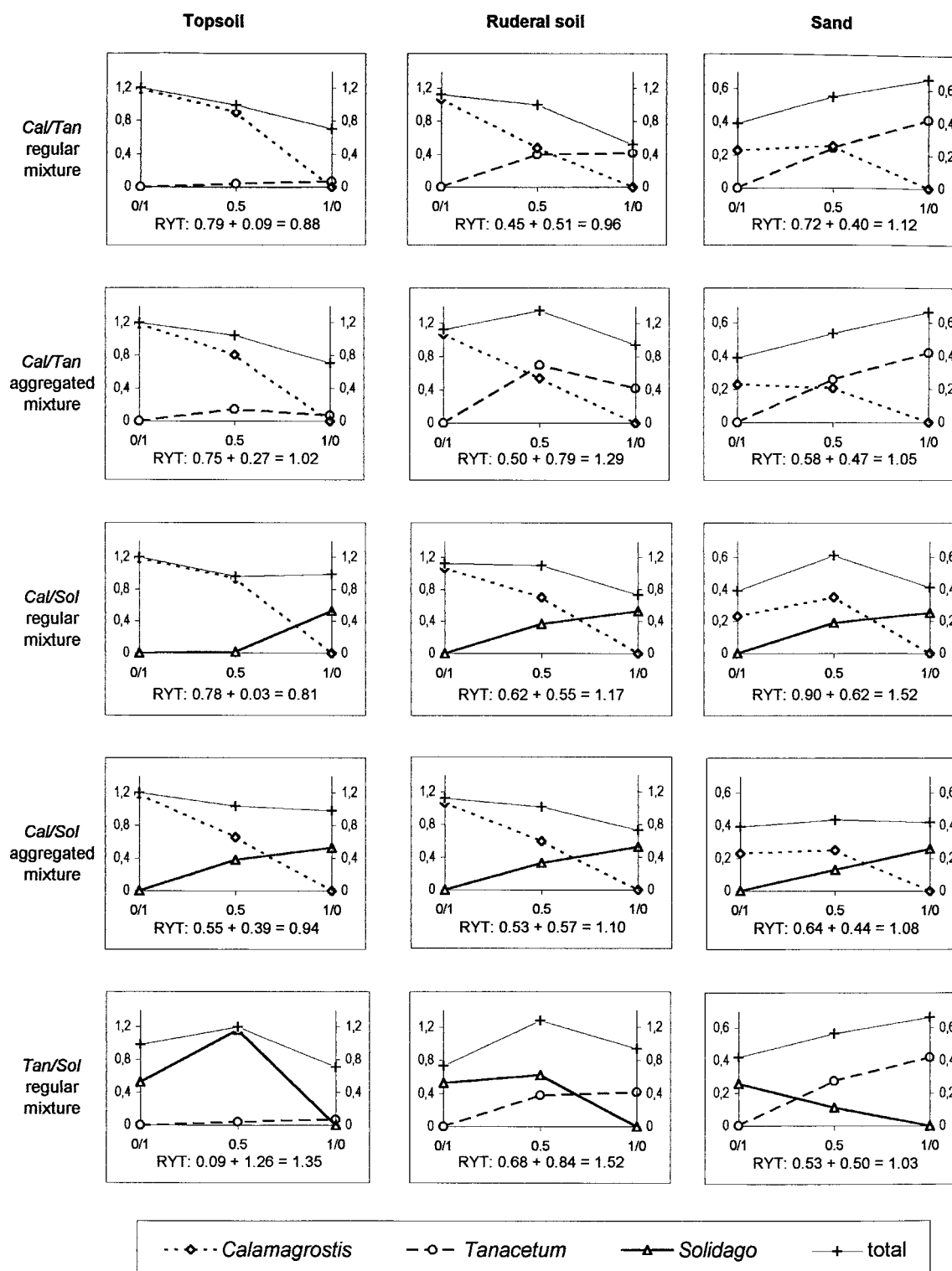


Figure 4. Replacement diagrams and Relative Yield Total (RYT) of total dry mass. The order of Relative Yields (RY) follows the order in the naming of mixtures.

ruderal soil and sand, but decreased in topsoil plots. Total Mg levels increased in topsoil and ruderal soil plots, but available Mg increased only in sand plots. Total and available P contents increased in ruderal soil plots; in topsoil plots total P decreased, but available P increased. In sand plots available P decreased. The pH values decreased slightly from 7.6 to 7.1 in topsoil, from 7.5 to 7.4 in ruderal soil, and from 7.5 to 7.0 in sand plots.

