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The effect of nutrient availability on biomass allocation patterns in 27 species of herbaceous plants

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Abstract

We investigated allocation to roots, stems and leaves of 27 species of herbaceous clonal plants grown at two nutrient levels. Allocation was analyzed as biomass ratios and also allometrically. As in other studies, the fraction of biomass in stems and, to a lesser extent, in leaves, was usually higher in the high-nutrient treatment than in the low-nutrient treatment, and the fraction of biomass in roots was usually higher under low-nutrient conditions. The relationship between the biomass of plant structures fits the general allometric equation, with an exponent $\neq 1$ in most of the species. The different biomass ratios under the two nutrient conditions represented points on simple allometric trajectories, indicating that natural selection has resulted in allometric strategies rather than plastic responses to nutrient level. In other words, in most of the species that changed allocation in response to the nutrient treatment, these changes were largely a consequence of plant size. Our data suggest that some allocation patterns that have been interpreted as plastic responses to different resource availabilities may be more parsimoniously explained as allometric strategies.

Key words: allometric strategies, biomass allocation, clonal plants, nutrient effects

Introduction

Plants may change their allocation patterns in response to the environment (Bloom *et al.* 1985). Availability of soil nutrients is one of the factors that may influence resource allocation patterns (Brouwer 1962). One hypothesis is that plants in low-nutrient environments should allocate proportionally more resources to roots to increase their uptake capacity for these limiting soil resources (Bradshaw 1965; Chapin 1980; Wilson 1988; Gedroc *et al.* 1996). Allocation of resources to different activities has been the central concept of life-history theory (Gadgil & Bossert 1970; Iwasa & Roughgarden 1984; Stearns 1992), and allocation patterns largely determine the ability of plants to capture resources (Poorter *et al.* 1990), to compete with neighbours (Grime 1979; Tilman 1988), and to produce vegetative offspring and seeds (Abrahamson & Gadgil 1973; Bazzaz & Reekie 1985; Schmid & Weiner 1993).

In this study, we ask whether resource allocation patterns are changed by nutrient availabilities in a wide array of clonal plant species grown under two different nutrient regimes. A comparative approach was chosen to look for generality in nutrient effects and to ask about variation in allocation pat-

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terns among species, rather than investigating patterns in fewer species more intensively. To eliminate different environmental effects among species – a major problem of many comparative studies (Wilson & Thompson 1989) – we took an experimental approach, with identical treatments for all species.

Most studies on resource allocation in plants have concentrated on the allocation of biomass. Biomass is easy to measure and the distribution of biomass is thought to reflect the distribution of other "currencies" such as nitrogen (Reekie & Bazzaz 1987). Resource allocation patterns have usually been described and interpreted in terms of the proportion of biomass in different structures. The use of such ratios to test biological hypotheses has recently been criticised (Jasienski & Bazzaz 1999). Resource allocation patterns may change with plant size (Pearsall 1927), i.e. they may be "allometric" in the broad sense, and it has been argued that some observed changes in allocation are primarily due to size (Weiner 1988; Coleman *et al.* 1994; Coleman & McConnaughay 1995). Simply put, if allocation to different structures changes with size, any factor that influences plant size will thereby change allocation.

We asked the following questions:

(i) How general is the predicted decrease in root:leaf, root:stem, and leaf:stem ratios with increased nutrient availability across a large number of clonal herbaceous plant species?

(ii) Can the optimal biomass ratios be explained by single allometric trajectories between the biomass components involved?

(iii) Do species differ in their allometric "strategies"?

Materials and methods

Study species and measurements

Twenty-seven herbaceous, clonal plant species from a wide systematic (20 genera out of 11 families) and ecological range, but all belonging to the central European flora, were investigated (Table 1). Seeds were obtained from the Botanical Gardens of Salzburg in Austria, and of Berlin, Frankfurt, Halle and Jena in Germany. Except for one species (*Apium repens*) all seeds had been collected from natural populations. Seeds were germinated on plates and placed on sand in small pots within the first day after germination. After up to three weeks of establishment in the small pots, seedlings of all species were transplanted into boxes of sand to allow for later harvesting of roots. They were brought into the experimental garden on 18 April 1994.

The species were placed into three groups according to their size and natural habitat: "wet" (five wetland species), "short" (ten short-statured species) and "tall" (12 tall species; Table 1). All species within a group were planted together, one seedling per species, in a box (wet, 30 cm × 40 cm × 20 cm; others 40 cm × 60 cm × 20 cm). The planting position of each seedling was randomly assigned. There were 20 replicated boxes in the wet group and 21 replicated boxes in both the

Table 1. Species cultivated in the experiment in three groups: wetland species, small and tall species. Seeds collected by Botanical Garden Berlin (b), Frankfurt (f), Halle (h), Jena (j), Salzburg (s) or from natural sites in the Swiss Jura mountains (n). Nomenclature follows Binz & Heitz (1990) for Swiss species.

