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Schippers, Peter; Olff, Han

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Biomass partitioning, architecture and turnover of six herbaceous species from habitats with different nutrient supply

Peter Schippers[1,*] & Han Olff[2]
[1]*Department of Theoretical Production Ecology,* [2]*Department of Terrestrial Ecology and Nature Conservation, Wageningen, The Netherlands; (*Present address: Netherlands Institute of Ecology, Rijksstraatweg 6, 3631 AC Nieuwersluis, The Netherlands) (E-mail: schippers@cl.nioo.knaw.nl)*

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Abstract

Three grasses (*Holcus lanatus, Anthoxanthum odoratum and Festuca ovina*) and three herbs (*Rumex obtusifolius, Plantago lanceolata* and *Hieracium pilosella*) were grown in a greenhouse at 3 nutrient levels in order to evaluate plant allocation, architecture and biomass turnover in relation to fertility level of their habitats.

Four harvests were done at intervals of 4 weeks. Various plant traits related to biomass partitioning, plant architecture, biomass turnover and performance were determined. Differences in nutrient supply induced a strong functional response in the species shoot:root allocation, but architecture and turnover showed little or no response. Architectural parameters like specific leaf area and specific root length, however, in general decreased during plant development.

Species from more nutrient-rich successional stages were characterized by a larger specific leaf area and longer specific shoot height (height/shoot biomass), resulting in a higher RGR and total biomass in all nutrient conditions. There was no evidence that species from nutrient-poor environments had a longer specific root length or any other superior growth characteristic. The only advantage displayed by these species was a lower leaf turnover when expressed as the fraction of dead leaves and a shorter specific shoot height (SSH) which might prevent herbivory and mowing losses.

The dead leaf fraction, which is a good indicator for biomass and nutrient loss, appeared to be not only determined by the leaf longevity, but was also found to be directly related to the RGR of the species. This new fact might explain the slow relative growth rates in species from a nutrient-poor habitat and should be considered in future discussions about turnover.

Introduction

The successional change in plant species dominance in grasslands depends on the balance between growth and losses of biomass. If the growth of a species exceeds its losses it will increase in biomass. Conversely, if biomass losses exceed growth, the biomass of a species will decrease.

The growth of a species depends on its ability to capture resources such as light and nutrients (Tilman 1985). Biomass senescence, mowing and herbivory determine the loss of nutrients and carbon to the environment. Plants may adapt to nutrient-poor environments either by increasing their ability to compete for nutrients or by reducing losses of nutrients by minimizing their biomass turnover (Berendse & Elberse 1990).

Various morphological traits determine the ability of species to compete for resources. Light capture in a vegetation is determined by the species height and the distribution of the leaf area over the height (Kropff & van Laar 1993). In turn, the total leaf area is determined by the specific leaf area (SLA $m^2\ g^{-1}$ leaf) and the dry weight of the leaves. The height of the plant depends on the specific shoot height (SSH cm g^{-1}

shoot) and the biomass present in the shoot (Schippers et al. 1999).

Root length is an important determinant to capture nutrients it too can be estimated from the root weight and the specific root length (cm g^{-1} root). The weight of the different plant parts depends on the biomass partitioning and the total plant weight. So we can distinguish two categories of plant properties. (1) Partitioning, which describes a plant's investment in organs and (2) Architecture, which describes the form of plant parts. Partitioning is ruled by direct trade-offs: biomass investment in a certain plant part cannot be used elsewhere. The plant's architecture is independent of allocation trade-offs and can be considered as a measure of how efficiently biomass is used. A species can make more leaf area and root length with the same amount of biomass by making thinner leaves and roots. But a more efficient plant architecture is often inversely related to tissue longevity (Berendse & Elberse 1990).

Various studies have been performed to relate plant properties to the nutrients status of species. In these studies two categories can be distinguished: (1) Short-term growth experiments, shorter than a month, involving a large number of species (25–35), concentrating on the species RGR and related parameters (Poorter & Remkes 1990; Gleeson & Tilman 1994; Werf van der et al. 1998) and (2) Longer term experiments covering one growing season or more concentrating on a few representative species (2–8). (Olff et al. 1990; Olff 1992; Vijver et al. 1993; Elberse & Berendse 1993; Ryser & Lambers 1995; Schläpfer & Ryser 1996). The current view from these studies is that fast-growing species, adapted to nutrient-rich environments, are characterized by a high SSH and SLA, whereas slow-growing species, adapted to nutrient-poor habitats, are characterized by low biomass turnover and a longer specific root length. We adapt this this current view about species characteristics as a working hypothesis for this study.

Although the above studies contribute a lot to our current understanding of succession little attention has been given to: (1) the change in architecture and allocation during plant growth and (2) the effect of nutrients on the architecture and allocation of species To clarify the points above we conducted a greenhouse experiment to examine the effect of nutrient availability on the architecture, allocation and turnover in time.

Table 1. Selected species and their habitat.

Habitat	Grasses	Forbs
(1) Nutrient-poor	*Festuca ovina* L. ssp. tenuifolia (Sibth.)	*Hieracium pilosella* L.
(2) Intermediate	*Anthoxanthum odoratum* L.	*Plantago lanceolata* L.
(3) Nutrient-rich	*Holcus lanatus* L.	*Rumex obtusifolius* L.