For the 1991 data, there are highly significant differences of total nutrient contents between substrate types ($P < 0.001$). Differences between cultures within a substrate type were only significant for phosphorus in ruderal soil ($P < 0.01$) and in sand ($P < 0.05$).

Temporal pattern of plant cover

On topsoil *Tanacetum* showed higher cover than *Calamagrostis* in regular and aggregated mixtures with *Calamagrostis* during years 1 to 4 with mean cover values ($n = 3$) up to more than 80% (Figure 3). In the fifth year the situation reversed dramatically and mean cover of *Tanacetum* decreased towards 2% in both regular and aggregated mixtures, whereas cover of *Calamagrostis* increased. On ruderal soil and sand *Tanacetum* obtained higher cover values than *Calamagrostis* in regular as well as in aggregated mixtures for all five years of investigation. Maximum mean cover values for *Tanacetum* were up to 70% on ruderal soil and up to 42% on sand. In mixtures with *Solidago*, *Tanacetum* also showed higher cover percentage on topsoil for the first four years and declined towards 3% cover in the fifth year as in mixtures with *Calamagrostis*. On ruderal soil the cover values of *Tanacetum* and *Solidago* are similar for years 1 to 3. In the fourth and fifth year *Solidago* had higher cover values than *Tanacetum*, but the decline of *Tanacetum* in year 5 was not as sharp as on topsoil. On sand *Tanacetum* showed higher cover values than *Solidago* during the five years of investigation with a continuous increase until year 4. In mixtures with *Calamagrostis*, *Solidago* obtained higher cover values on topsoil in regular and aggregated mixtures until year 3. However, in late summer of the third year there was a reverse. Cover of *Calamagrostis* increased and *Solidago* declined, approaching 0% in the fifth year in regular mixtures and 25% in aggregated mixtures. On ruderal soil *Solidago* had higher cover values during the five years of investigation in both regular and aggregated mixtures; but differences in cover were more pronounced in regular mixtures.

On sand *Solidago* showed increasing cover values during the five years, whereas cover of *Calamagrostis* was more constant.

In monocultures ($n = 3$), *Tanacetum* obtained up to 100% mean cover on topsoil for years 1 to 4, but declined to 4% in the fifth year, as was the case in mixtures. This sharp decline in all topsoil plots (monocultures as well as mixtures) was due to herbivory by slugs (*Arion ater*) during spring and early summer in the fifth growing season. On ruderal soil and sand there is also a decline of cover, but not as pronounced as on topsoil. *Solidago* also reached nearly 100% mean cover in the years 1 to 4 on topsoil and declined in the fifth year to a maximum mean level of 53%, whereas mean cover was higher (70%) on ruderal soil in that year. This was because *Solidago* plants growing in ruderal soil were less susceptible to summer drought than plants growing in topsoil. Maximum mean cover values of *Calamagrostis* were up to 94% on topsoil, 70% on ruderal soil and 20% on sand. Lowest values for topsoil and ruderal soil plots were recorded in the fifth year.

Ramet density, mean height and total biomass

A three-level nested ANOVA with soil type as the major classification, planting design within soil type, and neighbor species within planting design as factors showed significant effects of soil type on ramet density ($P < 0.001$), mean height ($P < 0.01$), and total biomass ($P < 0.01$) for the study species *Tanacetum*, *Solidago*, and *Calamagrostis* (Table 2). Ramet density, mean height, and total biomass increased with increasing soil fertility. There were also significant effects of the planting design on ramet density ($P < 0.01$), but not on mean height and total biomass ($P > 0.05$) for all three species. Significant neighbor effects on ramet density and total biomass ($P < 0.01$) were found for *Solidago*, showing that it is important whether *Tanacetum* or *Calamagrostis* is its neighbor within mixtures.