Wetland species (*n* = 5)	Small species (*n* = 10)	Tall species (*n* = 12)
Apium repens (f)	*Fragaria vesca* (s)	*Agrostis tenuis* (b)
Eleocharis palustris (s)	*Fragaria viridis* (s)	*Brachypodium pinnatum* (s)
Galium boreale (b)	*Luzula campestris* (j)	*Bromus inermis* (s)
Juncus compressus (s)	*Oxalis corniculata* (s)	*Carex arenaria* (b)
Juncus tenuis (s)	*Potentilla reptans* (s)	*Carex flacca* (h)
	Prunella grandiflora (n)	*Lolium perenne* (s)
	Prunella vulgaris (n)	*Mentha arvensis* (s)
	Trifolium fragiferum (j)	*Poa compressa* (s)
	Veronica officinalis (b)	*Poa pratensis* (h)
	Veronica serpyllifolia (s)	*Stellaria holostea* (b)
		Trifolium repens (s)
		Trisetum flavescens (s)

short and the tall groups. The positions of the boxes in the experimental garden were randomly changed once a week. The boxes in each group were randomly assigned to a high-nutrient (50 ml $^1/_2$ Hoagland's solution per plant per week; Arnon & Hoagland 1940) and a low-nutrient treatment (50 ml $^1/_8$ Hoagland's solution per plant per week). The final sizes of the plants were consistent with the range of sizes observed in the field, suggesting that the nutrient levels were within the range that these species experience in the field. The plants were also watered with tap water to avoid drought stress throughout the duration of the experiment.

After four months of growth (beginning on 16 August), before plants had attained sizes where competition among individual plants was apparent, all plants were harvested. The numbers of leaves and ramets were counted for all plants. Then the plants were partitioned into roots, leaves, stems, rhizomes and reproductive parts (for the few species that already flowered). All plant fractions were oven-dried at 80 °C for 36 h and weighed. For better comparison among different species, the stems, rhizomes and reproductive shoots were combined and are referred to as "stems", giving us three biomass compartments (Poorter & Nagel 2000).

Statistical analysis

The data were analysed with the general linear model (GLM) approach to analysis of variance (ANOVA; GENSTAT 5 General Statistical Program, release 5.3; Payne 1993). The model terms were fitted according to the hierarchical design of the experiment (individuals within boxes within species groups). For all but the allometric analysis, the treatment model consisted of group (g_i), nutrient (n_j), nutrient-by-group interaction ($(n \times g)_{ij}$), species (s_k) and nutrient-by-species interaction ($(n \times s)_{jk}$), i.e.

$$y_{ijk} = m + g_{i\,+}\, n_j + (n \times g)_{ij} + s_k + (n \times s)_{ijk}$$

The error model consisted of two terms, i.e.

$$y_{ikl} = m + (g \times b)_{il} + e_{ikl,}$$

where $(g \times b)_{il}$ is the deviation due to random box effects within groups, and b refers to box. Group effects, nutrient effects, and their interaction were tested against this "box-within-group" variance, whereas species effects (i.e. species differences) and nutrient-by-species interactions were tested against the residual variance (e_{ikl}). Differences between groups represent effects of position (because of blocking) and species attributes, which could not be separated according to our design. Whenever necessary, data were log-transformed to increase homoscedasticity and normality of residuals.

In addition to the overall analysis we also carried out separate ANOVAs for each species to analyse the different species-specific growth patterns and nitrogen responses in more detail. These analyses were done with the original variables and with percentages and ratios.

The species were also analysed, together and individually for allometric relationships between the biomasses of different structures (referred to below as *X* and *Y*). We looked at the allometric relationships between biomass compartments, not between compartments and total biomass, as some authors suggest (Poorter & Nagel 2000). Since total biomass includes stem biomass, these two variables are not likely to be independent. We used the classical allometric equation:

$$Y = \alpha X^{\beta},$$

where β is the allometric exponent and α is the allometric coefficient (Huxley 1932; Lumer 1936; Gould 1966). The allometric equation was log-transformed to yield a simple linear relationship:

$$Y = a X^{\beta} \Leftrightarrow \log(Y) = \log(\alpha) + \beta \log(X),$$

where the allometric exponent becomes the slope and the log of the allometric coefficient is the intercept.

Following Samson & Werk (1986) and Klinkhamer *et al.* (1990), *F*-tests were used to investigate proportionality of allocation and the influence of nutrients on these relationships. This was done using one component of biomass as the dependent variable (*Y*) and the other as the covariate (*X*) in the GLM models. Because there is no consensus about the most appropriate regression model for allometric analyses (Smith 1980; Seim & Sæther 1983; Schmid *et al.* 1994), we performed both least square (*LS*) and reduced major axis (*RMA*) regressions to estimate allometric slopes (b_i) for each species. Unlike *LS* regression, *RMA* regression assumes that there is error variance of the same magnitude in both the response variable and the covariate (Schmid *et al.* 1994).

Table 2. Influence of nutrient levels on biomass compartments, their ratios and allometric relationships. N and C × N refer to significance of nutrient and covariate × nuturient in the allometric analyses. Significance levels: +, $P < 0.1$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