Materials and methods

Experimental design

Six perennial species were selected (Table 1), from habitats with different nutrient availability according to Grime et al. (1988). Three seedlings of each species were planted in 3-l pots filled with a mixture of 33.3% sandy field soil and 66.6% washed river sand resulting in a sandy soil contained 1.1% carbon and 0.05% total nitrogen. Ten seedlings per species were measured at the start of the experiment to calculate the initial RGR. The pots were placed according to a random complete block design in 3 blocks in a greenhouse in Wageningen the Netherlands (latitude: 51.58°, longitude 5.40°). The initial pot density was 16 pots m^{-2} and decreased to 4 pots m^{-2} at the last harvest. The experiment was started on 28 February 1994. Plants were harvested four times at intervals of 4 weeks.

At the start of the experiment each pot were surrounded by mesh to prevent plant interaction between pots. As a result the area of growth was limited to 298 cm^2. The plants were given NPK fertilizer (15-12-24) at three rates, equivalent to 0, 5, and 20 g of nitrogen per m^2. (20 g is a normal fertilization rate for pastures in the Netherlands). These treatments will hence forth be referred to as N1, N2 and N3. Throughout the experiment the temperature of the greenhouse was kept above 15 °C and the soil was kept moist to avoid water limiting growth.

Measurements

At each harvest, plants were separated into flowers, stems, living leaves, dead leaves, taproots and roots. The organs were distinguished in a functional way. For instance, a leaf stalk or leaf sheath which has a carrying function were considered as a stem. Leafless flower stalks were classified as flowers. Roots that clearly had a storage function (visual judgement)

were considered as taproots (*Rumex obtusifolius* only). These taproots were treated separately in the analysis and were only used to calculate the total biomass production and RGR. The dry weight of plant organs was determined after drying at 70 °C for two days.

Leaf longevity was estimated by marking a just emerged leaf at harvest 1 (one per pot). The state of the marked leaves was recorded weekly. Leaves were considered as dead when more than 50% was not green anymore.

Root length was measured according to the method of Newman (1966). Leaves were harvested in layers of 5 cm and leaf area was measured with an electronic leaf area meter for each layer separately. The measured and calculated parameters are summarized in Table 2. We distinguished five groups of parameters: (1) partitioning parameters indicating where biomass is located at a certain moment, (2) architectural parameters indicating form or efficiency of biomass investment, (3) size related parameters which describe the plant's dimensions, (4) parameters of plant performance which indicate the growing speed and (5) parameters of turnover which comprise the dead leaf fraction and the leaf longevity.

Statistical analysis

Multiple linear regression was performed on partitioning and morphological parameters (Table 2) to search for trends caused by time and nutrient level. This was done for each species separately. Factorial analysis of variance was achieved on all parameters of the perennial plant species of harvest 4. Before this analysis the data were transformed (if necessary) according to Steel & Torrie (1981). Means were compared between species of each plant group (grasses or herbs) and within one nitrogen level using Tukey's procedure for pair wise comparison.

Results

Effect of nutrients

In all species the biomass roughly doubled when the nutrient supply was increased. The root fraction, however, decreased with the availability of nutrients (Table 3, Figure 1) resulting in an enlargement of both leaf and stem fractions in all species. The fraction of the biomass in the flowers and dead leaves was not affected by nutrients (Table 3).

The architecture reacted to nutrient supply less strongly than the partitioning (Figure 2). The observed specific root lengths were in agreement with the values found by Noordwijk & Brouwer (1991). In *Holcus, Festuca, Plantago, and Hieracium* the specific root length showed a functional response to the change in nutrients (Table 3). The specific leaf area was relatively insensitive to nutrients; only *Hieracium* showed some increase of this parameter in treatment N3. The increase in nutrients caused an increase of the specific shoot height (SSH in Table 4 and 5) in *Anthoxanthum*, *Rumex* and *Plantago* but had no significant effect in the other species.

Effect of time

The leaf fraction generally decreased over time, as the plants invested more in other organs like roots, flowers, and stems (Table 3, Figure 1). Leaf mortality contributed to this decrease, as it increased over time. *Hieracium* increased their investments in stems during the experiment, but the other species remained a constant level. The root fraction in the species from a nutrient-rich successional stage increased during the experiment. Only *Rumex* produced taproots (FRRES) during the experiment. The fraction of the biomass allocated in taproots increased over time. At harvest 4 *Rumex* had allocated 50–70% of the total biomass in its taproots.

Although the species architecture demonstrated low sensitivity for nutrients it changed considerably over time. In most of the cases both SRL and SLA decreased in time. Only in *Holcus* no significant trend was found in the SRL. During the experiment the SSH increased in *Rumex* and *Hieracium* but decreased in *Holcus, Anthoxanthum* and *Plantago*.

Differences between species

Noticeable was the similar productivity of species originating from habitats with the same nutrient availability. In all nutrient levels the species from a nutrient-rich environment had the highest productivity, followed by the species from an intermediate nutrient level, whereas the species from a nutrient-poor habitat had the lowest productivity.

In spite of its large sensitivity for nutrients, root fractions were similar among the perennial species at the same nutrient treatment (Tables 4 and 5). However, in treatment N3 in the grass and forb species from a nutrient-poor habitat invested less in the roots. The tested grasses showed a large difference in their

Table 2. Measured and derived parameters.