The mean total biomass ($n=22$) of living and dead plant material for monocultures as well as mixtures at the end of the fifth growing season was 2.8 kg m^{-2} for topsoil, 1.8 kg m^{-2} for ruderal soil, and 0.9 kg m^{-2} for sand. Higher biomass above-ground along the productivity gradient was the result of both higher ramet density and larger plants.

Table 2. F and P values from ANOVA for the effect of soil type, planting design, and neighbor species on ramet density, mean height, and total biomass for each species. Boldface values are significant

		Ramet density		Mean height		Total biomass	
	df	F	P	F	P	F	P
<i>Tanacetum</i>							
Soil type	2	36.37	0.000	10.17	0.001	10.94	0.000
Planting design	6	4.51	0.003	1.38	0.282	0.98	0.458
Neighbor species	1	0.18	0.679	0.03	0.869	0.00	0.978
<i>Solidago</i>							
Soil type	2	28.59	0.000	73.21	0.000	7.33	0.005
Planting design	6	10.56	0.000	2.65	0.056	0.81	0.578
Neighbor species	1	9.07	0.007	0.69	0.418	16.26	0.001
<i>Calamagrostis</i>							
Soil type	2	26.04	0.000	43.57	0.000	26.08	0.000
Planting design	6	4.17	0.005	0.89	0.516	2.14	0.085
Neighbor species	2	0.99	0.385	0.08	0.925	0.39	0.680

Outcome of the replacement experiment

Based on data of total biomass of plants harvested at the end of the fifth growing season (Replacement diagrams, Figure 4) and with respect to the cover data of the five years of investigation (Figure 3) the outcome of the experiment can be summarized as follows (Table 3): Within the five years there was only one case of competitive exclusion: *C. epigejos* excluded *S. canadensis* on the most fertile substrate in the fifth growing season in all replicates. In most cases the species still coexisted at the end of the experiment. Each of the three study species was able to dominate in at least one combination of substrate type and mixture. In all combinations of *Solidago* vs. *Calamagrostis*, *Calamagrostis* had higher total biomass at the end of the fifth growing season, but except on topsoil dominance did not lead to competitive exclusion. In mixtures of *Tanacetum* and *Calamagrostis*, *Calamagrostis* dominated on topsoil and on ruderal soil in regular mixed plantings. In aggregated plantings *Tanacetum* was dominant on ruderal soil and sand. Regular mixed plantings on sand showed codominance of *Tanacetum* and *Calamagrostis*. In mixtures of *Tanacetum* and *Solidago*, *Solidago* dominated on topsoil and ruderal soil and *Tanacetum* on sand.

Relative yield values (Figure 4) greater than 0.5 indicate positive net effects for a species grown in mixtures, values less than 0.5 show that the species was negatively affected, while values of 0.5 indicate

that the species grew equally well with either the same or a different species. Mean Relative Yield Totals of total biomass for all possible 15 mixtures are within a range from 0.81 to 1.52. Regular mixtures of *Calamagrostis* with *Tanacetum* and *Solidago* on topsoil show RYT values below 0.90 due to very low values of relative yield for *Tanacetum*, respectively *Solidago*. Seven mixtures have RYT values between 0.90 and 1.10. For six mixtures RYT values are higher than 1.10. The replacement diagrams (Figure 4) also show that in some cases overyielding of mixtures occurred, i.e. the yield of the mixture was higher than either of the monocultures. Overyielding was recorded for mixtures of *Tanacetum* and *Solidago* on topsoil and on ruderal soil, for aggregated mixtures of *Tanacetum* and *Calamagrostis* on ruderal soil and for regular mixtures of *Solidago* and *Calamagrostis* on sand.