	Root biomass	Leaf biomass	Stem biomass	No. of ramets	No. of leaves	Root: leaf	Root: stem	Stem: leaf	Root-leaf allometry		Root-leaf allometry		Stem-leaf allometry	
									N	C × N	N	C × N	N	C × N
Agrostis tenuis	*	**	*	*	**	*				**		*		
Apium repens	**	***	***	***	***	*	**							
Brachypodium pinnatum						*			+					
Bromus inermis	*	**	*	*	*						+	+	*	*
Carex arenaria				+	*									
Carex flacca	*	*	*		*									
Eleocharis palustris	*					***	**		***		**			
Fragaria vesca	***	***	***	***	***				+					
Fragaria viridis	***	***	***	***	***									***
Galium boreale	*	**	**		*									
Juncus compressus	*	*												
Juncus tenuis	**	***	***	*	*	*	***	*			*			*
Lolium perenne	**	***	***	***	***	***	*							
Luzula campestris	*	**	+											
Mentha arvensis														
Oxalis corniculata	*	***	***	**	**	***	***							
Potentilla reptans	***	***	***	***	***	***	**						**	*
Poa compressa	***	***	***	**	**	***	***				+			
Poa pratensis	**	***	+	*	**	**		*	*					
Prunella grandiflora						*		***	*				**	
Prunella vulgaris	*	*	**				+	*					*	
Stellaria holostea			+		+		+						**	
Trisetum flavescens	**	***	***	*	*	***	***	***	*					
Trifolium fragiferum			+			*	*				*			
Trifolium repens							**	+						
Veronica officinalis	***	***	***	**	***		*	***						
Veronica serpyllifolia	*	***	***		+	+	**	**	*		+			

The results of the separate analyses were used to determine the best fitting model for each species. In species that showed no significant ($P > 0.05$) nutrient effect in the separate analyses, slopes were estimated from a joint regression for both nutrient levels. In species with a significant nutrient effect but no significant covariate-by-nutrient interaction, parallel regression lines were fitted. If the interaction term in a species analysis was significant, the allometric exponents were estimated from separate regressions for each nutrient level. The calculation of all possible allometric relationships has the consequence that these analyses are not independent. Because our goal was to explore the variation in species allometries rather than to test a particular relationship, we did not use corrective measures for the dependence.

Results

Effects of nutrients and species on plant size

Pooled over all species, total biomass increased by 118% ($P < 0.001$) from the low- to the high-nutrient treatment. Despite this highly significant general pattern, species varied greatly in their biomass ($P < 0.001$) and in their response to nutrients (significant nutrient-by-species interaction, $P < 0.001$). When the species responses were tested individually, the increase from the low- to the high-nutrient treatment ranged from –16% to +640%. Nineteen of the 27 species showed a significant ($P < 0.05$) increase and none showed a significant decrease in total biomass in response to higher nutrient levels. The different components of biomass (i.e. biomass of roots, leaves, stems) showed similar patterns of variation. Pooled over all species there was a highly significant ($P < 0.001$) increase in all three biomass compartments in response to higher nutrient availability, as well as a high variance among species. In the separate analyses of species responses, 20 species showed a significant increase in root, 19 species in leaf, and 16 species in stem biomass (Table 2). In 7 species no significant effects of nutrient availability on any of the biomass components could be detected. In one species, *Eleocharis palustris*, root biomass was significantly lower at higher nutrient availability ($P < 0.05$).

Pooled over species, both the number of ramets and the number of leaves increased significantly in the high-nutrient treatment ($P < 0.001$). The same was true for most species if tested individually (Table 2). The number of leaves per ramet, however, remained unaffected by the nutrient treatment, suggesting that module size was less plastic than module number (i.e. plant size).

Patterns of biomass allocation considered as biomass ratios

The fraction of total biomass in aboveground organs (stems and leaves) very generally increased and fraction in roots decreased with higher nutrient availability. Thus, root:leaf and root:stem ratios were lowered by high nutrient availability. Further, stem:leaf ratios were increased by high nutrient availability. In addition to these common effects there was again significant variation among species in mean ratios and in responses of ratios to nutrients (Table 3).

Table 3. Analyses of variance tables for log-transformed biomass ratios. Significance levels: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$ (*df*, degree of freedom; *SS*, sum of squares; *VR*, variance ratio or *F*-value).

Source of variation		Root:leaf ratio			Root:stem ratio			Stem:leaf ratio		
	df	*SS*	*VR*		*SS*	*VR*		*SS*	*VR*	
Group	2	119.718	377.18	***	81.214	200.93	***	42.634	201.85	***
Nutrient	1	8.913	56.16	***	17.292	85.56	***	1.376	13.03	***
Group x nutrient	2	0.339	1.07		0.185	0.46		0.893	4.23	**
Box [group]	56	8.885	1.32		11.317	1.19		5.914	1.12	
Species [group]	24	100.533	34.82	***	348.563	85.86	***	318.985	141.57	***
Nutrient × species [group]	24	4.822	1.67	*	8.575	2.11	**	6.240	2.77	***
Residual	420	50.525			71.045			39.432		
Total	529	293.735			538.190			415.474		

In separate species analyses the lowered root:leaf ratio at higher nutrient availability was significant only in 12 species. One species, *Prunella grandiflora*, which typically occurs in nutrient-poor habitats and has a particularly conservative growth strategy (Birrer 1994), even had a significantly higher root:leaf ratio under higher nutrients. Root:stem ratios were also significantly lower under higher nutrient conditions for 12 species, whereas stem:leaf ratios were significantly higher in seven and lower in one (*Poa pratensis*) species at the higher nutrient levels (Table 2). A total of ten species out of the 27 species investigated did not show any significant ($P < 0.05$) change in biomass ratios of component organs in response to nutrient level.

