RESOURCE COMPETITION BETWEEN 12 SUCCESSIONAL GRASSLAND SPECIES

september 1990 - maart 1991

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Doctoraalverslag voor het Laboratorium voor Plantenoecologie van de Rijksuniversiteit Groningen.

ABSTRACT.

For twelve species from a successional series after cessation of fertilizer application with continued hay-making, competition against two competitors, Agrostis capillaris and Holcus lanatus, was studied at two nutrient levels using an additive design. The different pots were harvested three times with four weeks intervals.
For the first harvest the outcome of competition was strongly related to the seed weight of the target species. Competition for light was observed to be important for the outcome of the competition in the second harvest. For the third harvest the nutrient levels had decreased to a low level, wich probably caused competition to be mainly for nutrients.
The extinction coefficient and the lightintensity at the soil of a target species in controls without competition appeared to be good estimate for the outcome of the competition for light when also competition for nutrients was observed.
Species from nutrient rich soils were observed to have higher root fractions than species from nutrient poor soils. The outcome of competition for nutrients was positive correlated to the fractions of total biomass in roots of the species.
Therefore, early succesional species were both good light competitors and good nutrient competitors.

1. INTRODUCTION.

From the "Resource-Ratio hypothesis" (Tilman, 1988; Olff et al, 1990) it can be concluded that competition for nutrients will be important at low nutrient availabilities. While facing nutrient rich circumstances, competition for light is expected.
Depending on the kind and type of resource, a growth or responce curve can be determined. Given a loss rate of resources, the supply rate of the specific resource for the examined species can be determined.(R^*, Tilman, 1988). R^* can be viewed as the level of a resource to wich a species can reduce the total available amount of that resource. At R^* the increase in biomass (because of growth) compensates losses because of mowing, grazing or mortality.
According to the isocline-approach (Tilman, 1988) the outcome of competition between species for a certain resource will be determined by the different R^*'s of the species for that resource. The species with the lowest R^* will ultimatly win the competition. In case of competition for more than one resource, coexistence between species can occur when different species are limited by different resources. (Tilman, 1988).

The light reduction of a species for neighbour plants will be determined by the maximal height of that species and by the amount of the reduction of incoming light by a canopy of that species, and by the speed at which a species can obtain it's maximal height. The light intensity that reaches a leaf in a canopy at height h can be determined by the formula:

$$I^h = I_0 * e^{-kAh}$$

in which I_h = light intensity at height h;
I_0 = light intensity above the vegetation;
A_h = summed leafarea above height h;
k = extinction coefficient.
(Fliervoet, 1984).
Thus the extinction coefficient can be determined by the formula:

$$k = -\ln(I_h/I_0)/A_h.$$

The extinction coefficient is a quantification of the reduction of incoming light by a vegetation.

In this study R^* and L^* are studied under artificial conditions. Aim of this study is to determine a estimates for competitive ability for light and for nutrients to determine which plants traits explain differences in these estimates. Furthermore, the differences between species will be related to their position in a successional grassland series. In this succession series the nutrient availability is expected to decrease after stopping fertilizing wich will lead to a decrease in above-ground standing crop. This in turn will lead to an increase in light intensity at the soil.Based on the resource ratio hypothesis a shift from high shoot:rootratio's to low shoot:rootratio's is expected.
The importance of competition for nutrients is expected to increase in combination with a declining importance of competition for light.

Central questions in this research therefore are:

1. Are the extinction coefficient of light and the maximal plant height important determinants of competitive ability for light at high nutrient availability?
2. Is R^* a good estimate for the competitive ability for nutrients at low nutrient supplies and wich trades determine R^*?
3. What is the relation between the position of species in the succession after the cessation of fertilizer application, and their competitive ability at low and high nutrient availability.

2. MATERIAL AND METHODS.

Twelve dominant monocos from the grassland succession series were selected. The species were ranked in order of succesional age (Olff and Bakker, 1991). The successional age was computed by weighting the years in which each species occured by the cover percentages in each year. The selected species are listed in table 1.

Seeds of the species were sown on silver sand in a greenhouse in september 1990 and were watered regulary.
Twenty days after germination, the seedlings of the twelve species were transferred to round pots (O = 18 cm,
contents = 3.9 L) filled with "nutrient-rich" or "nutrient-poor" soils (10 plants per pot). All plants were potted with in one week.The two nutrient levels were created by mixing silver sand with pot-soil (mixtures 1:3 and 3:1). The nitrogen levels of the pots at the beginning of the experiment are given in table 7. By adding 10 seedlings of Agrostis cappilaris or Holcus lanatus a competitor was introduced. This way 6 treatments were created:

controls: LC: low nutrients, no competitor
HC: high nutrients, no competitor

LA: low nutrients, competition against A.capillaris
LH: low nutrients, competition against H.lanatus
HA: high nutrients, competition against A.capillaris
HH: high nutrients, competition against H.lanatus

Each treatment was replicated four times. In four high nutrient and four low nutrient pots no seedlings were transferred as controls to study the effect of watering on the nutrientlevels. The total number of pots was 272. The pots were placed in a greenhouse in october 1990 at 16 hours light and an average temperature of 25°C. The first ten days the pots were watered twice a day. After ten days the pots were watered once a day. The position of the pots was changed randomly every two weeks.