Designation	Description
Parameters of partitioning	
FRFL	Dry weight of the flowers divided by TDM(g/g)
FRLV	Dry weight of living leaves divided by TDM (g/g)
FRST	Dry matter fraction of morphological structures that carry leaves divided by the TDM (g/g)
FRTR	Fraction of biomass found in the taproot (R. obtusifolius only) (g taproot/(TDM + g taproot))(g/g)
FRRT	Dry matter of thread-like roots divided by TDM (g/g)
Architectural parameters	
SLA	Specific leaf area (dm^2 leaf/g leaf)
SRL	Specific root length (m wiry root/g wiry root)
SSH	Specific shoot height (height in cm $g^{-1/3}$ shoot)
Size related parameters	
HGT	Plant height (cm)
LA	Leaf area of all leaf layers (cm^2/pot)
RTL	Total root length (m/pot)
Parameters of plant performance	
RGR	Relative growth rate between start of the experiment and the first harvest after 4 weeks (d^{-1})
TDM	Total dry matter of living tissue without taproots (g/pot)
Parameters of leaf turnover	
LFMO	Leaf mortality (g dead leaves/(g dead leaves + living leaves))
LFLO	Leaf longevity (days)

Table 3. Partial standardized regression coefficients from a multiple regression analysis calculated individually for each species. Abbreviations according to Table 2.

Suc.-Sp.	Partitioning					Architecture		
	FRFL	FRLV	FRST	FRRT	FRTR	SRL	SLA	SSH
Effect of nutrients								
H. lanatus	–	0.272**	0.720***	−0.597***	–	−0.622***	0.054	−0.031
A. odoratum	–	0.357***	0.430*	−0.654***	–	−0.119	0.107	0.478*
F. ovina	–	0.637***	0.225	−0.62***	–	−0.369+	0.104	0.271
R. obtus	–	0.287***	0.455***	−0.652***	−0.219**	−0.107	0.089	0.607***
P. lanceolata	0.219	0.019	0.423**	−0.720***	–	−0.26+	0.153	0.398*
H. pilosella	0.229	−0.037	0.440***	−0.611***	–	−0.302+	0.373***	0.203
Effect of time								
H. lanatus	–	−0.888***	0.094	0.494***	–	0.084	−0.915***	−0.684***
A. odoratum	–	−0.834***	0.365+	0.392*	–	−0.428*	−0.910***	−0.321+
F. ovina	–	−0.516***	0.044	0.301+	–	−0.482*	−0.776***	0.283
R. obtus	–	−0.925***	0.104	0.648***	0.900***	−0.745***	−0.644***	0.593***
P. lanceolata	0.382	−0.918***	−0.120	0.326*	–	−0.659***	−0.828***	−0.49**
H. pilosella	0.647***	−0.914***	0.687***	0.226	–	−0.525**	−0.812***	0.55**

+ = $P<0.05$, * = $P<0.01$, ** = $P<0.001$, *** = $P<0.0001$.

Table 4. F values of a factorial anova on data of the perennial plants after 16 weeks of growth: the effect of species and nutrient application. Abbreviations according to Table 2.

	Grasses			Forbs		
	Sp.	Nutr.	N*P	Sp.	Nutr.	N*P
df	3	3	9	3	3	9
Parameters of partitioning						
FRFL	–	–	–	7.2*	2.5	0.7
FRLV	121.4***	48.7***	5.7*	2.6	0.9	3.4+
FRST	13.1**	25.8***	3.3+	1.3	28.6***	0.6
FRRT	12.1**	66.6***	5.1*	21.2***	121.7***	3.2+
Architectural parameters						
SLA	11.9**	0.3	0.3	231.7***	15.3***	0.427
SRL	7.6*	2.2	0.7	1.8	6.9*	2.9
SSH	19.5***	2.5	0.9	46.2***	12.5**	5.2*
Size related parameters						
HGT	50.1***	33.8***	0.7	84.9***	44.2***	5.1*
LA	44.9***	61.9***	1.0	70.0***	85.4***	1.4
RTL	52.1***	1.0	1.6	14.3**	2.9	3.1
Parameters of plant performance						
RGR*)	22.2***	3.9+	0.4	63.3***	1.9	0.2
TDM	82.8***	61.0***	0.8	123.5***	84.1***	1.4
Parameters of turnover						
LFMO	38.6***	0.7	2.4	5.1+	0.0	1.0
LFLO	5.4+	0.7	3.0+	29.2***	1.3	0.6

$+ = P<0.05$, $^{*} = P<0.01$, $^{**} = P<0.001$, $^{***} = P<0.0001$.
(*)The RGR was calculated over the first 4 weeks of growth.

shoot investment. In *Festuca* the decrease of the root investment caused by the increase in nutrient supply favoured leaf growth while in *Holcus* this decrease favoured stem growth. The latter effect caused large differences in leaf fraction in the grasses.