Patterns of biomass allocation considered as allometries

On the log-log-scale all allometric relationships between roots, leaves and stems varied significantly among species both in intercept (allometric coefficient) and slope (allometric exponent; significant species term and covariate-by-species interaction in Table 4). Nutrient availability only affected the intercept (allometric coefficient) of the stem-leaf allometry but had no other effects on allometric relationships, both overall and among the different plant species (nutrient term, covariate-by-nutrient interaction, covariate-by-nutrient-by-species interaction in Table 4). This is in stark contrast with the large effects of nutrient availability on biomass ratios. Thus, the different ratios represent different points (i.e. different plant size) on common allometric trajectories.

The results obtained from separate allometric analyses were consistent with the results of the combined analysis of all species. On the log-log-scale significantly ($P < 0.05$) different slopes (allometric exponents β_i; columns "C × N" in Table 2) in allometric regression lines for low- vs. high-nutrient treatments were found in only one out of 27 species for root-leaf allometry (Fig. 1a) and root-stem allometry, and in four species for stem-leaf allometry. There were significant differences in allometric coefficients (α_i; column "N" in Table 2) between low- and high-nutrient treatments in five species for roots vs. leaves (Fig. 1b), in three species for roots vs. stems, and in five species for stems vs. leaves. In all these species with the exception of *Prunella grandiflora*, less biomass was allocated to roots in high- than in low-nutrient treatment for any given amount of biomass allocated to leaves or stems.

Table 4. Sequential analyses of variance tables for allometric relationships. The biomass component mentioned first in each column head is the dependent variable, the other component the covariate. Significance levels: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

Change		Root-leaf allometry			Root-stem allometry			Stem-leaf allometry		
	df	*SS*	*VR*		*SS*	*VR*		*SS*	*VR*	
+ covariate	1	468.617	4993.50	***	344.804	3179.20	***	610.697	7378.20	***
+ group	2	109.973	310.50	***	116.654	243.33	***	28.433	139.78	***
+ nutrient	1	0.439	2.48		0.726	3.03		3.980	39.13	***
+ covar × group	2	0.059	0.16		4.472	9.33	***	8.940	43.95	***
+ covar × nutrient	1	0.000	0.00		0.040	0.18		0.005	0.05	
+ group × nutrient	2	0.687	1.94		0.305	0.64		1.006	4.95	*
+ covar × group × nutrient	2	0.479	1.35		1.224	2.55		0.268	1.32	
+ box [group]	56	9.917	1.87	***	13.425	2.21	***	5.696	1.23	
+ species [group]	24	73.364	32.21	***	173.086	66.50	***	305.118	153.60	***
+ covariate × species [group]	24	4.662	2.05	**	6.154	2.36	***	7.422	3.74	***
+ nutrient × species [group]	24	4.208	1.85	**	5.365	2.06	**	4.446	2.24	***
+ covar × nutri × spec [group]	24	2.021	0.89		3.207	1.23		1.984	1.00	
Residual	366	34.732			39.695			30.294		
Total	529	709.158			709.158			1008.290		