Four weeks after the potting, the maximal plant height and the lightintensity were measured every 3 cm in the canopy, using a linear light meter (10 cm).
The canopy was cut at a height of 3 cm. All plants were harvested wittin three days. The harvest of each pot was selected to species, seperatly for leaves and petioles. Leafareas were measured, using a Li-cor photo-electric area meter (model 3100). Dry weight of leaves and petioles were determined after drying at 80° for 16 hours. This was repeated four weeks after the first harvest and again five weeks after the second harvest.
At the third harvest also the dry weight of above ground biomass below 3 cm was determined per species. Roots of quarter pots were rinsed under a fine waterspray and dry weight was determined.
The mineral N concentrations (extraction with 1 M KCl) of all pots were determined after the third harvest. Nutrient deficiencies of the two soil mixtures were determined by a Bouma-Janssen pot experiment, using Holcus and Agrostis.

Data analysis.

From the rootdw per pot and the shoot:root ratio's of the species in controls the expected rootdw per species could be calculated for species in competition by using the formulas:

$ERDW_t = 4*(SDW_s/S/R_s)$
$ERWD_c = 4*(SDW_c/S/R_c)$
$TERDW = ERDW_s + ERDW_c$

in wich $ERDW_t$ = expected rootdw target species in competition
$ERDW_c$ = expected rootdw competitor in competition
TERDW = total expected rootdw
SDW_s = shootdw target species in competition
S/R_s = shoot:root ratio species in controls
S/R_c = shoot:root ratio competitorspecies in controls
(Berendse, 1981).

The calculated TERDW was compared to the observed rootdw in pots using a paired T-test.

The relative shoot yield per species was calculated by deviding the total shootdw of a species per pot per treatment by the mean total shootdw of the species in controls. The relative total yield was calculated for harvest 3 by deviding the total dw (total shootdw + $ERDW_t$) of a species per pot per treatment by the mean total dw of the species in controls. The relative shoot yield, relative total yield and the total dw were plotted against successional age of the target species seperatly for each competition of nutrient level and competitor.
Correlationcoefficients between the extinction coefficient k of controls, the maximal length of controls and of target species in competition and successional age with the relative shootyield were calculated for each harvest. Also the correlation of the seed weight (Grime et al, 1988) of three target species with the total shootdw was calculated for the three harvests. Furthermore correlations between the relative total yield with the extinction coefficient k of controls and the maximal length of controls and of target species in competition was calculated. The successional age of the target species and root fraction of the controls were correlated with the relative total yield. This was also done for the correlation between root fraction of controls with the relative shootyield and for the correlation of the seedweight with the total dw. Finally the correlation between the successional age of the target species with the root fractions of controls and the expected root fractions of target species in competition was calculated.

3. RESULTS.

Harvest 1.

From figure 1 it can be concluded that the total shoot biomass at high nutrient levels was higher than at low nutrient levels iboth with Holcus and Agrostis as competitors. Light reduction by Holcus was ore severe than by Agrostis (table 5), but for both species much less then in the next harvest.
Table 3 shows that the shootdw of the target species in competion is significant positive correlated to the seed weight of the target species.
Table 2 shows that relative shoot yield of target species at LA and LH was significant negative correlated to successional age of the target species and that the relative shoot yield at LH is signigficant possitive correlated to the extinction coefficient k of the target species in controls. This indicates competition for light.
The maximal length of target species without competition was not significantly correlated to the relative shootyield.

A significant negative dependence of the relative shootyield on the successional age of target species was found at HA and at LH (fig. 2a;b). The relative shootyield significantly increased with the the maximal length of target species in competition at LA.

Harvest 2.

Light reduction by both Holcus and Agrostis was more severe in this harvest. Holcus reduced the light more than Agrostis. Figure 4a and b show clear differences in total biomass per target species between low and high nutrient levels for both Holcus and Agrostis as competitors. This might indicate that the differences in the results of competition under high and low nutrient levels are caused by the differences in nutrient availability.
Table 2 shows that the relative shootyield of target species are significantly negative correlated to the extinction coefficient k of the target species in controls at LH and at HH. This indicates that the relative shoot yields in case of Holcus as competitor were the results of competition for light. At LA and LH the maximal length of target species in controls were significantly positive correlated to the relative shootyield. This also indicates that the results of the relative shootyields were caused by competition for light. The total shootdw of the target species under high nutrientlevels were still positive correlated to the seed weight of the target species (table 3). A significantly negative regression was found for the relative shootyield of target species on the succesional age at HH (fig 5). Later successional species did worse in competition at all treatments (table 2).

The relative shoot yield of target species showed a significantly negative dependence on the successional age at HH (fig 5). The relative shoot yield showed no significant dependence on the extinction coefficient k of the target species in controls (fig. 6).
Figure 7 shows that the relative shoot yield significantly depended negatively on the maximal length of target species in competition.