The specific leaf area (SLA) and the specific shoot height (SSH) were larger in the grass and forb species from a nutrient-rich habitat (Table 4 and 5). In the grasses the the SRL tended to be higher for *Holcus* in the N1 treatment; no clear trend was found in the forbs. The size-related parameters were, in general, higher in species from a more nutrient-rich successional stage (Tables 4 and 5). Only in the root length of the herbs was there no clear sequence. The total biomass at harvest 4 and the RGR, were generally greater in species from a nutrient-rich environment in all nutrient treatments. The pattern of the fraction of dead leaves differed between grasses and forbs. Grass species from a nutrient-poor successional stage had a lower dead leaf fraction compared to grasses from a nutrient-rich habitat (Tables 4 and Table 5). In the herbs *Rumex* had the highest leaf mortality followed by *Hieracium* whereas *Plantago* had lowest fraction of dead leaves at harvest 4 (Table 5). Surprisingly, the leaf longevity did not resemble the results of the dead leaf fraction (Table 5). The large differences in the grasses disappear whereas in the herbs *Plantago* and *Rumex* had the same leaf longevity and the slow growing *Hieracium* had the shortest leaf longevity of all species in the experiment.

Table 5. Mean values after 16 weeks of growth. N1, N2 and N3 are nutrient applications comparable with 0, 5 and 20 g of nitrogen per m^2. 'a b c' indicate significant differences (P=0.05) between grasses or herbs within a nutrient level.

		Grasses			Forbs		
		Holcus	*Anthox*	*Festuca*	*Rumex*	*Plant.*	*Hiera.*
Parameters of partitioning							
FRFL	N1	0	0	0	0^{a}	1^{ab}	3^{b}
(%)	N2	0	0	0	0^{a}	5^{ab}	6^{b}
	N3	0	0	0	0^{a}	12^{b}	9^{b}
FRLV	N1	20^{a}	28^{b}	29^{b}	30^{a}	47^{b}	40^{b}
(%)	N2	21^{a}	28^{b}	48^{c}	36	44	42
	N3	27^{a}	40^{b}	60^{c}	45	36	31
FRST	N1	20^{a}	25^{a}	14^{b}	13	9	12
(%)	N2	26	32	22	24	16	27
	N3	45^{a}	35^{b}	29^{b}	31	33	47
FRRT	N1	59	46	56	56	44	45
(%)	N2	52^{a}	40^{ab}	30^{b}	39^{a}	35^{a}	25^{b}
	N3	27^{a}	26^{a}	11^{b}	23^{a}	19^{b}	12^{c}
Architectural parameters							
SLA	N1	2.2^{a}	2.0^{a}	0.9^{b}	3.5^{a}	1.3^{b}	1.3^{b}
($dm^2\ g^{-1}$)	N2	1.8	1.7	1	3.5^{a}	1.4^{b}	1.3^{b}
	N3	1.7^{a}	2.0^{a}	0.9^{b}	3.9^{a}	1.9^{b}	1.9^{b}
SSH	N1	16.1^{a}	9.2^{b}	8.9^{b}	8.5^{a}	4.3^{b}	3.8^{b}
($cm\ g^{-1/3}$)	N2	17.9^{a}	8.5^{b}	9.8^{b}	10.0^{a}	6.2^{b}	3.9^{c}
	N3	16.5	13.1	12.5	12.5^{a}	12.8^{a}	3.6^{b}
SRL	N1	319^{a}	249^{b}	261^{b}	220	114	173
($m\ g^{-1}$)	N2	330	231	188	106^{a}	162^{b}	180^{b}
	N3	270	246	183	128	73	96
Size related parameters							
HGT	N1	29^{a}	16^{b}	11^{c}	16^{a}	8^{b}	5^{b}
(cm)	N2	42^{a}	19^{b}	17^{b}	25^{a}	15^{b}	6^{c}
	N3	58^{a}	34^{b}	27^{b}	43^{a}	41^{a}	8^{b}
LA	N1	666^{a}	625^{a}	135^{b}	572^{a}	552^{a}	224^{b}
(cm^2)	N2	1069^{a}	1201^{a}	424^{b}	1506^{a}	1442^{a}	385^{b}
	N3	2531^{a}	2599^{a}	995^{b}	3562^{a}	3132^{a}	824^{b}
RTL	N1	3698^{a}	1515^{b}	839^{b}	734	630	450
(m)	N2	5331^{a}	2708^{a}	648^{a}	558^{a}	1430^{b}	445^{a}
	N3	4268^{a}	2190^{a}	410^{b}	707^{a}	657^{a}	221^{b}
Parameters of plant performance							
RGR*	N1	0.146^{a}	0.119^{b}	0.121^{b}	0.166^{a}	0.101^{b}	0.114^{c}
($g\ g^{-1}\ d^{-1}$)	N2	0.150^{a}	0.129^{b}	0.130^{b}	0.167^{a}	0.095^{b}	0.124^{b}
	N3	0.152^{a}	0.127^{b}	0.137^{b}	0.171^{a}	0.104^{b}	0.130^{c}
TDM*	N1	18.1^{a}	12.2^{a}	5.5^{b}	18.6^{a}	11.1^{b}	4.7^{c}
(g)	N2	32.1^{a}	26.9^{a}	10.5^{b}	35.6^{a}	24.2^{a}	7.9^{b}
	N3	62.3^{a}	35.2^{b}	15.1^{c}	53.6^{a}	49.1^{a}	14.3^{b}

Table 5 continued.