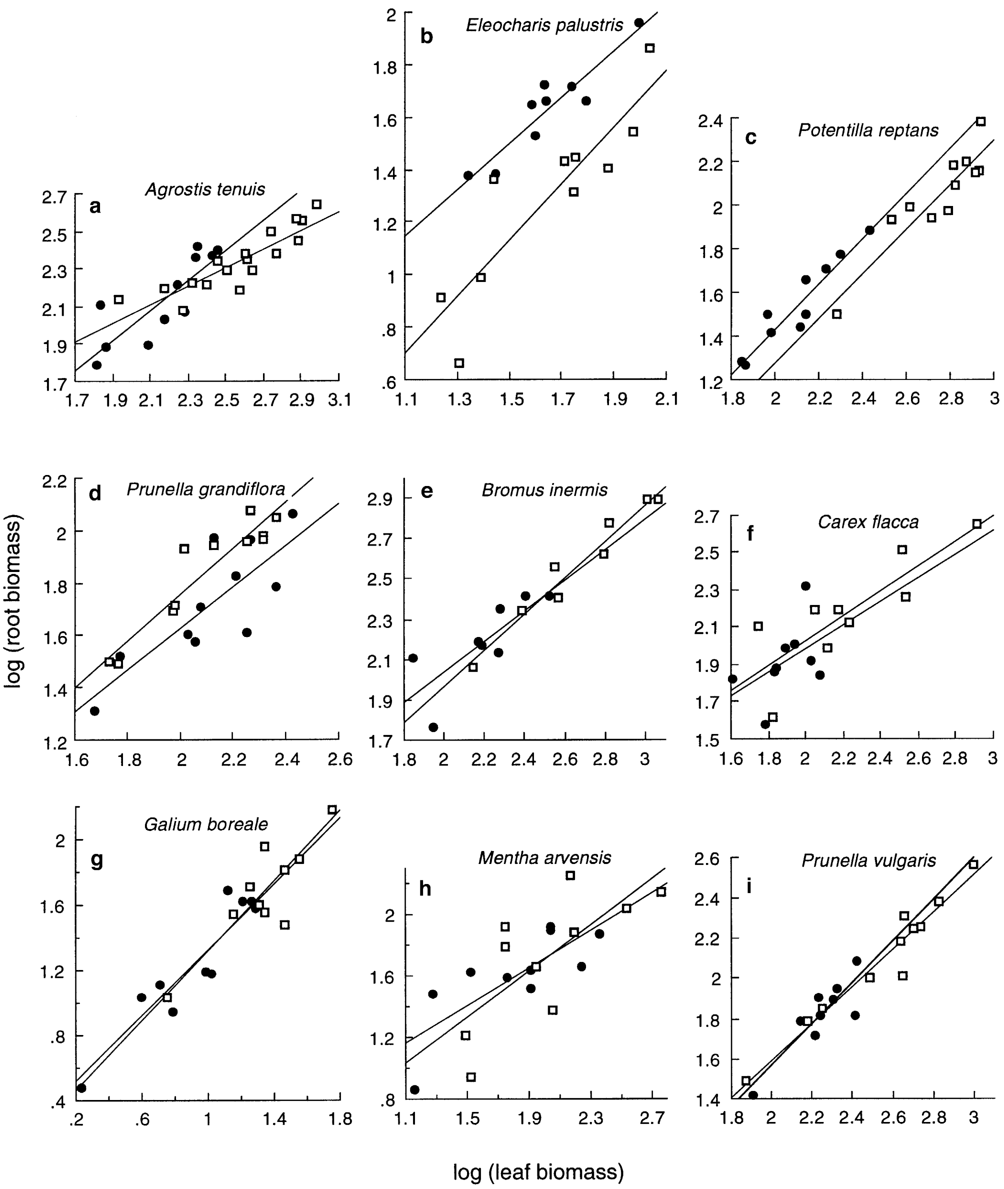

Fig. 1. Three types of effects of nutrient availability on the allometric relationship between root and leaf biomass. (a) Significant differences ($P < 0.05$) in allometric exponents between nutrient treatments, i.e. size-dependent effect (one species: *Agrostis tenuis*). (b)–(d) Significant differences ($P < 0.05$) in allometric coefficients between nutrient treatments, i.e. size-independent effect (five species). (e)–(i) No significant differences in allocation between nutrient treatments (21 species; ●, low-nutrient; □, high-nutrient treatment).

Table 5. Estimates of allometric exponents of best fitting model using least-square (*LS*) and reduced major axis regression (*RMA*). Model fitted: (I) no nutrient effect fitted, i.e. joint regression, (II) no interaction fitted, i.e. parallel regression lines, (III) full model, i.e. independent regressions. Significant departure from isometry: +, $P < 0.1$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. *Nl, Nh* refer to different estimates for low and high nutrient treatments.

	Root-leaf allometry							Root-stem allometry							Stem-leaf allometry						
	model fitted	*df*	r^2	β *LS*	*SE*	*LS*	*RMA*	*model* fitted	*df*	r^2	β *LS*	*SE*	*LS*	*RMA*	*model* fitted	*df*	r^2	β *LS*	*SE*	*LS*	*RMA*
Agrostis tenuis	III Nl	9	83.0	0.977	0.138			III Nl	9	70.7	0.943	0.188			I	26	75.9	0.769	0.083	**	
	III Nh	15	75.6	0.491	0.069	***	***	III Nh	15	36.0	0.386	0.122	***								
Apium repens	I	18	83.1	0.880	0.090			I	18	82.8	0.735	0.077	**		I	18	87.8	1.124	0.096		**
Brachypodium pinnatum	II	18	74.4	0.914	0.118		+	I	19	73.5	0.714	0.095	**		I	19	84.3	1.134	0.109		**
Bromus inermis	I	14	89.5	0.831	0.073	*		I	14	83.8	0.631	0.071	***	**							
								III Nl	6	80.6	0.443	0.081	***	***	III Nl	6	88.9	1.858	0.246	***	**
								III Nh	6	83.7	0.726	0.120	*		III Nh	6	94.4	1.148	0.105		+
Carex arenaria	I	17	70.0	0.968	0.148		*	I	17	69.9	0.601	0.092	***		I	17	93.3	1.558	0.098	***	***
Carex flacca	I	15	63.4	0.704	0.131	*		I	15	66.3	0.672	0.118	*		I	15	91.4	1.025	0.078		
Eleocharis palustris	II	16	75.8	1.021	0.156			II	16	71.4	1.005	0.173		*	I	17	90.8	0.940	0.070		
Fragaria vesca	I	17	96.0	1.011	0.049			I	17	91.6	0.956	0.068			I	17	92.1	1.010	0.054		+
	II	16	96.6	1.161	0.087	+	*														
Fragaria viridis	I	16	85.8	0.802	0.079	*		I	16	79.0	0.670	0.083	**	+	III Nl	5	96.4	1.488	0.116	***	**
															III Nh	9	93.0	0.951	0.082		
Galium boreale	I	18	86.9	1.039	0.092		*	I	18	88.2	0.984	0.082			I	18	96.0	1.043	0.049		+
Juncus compressus	I	16	66.6	0.992	0.168		*	I	16	70.6	0.883	0.137		+	I	16	75.2	1.010	0.139		*
Juncus tenuis	I	18	72.3	0.816	0.115			II	17	90.4	0.633	0.058	***	***	III Nl	8	88.9	2.204	0.258	***	***
															III Nh	8	58.6	1.094	0.295		*
Lolium perenne	I	18	59.2	0.431	0.081	***	**	I	18	50.4	0.323	0.072	***	***	I	18	66.0	1.021	0.166		**
Luzula campestris	I	17	46.7	0.627	0.153	*	*	I	17	59.0	0.602	0.116	**		I	17	67.6	0.963	0.155		**
Mentha arvensis	I	17	54.2	0.612	0.130	**		I	17	67.1	0.659	0.107	**		I	17	89.4	0.972	0.079		
Oxalis corniculata	I	17	72.4	0.581	0.084	***	*	I	17	63.2	0.413	0.073	***	***	I	17	83.9	1.216	0.125	+	**
Poa compressa	I	19	82.7	0.569	0.058	***	***	I	19	84.6	0.622	0.059	***	***	III Nl	8	93.3	1.027	0.091		
															III Nh	9	89.2	0.672	0.073	***	**
Poa pratensis	I	19	78.9	0.633	0.073	***	*	II	18	65.0	0.600	0.132	**		I	19	49.6	0.563	0.124	**	
Potentilla reptans	II	18	94.0	1.031	0.095			I	19	85.7	0.793	0.072	*		I	19	94.9	0.999	0.052		
Prunella grandiflora	II	17	72.5	0.842	0.12			I	18	56.1	0.566	0.112	**		II	17	70.8	1.044	0.167		*
Prunella vulgaris	I	18	92.4	0.933	0.061			I	18	75.0	0.760	0.10	*		II	17	88.4	0.919	0.102		
Stellaria holostea	II	16	76.6	0.599	0.076	***	*	I	16	76.7	0.622	0.083	***	*	I	15	98.7	0.921	0.029	*	*
Trifolium fragiferum	II	17	91.6	0.730	0.051	***	**	I	18	71.4	0.586	0.084	***	*	I	17	86.0	0.961	0.096		
Trifolium repens	I	19	69.6	0.936	0.137		*	II	18	70.2	0.849	0.122			I	19	77.1	1.019	0.123		*
Trisetum flavescens	I	18	77.7	0.583	0.071	***	**	I	18	68.3	0.398	0.062	***	***	I	18	85.6	1.282	0.120	*	***