Harvest 3.

Figure 8a and b show obvious differences in the total biomass per pot between low and high nutrient levels for both Agrostis and Holcus as competitor. This indicates that both nutrient treatments had so far impoverished that light
competition was less important than in the previous harvest.
Comparing figure 4 and 8 reveals that the total biomass at harvest 3 was lower than at harvest 2. Also, table 5 shows that the light intensity at 3 cm height (in percentage of total light availability above the canopy) was lowest at the second harvest for all treatments. At harvest 1 there were no differences in the light intensity at 3 cm height between the four treatments. This also counts for LA and HA at the second harvest. The light intensity at the third harvest was lower than at the second harvest at HA. There seemed to be no difference in light intensity between LA at harvest 1 and at harvest 3. At the third harvest, the light intensity at LH and HH was higher than at the second harvest.

Figure 10 shows that at the end of the experiment the total extractable N concentrations per pot showed were different between high and low nutrientlevels. The observed differences between species seemed to have no relation with the successional age or target species, ecept at HA were a significantly positive dependence of the total extractable N concentrations on the successional age of the target species was observed.
Table 2 shows that the relative shoot yield under high nutrient levels was significantly negatively correlated to the maximal length of target species in controls and that there were no significant correlations between the relative shoot yield and the extinction coefficient of target species in controls.
Although all plants probably faced nutrient poor conditions no significant correlation between the relative shootyield and the rootfractions of controls were found.

Table 4 shows that, except for Anthoxanthum odoratum at LA and for Poa pratensis and Juncus articularis at LH and HH, the expected total rootdw TERDW didn't differ significantly from the observed rootdw.
Using the $ERDW_t$ the total biomass and the relative total yields of the target species could be calculated.
Table 2 shows that, except at HH, there was a positive significant correlation between the root fraction of controls and the relative total yield of target species, again indicating competition for nutrients. This conclusion is furthermore supported by a significantly negative correlation between the relative total yield and the successional age at HA and at LH.

Though competition for nutrients seems to be important at this harvest, a significant negative correlation between root fractions of controls and the expected root fractions of target species in competition with the succesional age of target species was observed at HA and HH. For competition under low nutrient levels no significant correlations between root fractions and the succesional age were found.

So, although species with the highest allocation to roots were the best competitors at low nutrients availability, this were the earliest species in succession (from the richest stages).

Table 3 shows that a significant positive correlation was found

between the shoot biomass and the total biomass with seedweight of the target species, except at HH. A significant positive correlation between the maximal length of target species in competition and the relative shoot yield was found at LH and HH and at LA.
No significant dependence of the relative total yield on the rootfraction of target species in controls was observed (fig 9a;b).
The results of the Bouma-Janssen experiment show that N appeared to be the most limiting nutrient for both H.lanatus and A.capillaris high and low nutrientlevels. For A.capillaris also P and K were found to be limiting nutrients at low and high nutrient levels (figure 12 and 13).

4.DISCUSSION AND CONCLUSIONS.

From the results can be concluded that for the outcome of the competition of the first harvest, the seed weight was the main determining factor. For the second harvest, although there are found differences in total biomass between low and high nutrientlevels (figure 4), competition for light appeared to be the most important factor for all treatments. This conclusion is supported by the observed low light intensities at 3 cm height for both Agrostis and Holcus (controls) at low and high nutrient levels (table 5). From the significant negative correlation between relative shootyield and successional age can be concluded that the earlier species are better competitors for light, which is to be expected in a succession after the cessation of fertilizer application on (former) agricultural fields.
At high nutrient levels Holcus seems to be the ultimate (light)competitor. Though a significant negative correlation between the extinction coefficient of target species in controls and the relative shoot yield was found, no significant (negative) correlation between the maximal plant length of target species in controls and the relative shoot yield was observed. This suggest that the maximal growth rate of the species was the main determining factor for the outcome of competition but that the results were affected by the competition for light.
Although no significant negative correlation between the extinction coefficient k and the relative shootyield was observed at HA and LA, from table 5 can be concluded that competition for light appeared to be an important factor in determining the relative shoot yield.
From the differences in the relative shoot yield for Agrostis and Holcus as competitors between the 2 nutrient treatments (figure 4) must be concluded that beside competition for light also competition for nutrients occured. This conclusion is supported by the observed significantly negative correlation between the relative shootyield and the maximal length of target species in controls, meaning that the tallest target species are probably the best light competitors.
The main importance of competition for light instead of competition for nutrients at the low nutrient levels of the first two harvests must be explained by unexpected high extractable N contents at the start of the experiment (table 7). The potsoil appeared to be enriched with extra NO3-. Therefore nutrient limitation didn't appear to be important during the first two harvests. Nutrient limitation at low nutrient levels probably would have been more important for the outcome of competition when all pots would have been filled with silver sand and nutrientlevels were created by adding nutrient solutions.