		Grasses			Forbs		
		Holcus	Anthox	Festuca	Rumex	Plant.	Hiera.
Parameters of turnover							
LFMO	N1	27^{a}	23^{a}	12^{b}	30^{a}	11^{b}	19^{ab}
(%)	N2	38^{a}	12^{b}	7^{b}	24^{a}	9^{b}	14^{ab}
	N3	37^{a}	29^{b}	6^{c}	19	14	23
LFLO	N1	58	58	56	72^{a}	79^{a}	44^{b}
(d)	N2	37^{a}	56^{ab}	68^{b}	75^{a}	72^{a}	47^{b}
	N3	40	54	58	61^{a}	72^{a}	44^{b}

*For ROB including tap roots

Discussion

The experimental approach

In this study a greenhouse experiment was conducted to examine the effect of nutrient availability on the architecture, allocation and turnover in time. In this experiment, the effect of time is complex since plants change their own environment, as they grow bigger and the season is changing during the experiment. This implies that the time effect includes effects of nutrient depletion, size, ontogenetic changes and change of temperature and light. However, in the field, plants also deplete the soil during growth, also increase in size, and temperature and light are variable during the season. In this study therefore the time effect can be regarded as an example how seedlings may change their allocation and architecture during growth.

The effect of time and nutrients on the architecture

Although in *Festuca* and *Holcus* nutrients induced some responses in the specific root length the effect of nutrients on the architecture of grasses was generally limited. In the herbs there were only significant changes in the specific shoot height of *Plantago* and *Rumex* in response to the nutrient level. This effect was caused by a change in leaf angle of these rosette species. Plants growing in treatment N3 had more vertical leaves which resulted in taller plants while in treatment N1 the leaves and stems of both species had a more horizontal orientation.

Results showed that compared to the effects of nutrients, the effect of time on the architecture was more important. The SLA and SRL showed in general a strong downward trend during growth. The results with respect to the specific shoot height (SSH) were variable, but except *Festuca* all species showed significant change in time. These results indicate that in general architectural parameters show important changes during plant growth whereas they were less affected by nutrients.

The plant's architecture can be considered as a measure of how efficiently biomass is used to capture resources. A species with high values for its architecture can make more leaf area and root length with the same amount of biomass by making thinner leaves and roots. The decrease in SLA and SRL during growth, therefore, will induce a decrease of the plants efficiency during growth which in turn affects the competitive relationship between adults and seedlings in a vegetation.

The effect of time and nutrients on the allocation

It was the well known plasticity of the root allocation that was largely responsible for the substantial change in dry matter partitioning at different nutrient levels (Brouwer 1962; Levin et al. 1989; Van der Werf et al. 1993). With the increase of the nutrients the root fraction decreased in all species whereas the stem and leaf fraction increased. In the herbs especially the stem fraction profits from the decrease in root allocation whereas in the grasses both stem and leaf fractions increased.

The change of the partitioning in time, might also be explained as a functional response of the shoot:root ratio to the nutrient depletion effect. As plants grow bigger they use a larger part of the nutrients in the pots and will therefore encounter a lower nutrient level during growth. When this is true we would expect a decrease in the shoot:root ratio in both nutrient poor treatments during the experiment because it is unlikely that in the N3 treatment, with a application of