Discussion

Considering the outcome of the replacement experiment after five growing seasons one has to keep in mind that this is just a snapshot within an ongoing process of interactions between plants against the background of a fluctuating climatic and biotic environment. The course of the cover of living biomass above ground shows that competitive abilities may reverse within five years. Cover values, however, can only be used as an approximate measure of dominance

Table 3. Outcome of the replacement experiment after five years. Dominance means that the total dry matter yield of the species is at least 10% greater than that of the other species

Mixture	Topsoil	Ruderal soil	Sand
<i>Tanacetum</i> (T) vs. <i>Calamagrostis</i> (C)			
Regular	C dominant	C dominant	codominance
Aggregated	C dominant	T dominant	T dominant
<i>Solidago</i> (S) vs. <i>Calamagrostis</i> (C)			
Regular	competitive exclusion of S	C dominant	C dominant
Aggregated	C dominant	C dominant	C dominant
<i>Tanacetum</i> (T) vs. <i>Solidago</i> (S)			
Regular	S dominant	S dominant	T dominant

within a community. On topsoil, and in all mixtures of *Tanacetum* and *Solidago*, higher cover percentages during the fifth growing season were parallel to higher total biomass at the end of the season. In mixtures with *Calamagrostis* on ruderal soil and sand, higher mean cover percentages of *Tanacetum* and *Solidago* during the growing season of the last year were not correlated with higher total biomass at the end of the season. Total biomass is the result of the full growth period and biomass below ground also has to be taken into account.

One can not directly relate net effects indicated by relative yields in replacement series to competitive mechanisms. Comparing total biomass of mixtures with that of monocultures reveals that also other effects apart from competition have to be considered. This is obvious when yields of monocultures are equally low as yields of mixtures or when overyielding occurs, a phenomenon which is well known from mixed cropping in agriculture (Trenbath 1974).

Analyzing the course of growth of the three species in monocultures and mixtures and the outcome of the replacement experiment after five years, we can distinguish various kinds of biotic interactions and competitive mechanisms:

Competitive exclusion through asymmetric competition for light

Using plant cover as an indicator of dominance, the course of the cover during five years shows that *Solidago* was dominant in regular mixtures with *Calamagrostis* on the topsoil plots until the beginning of

the third growing season. From late summer of the third year, *Calamagrostis* dominated over *Solidago* and excluded *Solidago* at the end of the fifth year (Figures 3, and 4). A dense stand of living and dead plants of *Calamagrostis* might have further inhibited new germination and establishment of *Solidago*. *Calamagrostis* itself is able to penetrate the dense litter sward with its leaves and culms. There is evidence for strong competition for light, which *Calamagrostis* had won after five years. The inhibition of new recruitment of *Solidago* seedlings by a dense *Calamagrostis* stand and litter accumulation can be interpreted as a kind of interference competition (Aarssen 1983). Inhibition by litter is most commonly observed in highly productive but undisturbed environments, where litter accumulation can be quite high (Foster & Gross 1998).

Considering the result after five years competition is one-sided or asymmetric in the sense of Weiner (1986, 1990). The basic concept of competitive asymmetry is that larger plants have a competitive advantage over smaller plants and that differences among species in resource acquisition rates, once established, are maintained and magnified during competition. However, in my experiment the one-sided result was not caused by an initial advantage of *Calamagrostis* plants. Over more than two years *Solidago* dominated. The switch in dominance was probably caused by the summer drought of the very dry year 1989, which heavily affected *Solidago* plants growing in topsoil. The loss of green leaves diminished reserve supply of *Solidago* and enhanced light acquisition for *Calamagrostis* plants. This casual advantage was magnified

during the following years and led to competitive exclusion of *Solidago*.

Wilson (1988) showed that asymmetric competition is a feature of competition for light, and does not apply to nutrient competition. In this experiment asymmetric competition for light and competitive exclusion occurred only on the most productive soil. These results are consistent with those of Keddy et al. (1997) who found that interspecific competitive asymmetry increases with soil productivity. The fact that only one case of competitive exclusion was observed may be due to the circumstance that all study species are long-lived tall clonal species with similar competitive abilities. The probability of observing competitive exclusion may increase with the number of species examined, especially when less similar species are included. Weiher & Keddy (1995) examined 20 species of wetland communities in 24 different habitat treatments over five years and found that only 14 species persisted. There were strong and consistent effects of fertility, water level, and leaf litter on community composition.