From the results of the third harvest it must concluded that competition for nutrients was the most determining process. Except at HH, significant negative correlations between the root fractions of controls with the relative total yield was found.
So species allocation more to roots did worse in competition.

Yet, at HH there was a significant negative correlation between the maximal length of target species in controls with the relative total yield and a significant positive correlation between the extinction coefficient k and the relative total yield (table 2), also indicating competition for nutrients.
Although competition for nutrients was an important factor for the outcome of competition in case of high nutrients, from table 5 can be concluded that also competition for light occured for both Agrostis and Holcus as

competitor under high nutrients.
The competition for nutrients at the third harvest was strongest at low nutrientlevels.

From the significant negative correlation between the root fractions and the successional age of the target species at high nutrient levels (table 3) in combination with a possitive correlation between the root fractions and the relative total yield (significant except at HA (table 2)) must be concluded that the earlier succesional species from the range beside competition for light also were the best nutrient competitors.

The extinction coefficient k of target species in controls appeared to be a usefull estimate for the outcome of competition for light, given nutrient competition is not very important, although from table 6 can be concluded that also light at 3 cm height is a useable and more easy determinable estimate.
The maximal length of target species in competition appeared to be a significant estimate for the outcome of competition for light when also competition for nutrients occures.

Contrary to the predictions of the resource-ratio hypothesis in this study higher root fractions are observed for earlier successional species. This was also found by Olff, van Andel and Bakker (1990). This explaines why earlier species from the successional series also win the competition for nutrients. Although a significant positive correlation between the relative total yield and the extinction coefficient was observed (table 3), it's striking that species with lower shoot:rootratio's are able to win the competition for light.
From these results must be concluded that the resource-ratio hypothesis gives no explanation for the succession after cessation of fertilizer application on hay-fields and continuing hay making.

This leaves the question why species with higher root fractions lose the supposed competition for nutrients in the field. Suggestions herefore are done by Olff, van Andel and Bakker (1990) who concluded that differences in allocation patterns increase in importance with successional age. However, the allocation patterns observed in this experiment give no explanation for the observed successional range of species in the field. This is also the case with the transient dynamics theory of Tilman (1988).

Another possibility might be that an allocation trade off in the roots is of more importance than the trade off between shoot and root (Olff, van Andel and Bakker) This concurs results of Berendse and Elberse (1989) who indeed observed higher specific rootlength's for species of poorer soils. Other suggestions are done by Abrahamson and Caswell (1982) and by Reekie and Bazzaz (1987) who suggested that the allocation of nutrients don't reflect the allocation of carbohydrates.

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Table 1: Selected species from the succesion after the cessation of fertilizer aplication in the Drentse A area, their successional age (succ. age in years) and seed weight.

SPECIES	CODE	SUCC. AGE	RANKORDER	SEEDWEIGHT (mg)
Lolium perenne	Lp	5.91	1	1.79
Elymus repens	Er	7.65	2	2.02
Poa pratensis	Pp	10.92	3	0.25
Dactylis glomerata	Dg	10.98	4	0.51
Festuca pratensis	Fp	11.68	5	1.53
Cynosurus cristatus	CC	12.98	6	0.70
Holcus lanatus	Hl	13.45	7	0.32
Festuca rubra	Fr	14.40	8	0.79
Juncus effusus	Je	14.88	9	0.01
Anthoxan-thum odoratum	Ao	15.27	10	0.45
Agrostis capillaris	Ac	20.37	11	0.06
Juncus articula-tus	Ja	31.46	12	0.02

Table 2: Correlationcoefficients and level of significance (sign.) of extinction coefficient (K), maximal length (max L), successional age (succ. age) and root fraction (root fract.) with relative yields for 3 harvests.
* - p <.05;** - p <.01;*** - p <.001.

			HARVEST 1			
	FACTOR		HIGH	NUTR.	LOW	NUTR.
			COMP=Ac	COMP=Hl	COMP=Ac	COMP=Hl
RY SHOOTDW	K		-0.1621	-0.2019	-0.1837	-0.2618
	SIGN.		ns	ns	ns	*
	MAX. L	IN COMP.	0.2652	0.1618	0.5199	0.5337
		SIGN.	*	ns	***	**
		CONTROL	0.2101	0.0418	-0.0946	-0.1214
		SIGN.	ns	ns	ns	ns
	SUCC. AGE		-0.4448	-0.3302	-0.6626	-0.5888
	SIGN.		**	*	***	***

			HARVEST 2			
			HIGH	NUTR.	LOW	NUTR.
			COMP=Ac	COMP=Hl	COMP=Ac	COMP=Hl
	K		-0.1747	-0.4669	-0.2611	-0.3347
	SIGN.		ns	**	ns	*
	MAX. L	IN COMP.	0.4506	0.6914	0.2688	0.8659
		SIGN.	**	***	*	***
		CONTROL	-0.3485	-0.1452	0.7402	0.6048
		SIGN.	*	ns	***	***
	SUCC. AGE		-0.4082	-0.6154	-0.2867	-0.4332
	SIGN.		**	***	*	**

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Continuation table 2.