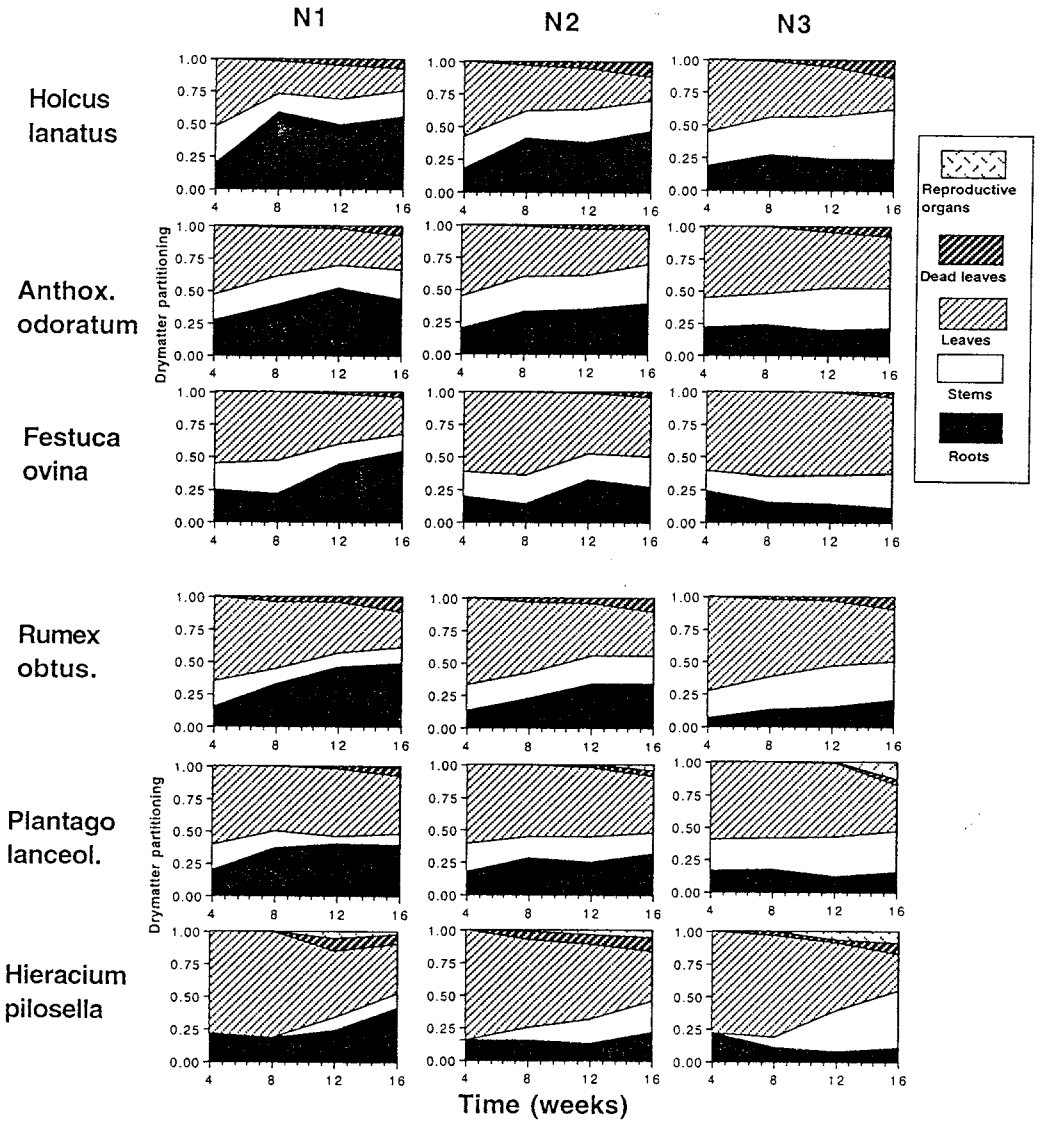

Figure 1. Dry matter partitioning of 6 species over time at 3 nutrient levels N1, N2 and N3 equivalent to 0, 5 and 20 g of nitrogen per m^2.

20 g N m^{-2}, nutrient limitation was important. Results of the experiment generally confirm this expectation which indicates that the partitioning was primarily affected by the nutrient availability as a result of the functional response of the shoot:root ratio.

The increase of the taproot fraction in *Rumex* and the increase of the stem fraction in *Hieracium*, however, may have developmental causes. Probably both species do not invest in these relatively unproductive organs as a seedling to keep up their RGR which can be regarded as essential during the establishment of species (Grime 1979).

Species characteristics

In this paper we have adapted the hypothesis that fast-growing species, adapted to nutrient-rich environments, are characterized by a high SSH and SLA, whereas slow-growing species, adapted to nutrient-poor habitats, are characterized by low biomass turnover and a longer specific root length. Light is generally considered to be the limiting resource in nutrient-rich environments which is why we expected species from a fertile successional stage to have high values for their shoot architecture (Tilman 1985). The results for the shoot architecture generally confirm