A total of 14 species showed a significant departure from isometry in roots-leaf allometry, if allometric exponents were estimated with least square regression (i.e. $\beta_{LS} \neq 1$). All these species decreased allocation to roots with increasing allocation to leaves, i.e. their allometric exponents were significantly smaller than one (Table 5). A somewhat different pattern was observed in the exponents calculated from reduced major axis regression. In nine of the above 14 species β_{RMA} was also significantly smaller than one, but seven other species had β_{RMA} significantly greater than one (Table 5). The amount of biomass allocated to roots increased significantly less than the amount allocated to stems in 21 species using *LS* regression (i.e. $\beta_{LS} < 1$); nine of these species retained this pattern when analysed with *RMA* regression (Table 5). The allometric relationship between stems and leaves showed a more variable pattern: in *LS* regression analyses, the allometric exponent was >1 in six species (Fig. 2), with *RMA* regression this number increased to 14 species (Table 5).

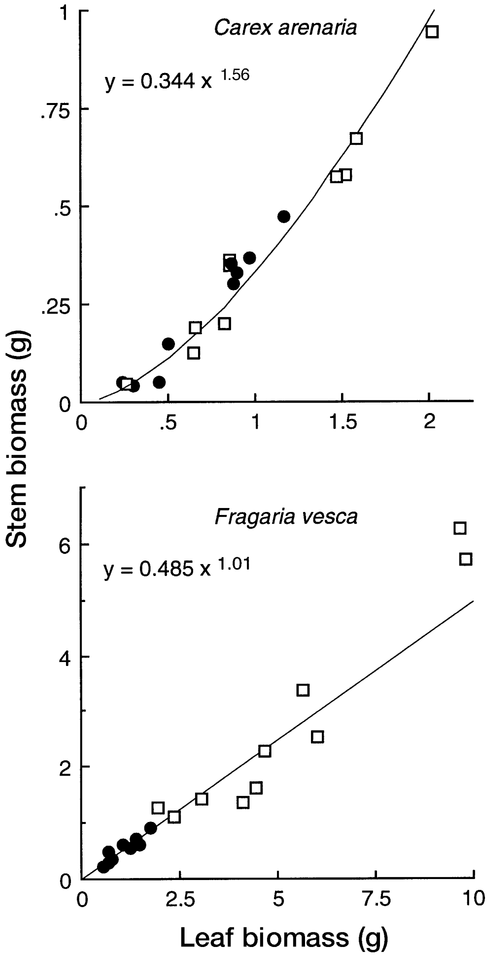

Fig. 2. Size-dependencies of biomass allocation. Allometric (i.e. size-dependent) pattern of biomass allocation in *Carex arenaria.* Isometric pattern of biomass allocation in *Fragaria vesca* (●, low nutrient treatment; □, high nutrient treatment). Allometric equations and correlation coefficients estimated by least-square regression.