			HARVEST 3			
			HIGH NUTR.		LOW NUTR.	
			COMP=Ac	COMP=Hl	COMP=Ac	COMP=Hl
	K		0.1992	-0.1864	-0.0323	-0.2320
	SIGN.		ns	ns	ns	ns
	MAX. L	IN COMP.	0.1995	0.6704	0.0940	0.7047
		SIGN.	ns	***	ns	***
		CONTROL	-0.4044	-0.3207	-0.0676	0.1592
		SIGN.	**	*	ns	ns
	SUCC. AGE		-0.0769	0.2171	-0.0119	-0.3614
	SIGN.		ns	ns	ns	**
	ROOT FRACT. CONTROL		0.2305	-0.1651	0.2465	0.2959
	SIGN.		ns	ns	ns	*
RY TOTALDW	K		0.4605	0.3791	-0.0856	-0.1982
	SIGN.		**	**	ns	ns
	MAX.L	IN COMP.	0.3971	0.4677	0.2107	0.6402
		SIGN.	**	**	ns	***
		CONTROL	-0.5227	-0.2926	0.0634	0.0866
		SIGN.	***	*	ns	ns
	SUCC. AGE		-0.2577	0.0560	-0.1774	-0.4527
	SIGN.		*	ns	ns	**
	ROOT FRACT. CONTROL		0.4357	0.0661	0.3521	0.3058
	SIGN.		**	ns	*	*

Table 3: Correlationcoefficients and level of significance (sign.) of seed weight with totaldw and total shootdw and successional age with root fractions (root fract.) for 3 harvests.
* - p <.05;** - p <.01;*** - p <.001.

	FACTOR	HARVEST 1 HIGH COMP=Ac.	NUTR. COMP=Hl.	LOW COMP=Ac.	NUTR. COMP=Hl.
SHOOTDW.	SEEDWGHT.	0.3918	0.7576	0.5045	0.6688
	SIGN.	**	***	***	***
		HARVEST 2 HIGH COMP=Ac.	NUTR. COMP=Hl.	LOW COMP=Ac.	NUTR. COMP=Hl.
SHOOTDW.	SEEDWGHT.	0.3250	0.4089	0.0309	-0.0199
	SIGN.	*	***	ns	ns
		HARVEST 3 HIGH COMP=Ac.	NUTR. COMP=Hl.	LOW COMP=Ac.	NUTR. COMP=Hl.
SHOOTDW.	SEEDWGHT.	0.3371	-0.0275	0.2592	0.3495
	SIGN.	*	ns	*	*
TOTALDW.	SEEDWGHT.	0.4793	0.0684	0.3839	0.5983
	SIGN.	***	ns	**	***
ROOT-FRACTIONS CONTROLS	SUCCESIO-NAL AGE	-0.4124	-0.4359	-0.1327	-0.1601
	SIGN.	**	**	ns	ns
ERDWt	SUCCESIO-NAL AGE	-0.3858	-0.4213	-0.1715	-0.1940
		**	**	ns	ns

Table 4: Paired T-Test for Total Expected Rootdw with found rootdw. * - p <.05;** - p < .01;*** - p <.001

TAR-GET	COMP.	NUTR.	DIF.	sd	t-VA-LUE	df	PROB.	SIG.
Lp	Ac	H	0.459	0.441	2.20	3	0.115	ns
Er	Ac	H	0.334	0.653	1.02	3	0.382	ns
Pp	Ac	H	-0.462	0.219	-0.42	3	0.701	ns
Dg	Ac	H	0.880	0.859	0.20	3	0.851	ns
Fp	Ac	H	-0.116	0.217	-1.07	3	0.362	ns
Cc	Ac	H	-0.166	-0.211	-0.16	3	0.884	ns
Hl	Ac	H	0.544	1.180	0.92	3	0.424	ns
Fr	Ac	H	0.421	0.458	1.83	3	0.164	ns
Je	Ac	H	0.011	0.237	0.09	3	0.931	ns
Ao	Ac	H	1.590	0.884	3.60	3	0.037	*
Ac	Ac	H						
Ja	Ac	H	-0.056	0.102	-1.10	3	0.352	ns

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Continuation table 4.