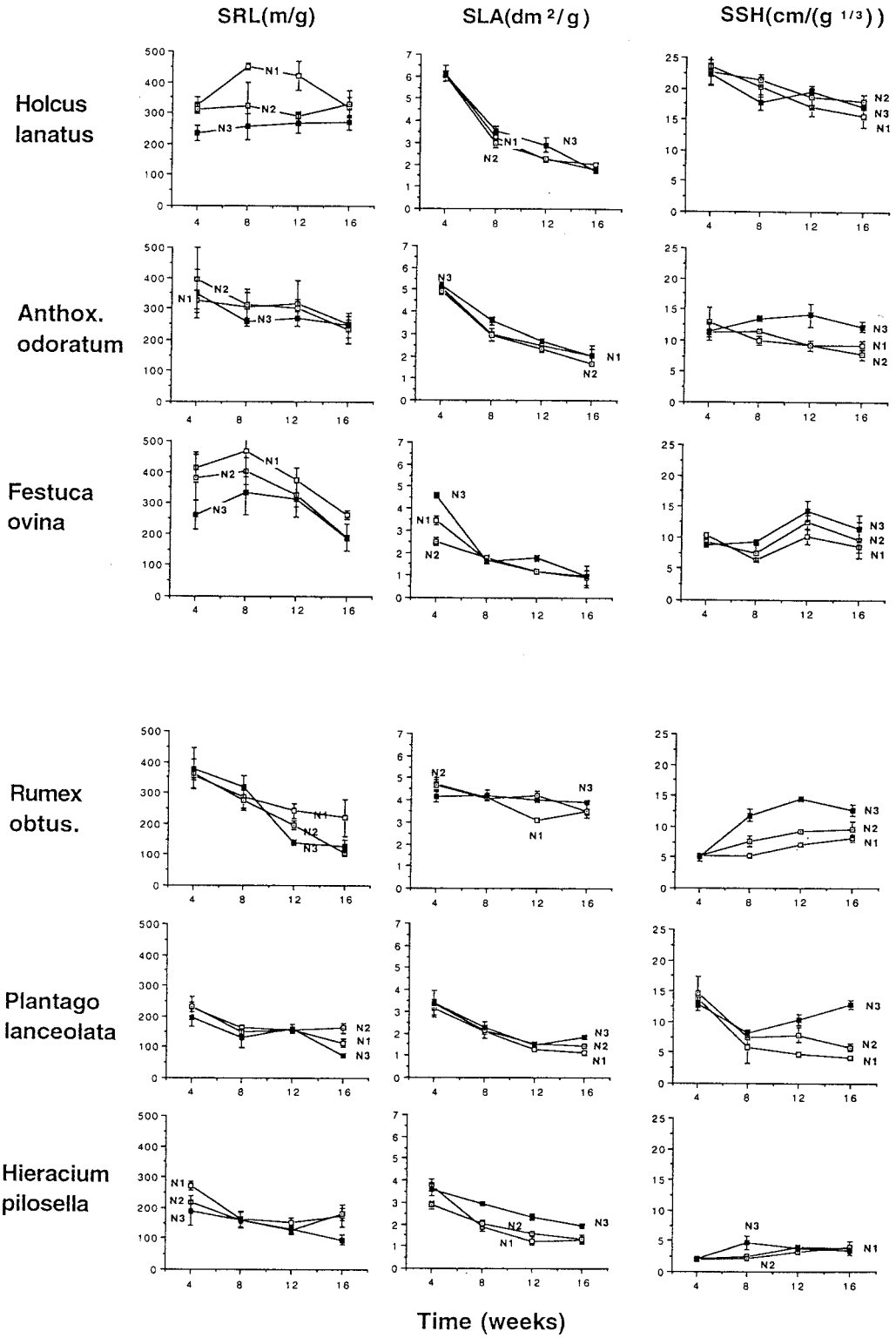

Figure 2. Temporal change of three important architectural related parameters of 8 species. SRL = specific root length, SLA = specific leaf area. SSH = specific shoot height. N1, N2 and N3 are nutrient applications equivalent to 0, 5 and 20 g of nitrogen per m^2.

these expectations: specific shoot height and specific leaf area were greater in species from a fertile environment. Our results, however, do not support the view that species from a nutrient-poor habitat are better competitors for nutrients (Tilman 1985; Elberse & Berendse 1993). These species did not invest more in there root system as suggested by Gleeson & Tilman (1994) or have a higher specific root length as suggested by Elberse & Berendse (1993). Nor in the results of the grasses, nor in the herbs such sequence was found. Ryser & Lambers (1995) also found that *Dactylis glomerata*, a species from a nutrient-rich habitat, had a longer SRL than *Brachypodium pinnatum*, from a nutrient-poor habitat. This leads to the conclusion that there is little evidence to accept the hypothesis that species from a nutrient-poor habitat are specialized in competing for nutrients or generally have a longer specific root length. This means that species from a nutrient-rich habitat, in general, have a superior architecture compared to species from a nutrient-poor habitat. Therefore these species are more efficient (size/gram biomass) in increasing their size related parameters such as leaf area, height and root length which enables to have a higher RGR (Grime & Hunt 1975; Poorter & Remkes 1990). This brings about a higher biomass, even in nutrient-poor conditions, as shown by our results.

Our hypothesis predicts that species from a nutrient-rich environment have a higher turnover speed compared to species from a nutrient-poor habitat (Berendse & Elberse 1990; Aerts 1995; Schläpfer & Ryser 1996). When the fraction of dead leaves (LFMO) is considered results with respect to the grasses confirm this view. In the herbs, however, the results were not what we expected. *Plantago* had the lowest LFMO, *Rumex* produced the most dead leaves whereas *Hieracium* had intermediate LFMO values. Evaluating these results we have to consider that measured turnover values were caused by natural senescence of the leaves without any external loss factors like herbivory or mowing which can be considered as important loss factors in grasslands (Berendse et al. 1992; Fan & Harris 1996; Coffin et al. 1998). It seems likely that taller species like *Rumex* and *Plantago* will suffer more from external loss factors than *Hieracium*. This may explain these unexpected results in the dicots.

Turnover parameters

There was a striking difference between the results of both turnover parameters. Species, with about equal leaf longevity (i.e., *Rumex* and *Plantago*), had very different values for their LFMO (*Rumex* > *Plantago*). To analyse the cause of these differences we calculated the LFMO after 16 weeks of growing with simple simulations using fixed leaf longevity- and initial RGR (RGRi) values which were chosen close to the experimental situation. We used three standard growth models: exponential, exponential-linear and logistic (see Appendix 1 for precise description) to analyse various growing conditions.

These simulations surprisingly demonstrate that the dead biomass fraction was not only dependent on biomass longevity but also on the RGRi (Figure 3). The exponential equation (Appendix 1) does not explain the differences in the turnover parameters since the increase in RGRi would lead to lower dead leaf fractions. In our results, however, the fraction of dead leaves was higher in species with high RGRi. At lower RGRi values the other growth models gave the same results as the exponential model but at higher RGRi values the fraction of dead biomass increased strongly with the RGRi. This means that species, with faster RGRi values in this range, will have a higher dead leaf fraction although their leaf longevity are the same. This perfectly explains the contradictory results in both turnover parameters. This is even more convincing when we are aware of the fact that the growing curve of the experiment is best described by the exponential-linear model and the experimental RGRi values are positioned in the range where dead biomass fraction is increasing with the RGRi (Table 5).

This fundamental difference between both turnover parameters raises the question which parameter should be measured to characterize the turnover of a plant species? In principle the longevity is a parameter which not directly related to the RGRi of a species and can therefore be classified as a good parameter describing the intrinsic senescence of a species.