Difference between ratio and allometric analyses

There were notable differences between the analyses of biomass ratios and the allometric analyses. Overall, the influence of nutrient availability on biomass allocation patterns as represented by biomass ratios was pronounced, but in allometric analyses the nutrient effects mostly disappeared, even though allometric analyses fit better, i.e. explained more of the total variation. The adjusted r^2

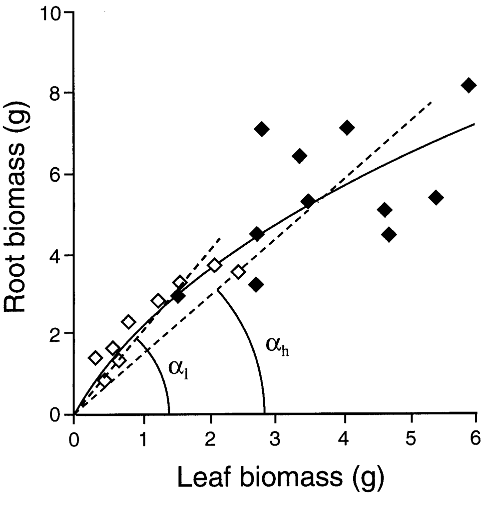

Fig. 3. Differences in biomass allocation to roots vs. leaves in *Trisetum flavescens* depending on nutrient treatment. Analysis of biomass ratios indicates a significant ($P < 0.001$) difference in allocation between nutrient treatments (α_h = mean ratio high-nutrient < α_l = mean ratio low-nutrient). In contrast, allometric analysis of the same data indicates no significant difference between nutrient treatments. Solid line represents the joint allometric regression line for both treatments (◇, low-nutrient level; ◆, high-nutrient level).

was higher for the allometric analyses than for the ratio analyses in all three investigated relationships, i.e. 92.9% (allometric analyses) vs. 78.3% (ratio analyses) for the relationship between root and leaf biomass, 91.9% vs. 83.4% for the relationship between root and stem biomass and 95.7% vs. 88.0% for the relationship between stem and leaf biomass.

In 22 of the 33 analyses that showed significant differences in biomass ratios between nutrient treatments, there were no differences in the allometric relationships (e.g. *Lolium perenne*, *Oxalis corniculata* or *Trisetum flavescens*; Fig. 3). The opposite case – no significant differences in ratios between nutrient treatments but significant differences in allometries – was found in only six of the total of 81 analyses.

Discussion

Plant size and biomass allocation

Models of optimal biomass allocation in plants predict decreasing root allocation with increasing nutrient availability (Bloom *et al.* 1985). Because nutrient availability commonly decreases and light competition increases during occupation of an open site by plants in secondary succession, a typical allocation trajectory in the root-stem-leaf allocation triangle is predicted (Tilman 1988). A number of empirical studies are in agreement with these predictions (Chapin 1980; Olff *et al.* 1990; Tilman & Wedin 1991; Aerts *et al.* 1992; Olff 1992; van de Vijver *et al.* 1993). However, there is also large variation in biomass allocation patterns within and among studies (Körner & Reinhardt 1987; Olff *et al.* 1990; Poorter & Remske 1990; Aerts *et al.* 1992; Olff 1992; van de Vijver *et al.* 1993).

In our own study we confirmed the general applicability of the predicted relationships to a large number of species, but also found variations on the theme. More "opportunistic" species (e.g. *Eleocharis palustris, Juncus tenuis, Lolium perenne, Oxalis corniculata, Poa compressa, Trisetum flavescens* or *Veronica serpyllifolia*) showed a larger response to nutrient availability in their allocation patterns than did other species (e.g. *Carex flacca, Fragaria vesca, Luzula campestris* or *Mentha arvensis*). One species from nutrient-poor habitats, *Prunella grandiflora*, was so conservative that it even increased its root:leaf ratio under higher nutrients.

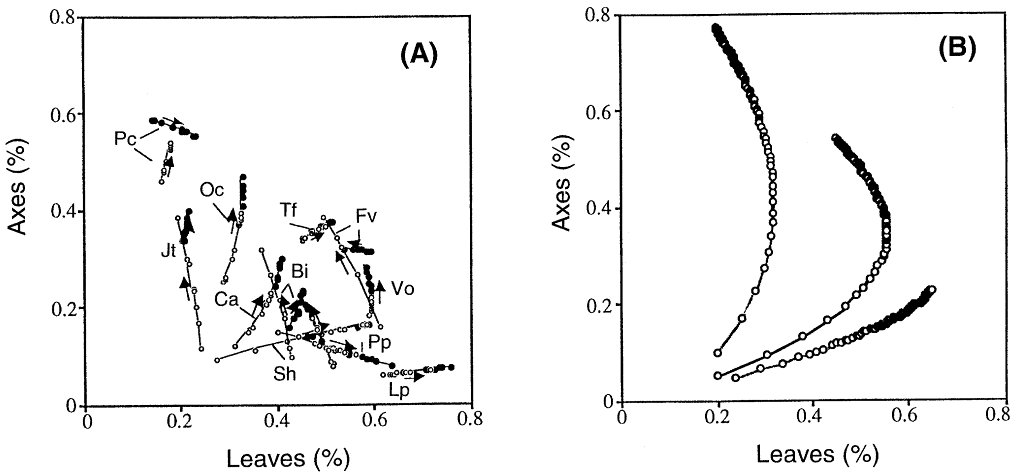

Fig. 4. Changes in allocation patterns caused by allometric relationships. (a) Allocation patterns of species with size-dependent biomass allocation. Points represent fitted values of the best-fitting allometric model, arrows indicate the progression with increasing size. Species names: Bi, *Bromus inermis*; Ca, *Carex arenaria*; Fv, *Fragaria viridis*; Jt, *Juncus tenuis*; Lp, *Lolium perenne*; Oc, *Oxalis corniculata*; Pc, *Poa compressa*; Pp, *Poa pratensis*; Sh, *Stellaria holostea*; Tf, *Trifolium fragiferum*; Vo, *Veronica officinalis.* (b) Allometric changes calculated for three pairs of possible allometric exponents. Curve to the left: $\beta_{\text{axes v. leaves}} = 1.2$, $\beta_{\text{roots v. leaves}} = 0.7$; center: $\beta_{\text{axes v. leaves}} = 1.1$, $\beta_{\text{roots v. leaves}} = 0.5$; right: $\beta_{\text{axes v. leaves}} = 1.05$, $\beta_{\text{roots v. leaves}} = 0.75$.