TARGET	COMP.	NUTR.	DIF.	sd	t-VALUE	df	PROB.	SIG.
Lp	Ac	L	-0.049	0.244	-0.40	3	0.713	ns
Er	Ac	L	-0.105	0.968	-0.22	3	0.742	ns
Pp	Ac	L	0.255	0.111	4.58	3	0.020	*
Dg	Ac	L	0.017	0.408	0.08	3	0.938	ns
Fp	Ac	L	-0.311	0.431	-1.44	3	0.246	ns
Cc	Ac	L	0.104	0.164	1.27	3	0.293	ns
Hl	Ac	L	0.259	0.279	1.84	3	0.164	ns
Fr	Ac	L	-0.228	0.184	-2.48	3	0.089	ns
Je	Ac	L	-0.047	0.077	-1.22	3	0.311	ns
Ao	Ac	L	-0.295	0.407	-1.45	3	0.243	ns
Ac	Ac	L						
Ja	Ac	L	0.139	0.244	1.25	3	0.300	ns
Lp	Hl	H	0.202	0.323	1.25	3	0.299	ns
Er	Hl	H	0.169	1.198	0.28	3	0.798	ns
Pp	Hl	H	0.187	0.515	0.73	3	0.520	ns
Dg	Hl	H	0.333	0.942	0.71	3	0.530	ns
Fp	Hl	H	0.661	0.627	2.11	3	0.126	ns
Cc	Hl	H	0.213	0.361	1.18	3	0.323	ns
Hl	Hl	H						
Fr	Hl	H	-0.282	0.649	-0.87	3	0.449	ns
Je	Hl	H	-0.143	0.553	-0.52	3	0.640	ns
Ao	Hl	H	0.829	0.721	2.30	3	0.105	ns
Ac	Hl	H	0.544	1.180	0.92	3	0.424	ns
Ja	Hl	H	-0.553	0.785	-1.41	3	0.254	ns

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Continuation table 4.

TARGET	COMP.	NUTR.	DIF.	sd	t-VALUE	df	PROB.	SIG.
Lp	Hl	L	-0.198	0.332	-1.20	3	0.318	ns
Er	Hl	L	0.094	0.521	0.36	3	0.741	ns
Pp	Hl	L	0.026	0.127	0.41	3	0.711	ns
Dg	Hl	L	0.949	1.006	-1.89	3	0.156	ns
Fp	Hl	L	0.176	0.237	1.48	3	0.235	ns
Cc	Hl	L	-0.363	1.544	-0.47	3	0.670	ns
Hl	Hl	L						
Fr	Hl	L	0.133	0.537	0.49	3	0.655	ns
Je	Hl	L	0.394	0.382	2.06	3	0.132	ns
Ao	Hl	L	0.200	0.454	0.88	3	0.443	ns
Ac	Hl	L	0.256	0.279	1.84	3	0.164	ns
Ja	Hl	L	0.518	0.87	11.89	3	0.001	***

Table 5: Mean light at 1 cm height (in % of total light availability above the canopy) +/- sd for *A. capillaris* and *H. lanatus* (controls) at high and low nutrient levels for three harvests.

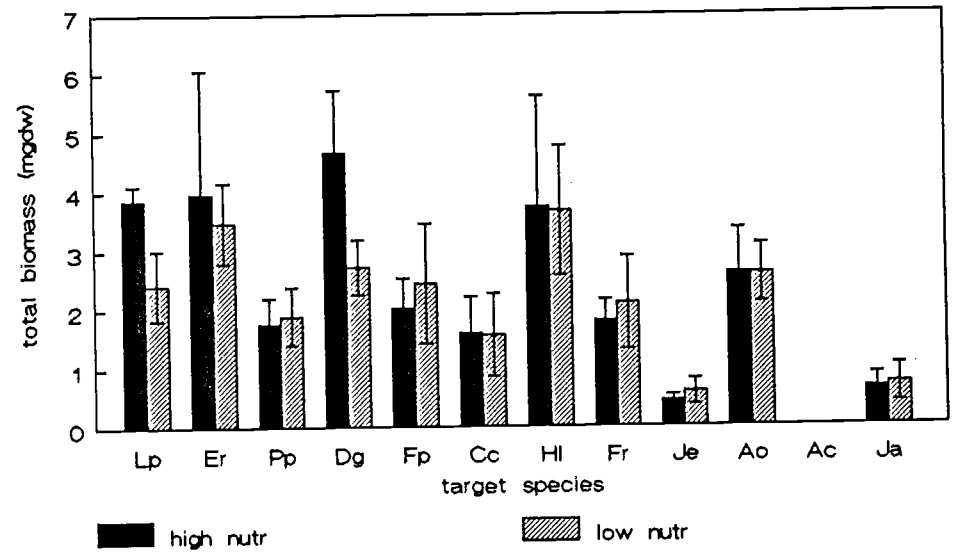
NUTR.	SPECIES	HARVEST 1	HARVEST 2	HARVEST 3
HIGH	Ac	72.74 +/-8.24	48.82 +/-10.73	55.81 +/-9.84
HIGH	Hl	36.08 +/-4.17	14.04 +/-5.19	33.95 +/-10.93
LOW	Ac	75.58 +/-3.41	49.82 +/-15.82	74.93 +/-09.70
LOW	Hl	27.45 +/-5.19	18.15 +/-5.41	50.61 +/-7.87

Table 6: Correlation and significance between light at 3 cm height and the relative shoot yield.
ns - not significant;* - p <0.05;** - p <0.01;
*** - p <0.001

NUTRIENTS	COMPETITOR	CORRELATION	SIGNIFICANCE
HIGH	A. capillaris	-0.5833	***
HIGH	H. lanatus	0.0488	ns
LOW	A. capillaris	-0.4100	**
LOW	H. lanatus	-0.4200	**

Table 7: Extractable N levels (mg.kg soil^{-1}) +/-sd of blanks at the beginning of the experiment and after one month watering.