The fraction of dead tissue can be considered as a direct measure to characterize biomass and nutrient loss of a species. The effect of the RGRi on the fraction dead biomass in our simulations demonstrated that the RGRi was an important determinant of the turnover in our experiment experiment but would the RGRi also affect the turnover of perennials in the field? In our view the RGRi might also affect the

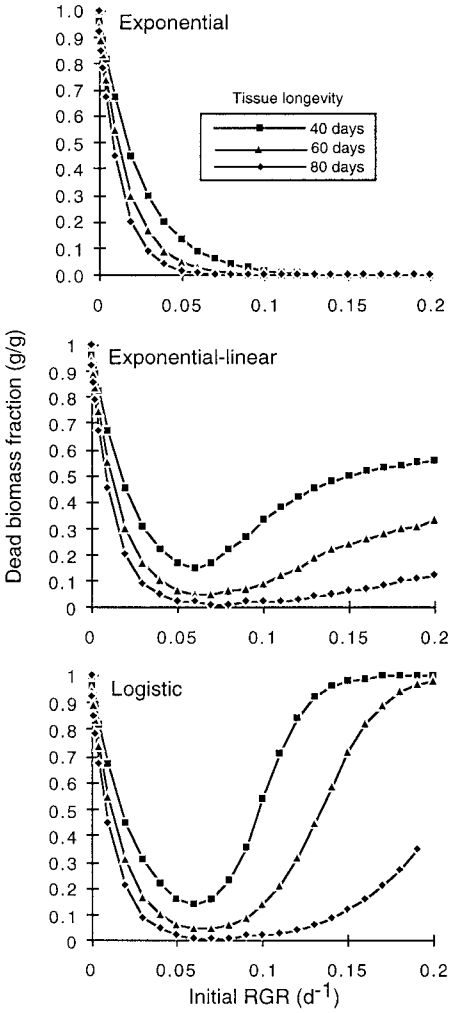

Figure 3. Simulated fractions of dead tissue after 16 weeks in relation to the initial relative growth rate (RGRi) usign 3 growth models: exponential, exponential-linear and logistic. Different lines indicate different values for the leaf longevity. For description of simulations see Appendix.

turnover in the field since exponential-linear or sigmoid shaped growing curves are common in the life cycle of perennial plants due to seasonal change (see, e.g., Schippers et al. 1999). This indicates that species with a slow RGRi will take up their nutrients later in the season and release them later in the season. This difference in timing of nutrient uptake and release may be an important factor in the competition between fast and slow growing perennials and might even explain why species from a nutrient-poor habitat have slower growth rates.

To our knowledge the direct effect of RGRi on turnover as shown in figure 3 has received no attention in literature (e.g., Aerts & Caluwe 1995; Schläpfer & Ryser 1996). In our view these direct effects of the RGR should be discussed in future literature dealing with turnover.

Conclusions

In this research we examined biomass allocation, architecture and turnover of species from different successional stages and found that the availability of nutrients primarily affected the shoot-to-root ratio of the species whereas it had a limited effect on the plant architecture. The plants architecture, however, was in general strongly decreasing during the plants development while the partitioning was less effected. Our results support the view that species from a nutrient-rich successional stage generally have a larger specific leaf area and higher specific shoot height. We did not find that species from a nutrient-poor successional stage to have a longer specific root length nor did we find evidence for any compensating growth-related properties to make them superior to species from a nutrient-rich successional stage. The only advantage which later successional had was a slower biomass turnover expressed as the dead leaf fraction and a shorter specific shoot height (SSH) which might prevent herbivory and mowing losses. Surprisingly the dead leaf fraction was not only positively related to the leaf longevity but also to the RGR of the species. This effect can be considered as important for the timing of nutrient uptake and release during the season. This may affect the competition between fast and slow growing perennials.

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Appendix 1. Description of simulations depicted in Figure 3

Exponential case

The dead biomass fraction in exponential growing plants can be derived as:

$$Fd = \exp(-LO^{*}RGRi)$$

In which LO = tissue longevity (d), RGR = relative growth rate in (d^{-1}).

Exponential-linear growth

The exponential linear growth is based the exponential linear equation of Goudriaan (1994).

$$dW/dt = P^{*}(1 - \exp(-(RGRi/P)^{*}W))$$

where W = total biomass of a plant (g), $RGRi$ = initial RGR (d^{-1}), P = productivity of a closed canopy (20 g m^{-2} d^{-1} = normal potential plant production value).

This Exponential-linear equation was used for the simulations of Figure 3 with: Initial weight = 0.56 g m^{-2} at t=0 (= mean starting value in the experiment). Taking the dead biomass fraction Fd at time=120 (= harvest time of experiment). Time step = 1 day. The biomass grown at time = T died at time = $T + LO$. The dead biomass fraction Fd was estimated at time = 120 by:

$$Fd = Wd/W$$

where: Wd = dead biomass, W = living biomass + dead biomass.

Logistic growth

The standard logistic differential equation was used:

$$dW/dt = W^{*}RGRi^{*}(K - W)/K$$

in which: K = carrying capacity.

Al other calculations resamble the logistic calculations. The K value was assumed to be 1000 g m^{-2} which is between the total productivity of both high nutrient levels.