Founder effect in aggregated mixtures

Competition for 'space' or a founder effect (Yodzis 1986) may further play a role for delaying the process of competitive exclusion. In the case of aggregated *Solidago/Calamagrostis* plantings on topsoil coexistence continued until the end of the experiment (Figures 3 and 4). Despite the guerrilla growth of *Calamagrostis*, which invaded the side planted with *Solidago* seedlings within one growing season there is some kind of founder effect. Though it is possible that *Calamagrostis* would have outcompeted *Solidago* later on, within-species aggregation of *Solidago* slowed down competitive exclusion through *Calamagrostis*.

A founder effect for *Solidago canadensis* in aggregated mixtures with *Urtica dioca* was already shown by Schmidt (1981) in a three year field replacement experiment. Aggregated mixtures are not only an artifact of planting designs in experimental studies. In natural communities species are not always well mixed, but often aggregated or clumped (Kershaw & Looney 1985). Silvertown et al. (1992) showed with cellular automaton models of interspecific competition for space that the spatial pattern and configuration of competing species may be just as important as the density and frequency of competitors in determining the outcome. Founder effects can delay competitive

exclusion and hence promote coexistence (Silvertown 1987; Wilson 1990).

Symmetric competition for soil nutrients

Competition for limiting soil nutrients has been assumed to play an important role on substrates of low fertility. However, analysis of nutrient contents revealed that there was only one case with evidence for competition of soil nutrients in short supply. In relation to monocultures of *Solidago*, contents of P, Ca and Mg were lower in *Solidago* plants growing in mixtures with *Tanacetum* on sand. On the other hand, nutrient contents were elevated in *Tanacetum* plants (Rebele 1996b). Also, available P and Ca contents in the soil were lower than at the start of the experiment (Table 1).

These results indicate that resource reduction and competition for soil nutrients which were in short supply might have occurred. Despite this kind of antagonistic exploitation competition, species coexisted until the end of the fifth growing season. Because there is only a slight effect on total biomass, one can assume that competition is not as severe as in the case of competition for light mentioned above. Competition for soil nutrients is reciprocal or symmetric (Weiner 1990) where smaller individuals can maintain their relative sizes through time.

There is a debate whether root competition for soil resources is important when nutrient (and water) supply is low (Grime 1973; Newman 1973; Grubb 1985; Fowler 1986; Belcher et al. 1995; Peltzer et al. 1998). In this experiment there is only weak evidence that plants compete for soil nutrients, but it seems to be most relevant on the substrate of low fertility.

Positive interactions

Relative Yield Totals higher than unity and overyielding indicate that positive effects are greater than negative effects in mixtures. RYT's greater than 1.1 occurred for six possible mixtures (Figure 4). For even more, for 9 of the 15 pairwise combinations, biomass and also nutrient levels were more than 10% higher in mixtures both for the dominant and for the subordinate species, or for the codominant species (Rebele 1996b). I.e., the performance of plants in mixture was better than in monoculture.

RYT's higher than unity are normally interpreted that resources in mixtures are used more efficiently due to niche separation (Wilson 1988). Niche separation can be realized in various ways, e.g. different

rooting depth, differing seasonal patterns of growth, or different resource use of particular resources (Trenbath 1974). The result is that resources are used more completely in mixtures compared to monocultures. In this experiment there is evidence for a stimulation of nutrient uptake and differential resource use in mixtures (Rebele 1996b). However, positive non-uptake effects, e.g., reduced evapotranspiration in mixtures, should also be taken into account. During strong summer droughts *Solidago* plants grown in mixture were less affected by water stress than plants of monocultures.