N level	NO3+NH4 mg.kg-1	sd	NH4 mg.kg-1	sd
HIGH begin	321.08	13.58	7.02	1.60
LOW begin	31.31	1.84	2.09	0.33
HIGH 1 month	9.32	4.89	7.27	1.40
LOW 1 month	2.42	1.98	1.19	0.24



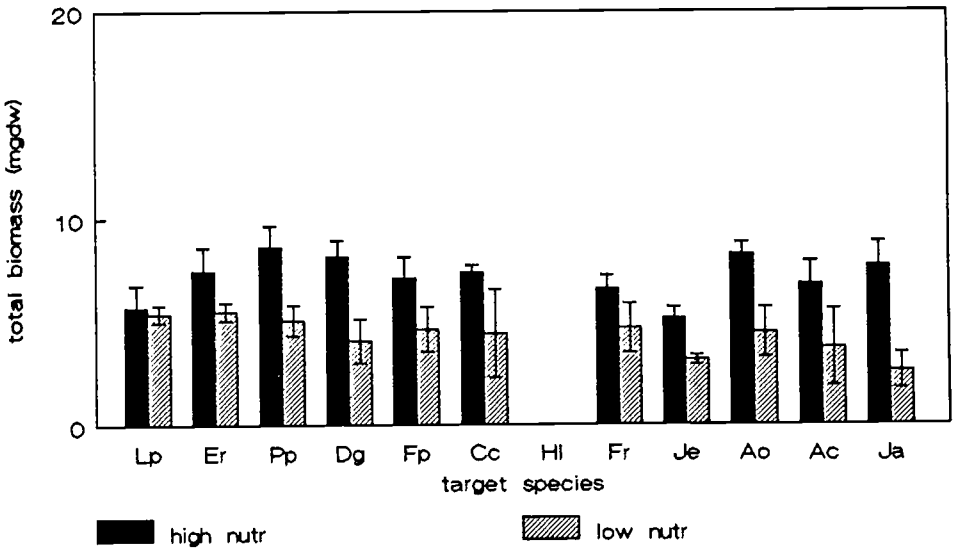
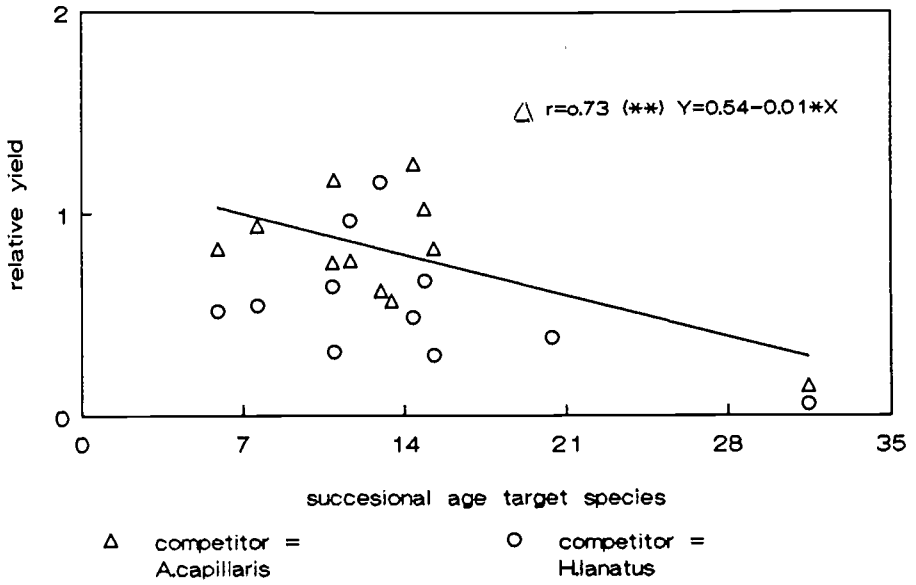


FIGURE 1: Mean shoot biomass (mgdw) of the first harvest (stem base excluded) per nutrient level for each target species.
a. Competition against A. capillaris.
b. Competition against H. lanatus.