Allometry of biomass allocation

Most empirical studies of allocation have analysed only biomass ratios. We could show by allometric analyses that the different ratios under low and high nutrient availability can be achieved with a single allometric strategy in the great majority of plant species. This means that biomass ratios vary with overall plant size in a way that is generally adaptive. At small sizes (early in life or under low nutrient availability) allocation to roots is highest, but later on allocation is shifted more towards the leaves and eventually to the stem. This trajectory is the same as that predicted by Tilman (1988) for communities of plant species, except in this case it occurs within individuals of a species (Fig. 4).

Allometric analyses have been widely used to study plant architecture and size-dependencies of various processes (Gould 1966; Niklas 1994 and references therein), but they are also well suited to test for size-dependency in resource allocation, and have been successfully applied to reproductive allocation (Samson & Werk 1986; Klinkhamer *et al.* 1990; Schmid & Weiner 1993; Schmid *et al.* 1994). Sulfur dioxide did not alter root-shoot allometry in *Raphanus sativus* (Coleman & McConnaughay 1995). Nutrient level influenced root-shoot allometry in *Abutilon theophrasti* and *Chenopodium album* when nutrients levels were kept constant, but not when the nutrient regime was altered during growth (Gedroc *et al.* 1996). Competition has been shown to alter several aboveground allometries in annual plants (Weiner & Thomas 1992; Weiner & Fishman 1994).

The allometric exponents estimated from the separate allometric analyses for the species (Table 5) clearly demonstrate size-dependency of allocation patterns for many of the species in our experiment (e.g. 21 out of 27 for allocation to roots vs. stems), although there was considerable variation in the size-dependency of biomass allocation among species. This variance in allometric exponents among species is consistent with data on biomass allocation for seedlings of herbaceous species from Canadian wetlands (Shipley & Peters 1992) and for mangroves species (Turner *et al.* 1995). Despite the great variance in allometric exponents among species, the general trend of (1) decreasing allocation to roots and increasing allocation to leaves and stems (i.e. $\beta_{\text{root-leaf}} < 1$ and $\beta_{\text{root-stem}} < 1$) with increasing size, and (2) allocation to stems increasing more with size than allocation to leaves (i.e. $\beta_{\text{stem-leaf}} > 1$), were remarkably similar in most species. In Shipley & Peters' (1990) results, the effect of size on allocation to roots vs. allocation to shoots was less consistent among species; some species increased and some species decreased allocation to roots with an increase in size. Shipley & Peters measured their plants at a much younger age (30 days) than we did (>120 days), which might explain some of the differences between their results and ours.

The allometric analyses revealed only minor effects of nutrient supply on allocation patterns. Looking across all species, there was no effect of nutrient supply on root-leaf or root-stem allometry. This means that a common allometric relationship can be used to describe allocation in both nutrient treatments. An effect of size itself on allocation patterns is indicated by an allometric exponent different from one. The allometric coefficient of the allocation to stems vs. leaves was increased by nutrient application; plants in high-nutrient environment allocated more biomass to stems irrespective of plant size (same allometric exponent in both nutrient treatments).

It is remarkable that the allometry of biomass allocation was rarely affected by nutrient availability. While there are some documented cases in which nutrient levels do alter root:shoot ratios at the same plant size (e.g. Ericsson 1995), many plants seem to be "form-conservative", i.e. the form and therefore the allocation of biomass of a plant at a given size is the same irrespective of the nutrient environment. In this case, the optimal biomass allocation in the proportional sense must be achieved by the plant via an adjustment of its size (Poorter & Nagel 2000). It may be more parsimonious for plants to have an evolved simple allometric strategy than an evolved programme of how to adjust to particular resource availabilities. Since plants are usually small under low and large under high nutrient conditions, a single allometric strategy can produce the required optimal high and low root:shoot ratios. Similarly, optimal stem:leaf ratios may often be achieved with a single stem – leaf allometric strategy. It is known that the investment of biomass to mechanical support increases more with size than does the investment in photosynthetic tissue (Niklas 1994, p. 155). Allometric analyses are tools to explore the role of size

(Gould 1966), not necessarily to “remove” the effects of size.

Whereas allometries represent relationships of plant form, in clonal plants size is also related to number of modules, offering these plants another way to respond flexibly to the environmental conditions and to overcome allometric constraints (Silvertown 1983; Schmid 1990). In our study the numbers of both ramets and leaves increased greatly with higher nutrient supply, but the internal architecture of a ramet, i.e. number of leaves per ramet, was remarkably constant.

The two types of analyses presented in this study reflect two different conceptions of allocation in plants. In the “ratio” view, a plant has a certain biomass at any point in time and allocates it proportionally to different structures. In the allometric view, allometry is seen as the quantitative translation of growth into allocation. Plants evolve allometric patterns in response to numerous selection pressures and constraints. The specific allometric relationships of biomass allocation of a genotype are fundamental aspects of the genotype’s “strategy”, which is the result of natural selection (Weiner 1988).

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