Facilitative effects have been demonstrated for a wide variety of environments and communities over the world (Fowler 1986; Gigon & Ryser 1986; Callaway 1995; Brooker & Callaghan 1998). Even species with high competitive ability like *Typha latifolia* L. have the potential to facilitate neighbors (Callaway & King 1996).

It is important to realize that replacement series show only net positive, net negative, or no net effects. This means that negative competitive effects can be overlaid by positive facilitative effects and the result is a mitigated negative effect or even a positive net effect.

Apparent competition produced by selective herbivory

Selective herbivory is an important factor for structuring communities because it may change dominance and diversity within plant communities (Tansley & Adamson 1925; Crawley 1983; Cottam 1985; Louda et al. 1990). Herbivores not only select specific plant species, but also may prefer more palatable organs or specimens within populations. Because nitrogen is scarce and a limiting nutrient for many herbivores, vertebrates as well as invertebrates, N content of plants is a crucial factor for feeding animals (Mattson 1980). Selective herbivory may override competitive relationships between plants and cause a shift in dominance or even eliminate a species within a community. The effect of this process can be seen as some kind of 'apparent competition' (Holt 1977, Connell 1990).

Apparent competition produced by selective herbivory also played a role in this study. On topsoil *Tanacetum* was dominant in mixtures with *Solidago* and *Calamagrostis* from the first until the fourth year (cf., Figure 3). In the fifth year however, cover and biomass decreased dramatically in mixtures and to the same degree also in monocultures. This was due to selective herbivory by slugs (*Arion ater*), which ate

nearly all of the fresh *Tanacetum* leaves during spring in all topsoil plots (monocultures as well as mixtures). Herbivory by slugs in the fifth growing season may have been favored by the relatively cool and moist spring of that year compared with other years.

It was surprising that *Tanacetum* plants growing on ruderal soil and on sand were hardly affected and developed well until the end of the growing season. The slugs obviously preferred *Tanacetum* leaves with higher N-concentrations, which contained, e.g., 3.01% N in the nutrient-rich topsoil plots, but only 1.83% N in the ruderal soil, and 1.85% N in the sand plots (Rebele 1996b).

Reversal of rank order during time, with soil properties, and neighbors

Among ecologists studying plant competition there is a controversy whether 'competitive power' or 'competitiveness' is an inherent trait of particular species and whether constant rank orders exist within plant communities. That means that the relative suppressive effects of species on each other are not variable. Campbell & Grime (1992) found that the best competitors in productive condition tended to keep their place in the biomass hierarchy under low fertility. Shipley & Keddy (1994) stated that the available empirical evidence is strongly weighted towards the conclusion that constant rank orders and transitive competitive networks are the most common multi-species patterns among plants. Contrary to this view, Harper (1963) already argued, that the concept of an innate quality of 'competitiveness' as a property of species and not an association of the species with any particular competitor, may have no real meaning. Aarssen (1988) showed that rank order of suppressive effects on a given target species differed depending on which species was the target. Fowler (1982) found that soil fertility and time of year affected the intensity and the outcome of competition. In two of six pairs of grassland species, one species was dominant in one environment, but the other species became dominant in another environment.

This five year field experiment revealed that rank orders changed with soil properties, during time and with the interacting neighbor species. Each of the three species is able to dominate in at least one position along a nutrient gradient. Competitive abilities depend on site factors (nutrient regimes, climatic fluctuations, feeding animals, etc.) and on the particular species

in competition. It is therefore only possible to talk about relative competitive abilities within a given set of species and a given environment. In my study, this result may be due to the fact that the species had very similar morphologies. Shipley & Keddy (1994) predicted that species with very similar morphologies would be most likely to show switches in competitive dominance.

Relative importance of competition and positive interactions along a nutrient gradient

This experiment gives evidence that competition for light is important on the substrate of high fertility, and competition for soil nutrients may play a role on nutrient-poor sandy soil. Competitive exclusion has to be kept in mind, but it occurred only in one mixture over the five years of investigation. It was related to strong asymmetric competition for light in combination with a kind of interference or inhibition competition. In most cases, species coexisted and positive effects of species in mixtures were more important than negative competitive effects. Obviously, the relative importance of root competition for soil nutrients, competition for light and positive interactions changes with soil fertility.

Grime (1973, 1979) predicts an increase in both root and shoot competition along a gradient of increasing soil resources. In contrast, Tilman argues that root competition should decrease and shoot competition should increase along a gradient of increasing soil resources whereas total competition should remain constant (Tilman 1985, 1987, 1988). Results from experiments along gradients testing these hypotheses are contradictory (for review see Belcher et al. 1995; Peltzer et al. 1998). The controversy debate whether competition intensity will or will not increase with an increase in biomass may be due to the fact that investigations have not always been carried out at the upper range of the productivity scale (Bonser & Reader 1995).

Wilson & Keddy (1986); Wilson (1988); Kadmon (1995), and Twolan-Strutt & Keddy (1996) found that competition intensity increased along an increasing gradient of productivity. Twolan-Strutt & Keddy (1996) also found that belowground competition was constant among habitats and they predicted that the relative importance of belowground to aboveground competition intensity decreases with increasing productivity, primarily due to an increase in aboveground competition.

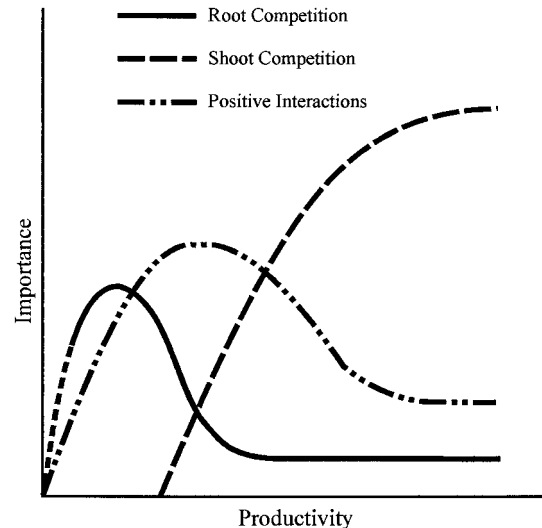


Figure 5. Conceptual model of the relative importance of root competition for soil nutrients, shoot competition for light, and positive interactions among plants along a soil fertility gradient.

This study confirms this prediction. There is evidence that root competition for soil nutrients and shoot competition for light are not of equal importance, especially with respect to competitive exclusion. The probability of competitive exclusion is much higher on substrates of high fertility where asymmetric competition for light might turn into one-sided inhibition of the subordinate species. However, competitive exclusion is not always restricted to highly productive habitats. Wedin & Tilman (1993) found that competitive exclusion can also occur on low-N soils.

The controversy debate of Grime and Tilman about competition intensity along productivity gradients did not relate competition to other kinds of interaction. Kareiva & Bertness (1997) pointed out that positive interactions are pervasive forces in communities and that incorporating them into our understanding of natural systems may resolve many long-standing conceptual problems in ecology. Belcher et al. (1995) presented a graphical model in which changes of mutualism/facilitation and competition intensity along a gradient of increasing biomass and decreasing stress were hypothesized. In that model, facilitation plays a role only in low biomass/high stress sites. However, in my opinion positive interactions should be considered as being important over a broad range of the productivity gradient. Only when shoot competition for light is overwhelming, does the relative importance of positive interactions within communities decline.

Figure 5 shows a modified model of the relative importance of competitive and positive interactions along a productivity gradient. Root competition for soil nutrients plays a greater role on the nutrient poor substrate, but its importance decreases when soil nutrients are plentiful. In contrast, shoot competition for light is absent as long as plant cover is sparse, but increases sharply when cover is dense and species in mixtures are overshadowed by superior competitors or covered with litter. Positive interactions play a role over a broad range of the productivity scale with a peak at intermediate levels of fertility.

This view also contradicts in part the model of Bertness & Callaway (1994) where positive interactions are predicted to be important under harsh physical stress conditions and under intense consumer pressure but not at intermediate levels of physical stress (cf., also Bertness & Leonard 1997). In my model, it is the broad range of intermediate levels of nutrients and physical stress (which are often combined) where positive interactions dominate over negative competitive effects. On sites of high stress and low nutrients facilitative nonuptake effects may play an important role but competition for soil resources may occasionally be more important than such positive effects.

The role of positive effects on sites of high productivity is overlaid by the negative effects of competition for light, but sometimes facilitative effects are also evident. A positive effect of mixtures on topsoil was evident during severe drought periods. *Solidago* was more affected by drought on topsoil plots than on plots of lower fertility and was more affected in monocultures than in mixtures with other species, even when the other species was the superior competitor.

Competition and coexistence of core species with similar morphologies

Analyzing the results of this five year field experiment it is obvious that the three tall perennial species coexisted longer on soils of low and intermediate fertility whereas competitive exclusion and apparent competition occurred on the high-N substrate.

There could be two main reasons for coexistence. The first, a very simple, is that time was not long enough for competitive exclusion. The second explanation is that niche separation may play a role, at least in cases where overyielding occurred. Niche differentiation however could hardly be the result of past competition selection for specialization as it is assumed in the traditional niche concept, because pop-

ulations of the three species introduced from different biogeographical regions have no long common history. The alternative concept of resource partitioning and differential distribution along environmental gradients proposed by Keddy (1989) hypothesizes that species in the core habitat coexist because they share identical growth form. The core habitat is the habitat of highest productivity with light as a limiting resource (Wisheu & Keddy 1992).

All three study species are tall perennials with clonal growth and are approximately competitive equivalent. All species performed best at high fertility levels under optimal environmental conditions. However, the three species responded in different manner to severe drought and herbivore pressure. *Calamagrostis* was less affected by drought and herbivore pressure over the five years of investigation. There is also evidence that slight differences in tolerating low resource levels and in resource acquisition exist between *Tanacetum* and *Solidago* (Rebele 1996b).

Despite very similar morphologies and growth form, *Calamagrostis* was the most successful of the study species in the long run. It dominated in 9 of 12 mixtures after five years. Rare events during time caused a switch in competitive ability even for species with similar morphologies. Although *Tanacetum* and *Solidago* are highly productive for a distinct period on the substrate of high fertility, these species are better adapted and persist longer on the less productive sites. High productivity of these species is combined with high susceptibility to environmental constraints or herbivore pressure and only *Calamagrostis* is able to persist on the most productive soil because it is less affected by drought and/or herbivores.

There are also slight differences in growth strategy. The guerrilla growth type of *Calamagrostis* allows a more rapid lateral spread. Gaps where *Solidago* or *Tanacetum* died back can rapidly be filled by *Calamagrostis*. High production of aboveground biomass and litter further inhibits germination and/or growth of the subordinate species.

These results are consistent with the centrifugal organization model (Keddy 1989, Keddy & Wisheu 1992). *Calamagrostis* is competitively superior in the core habitat with light as a limiting resource. *Solidago* and *Tanacetum* still coexist in the peripheral habitats of lower fertility. However, there remains an open question: The centrifugal organization model assumes that competitive abilities are negatively correlated with fundamental niche width. This is not the case for *Calamagrostis*, the superior competitor in the core habitat.

Calamagrostis shows high competitive ability in high-N habitats but is also able to tolerate low resource levels (see also Rebele 1996a). Further work is needed to answer this question.

Conclusions

Experiments on competition and coexistence should consider all kinds of interactions among plants and evaluate their relative importance which changes along gradients. The present study also shows that the competitive superiority of very similar species can only be seen in the long run. Environmental fluctuations can cause switches in dominance and reverse the rank order in competitive hierarchies. High productivity can be combined with high susceptibility to drought or other environmental constraints. The example of *Tanacetum* on the high-N site reveals that biotic fluctuations are also important. The stands of *Tanacetum* growing in the nutrient rich substrate showed a rapid breakdown after having been attacked by slugs, but developed well on the substrates of moderate and low fertility. One can predict that it is not always best for plants to grow on the upper range of the productivity scale.

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