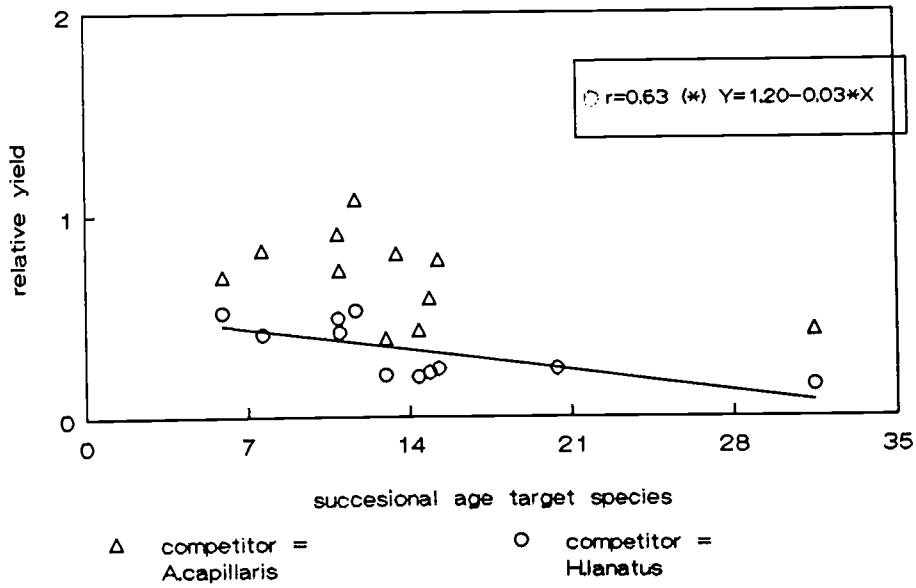
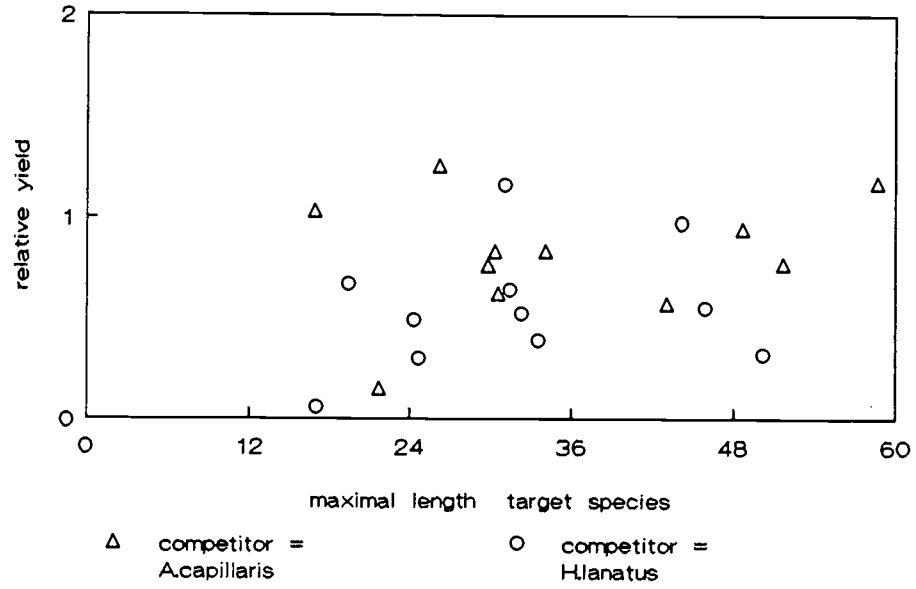


FIGURE 2: Mean relative shoot yield of target species as function of the successional age of target species at competition against A. capillaris and against H. lanatus the first harvest.
a. High nutrients.
b. Low nutrients.



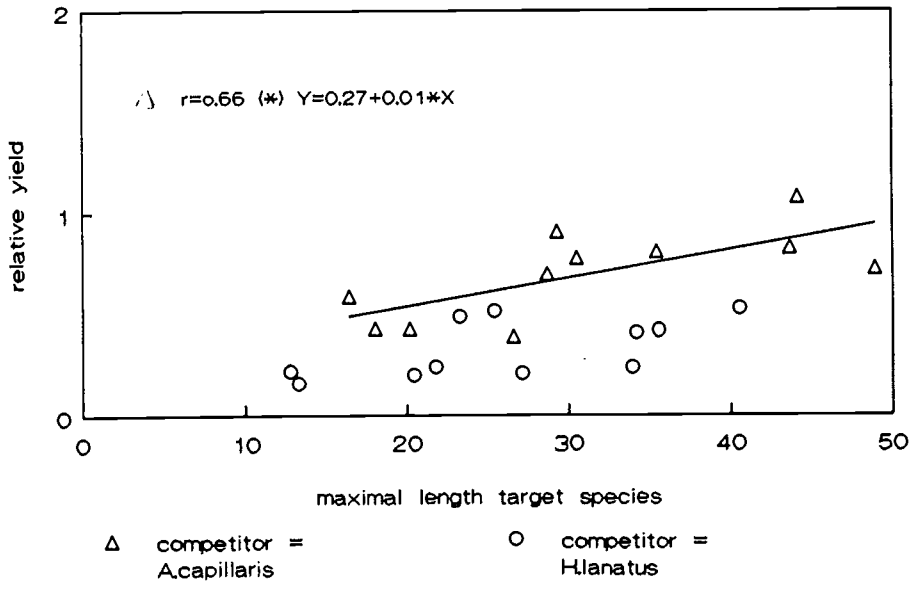


FIGURE 3: Mean relative shoot yield of target species as function of the mean maximal plant length of target species at competition against A. capillaris and against H. lanatus for the first harvest.
a. High nutrients.
b. Low nutrients.

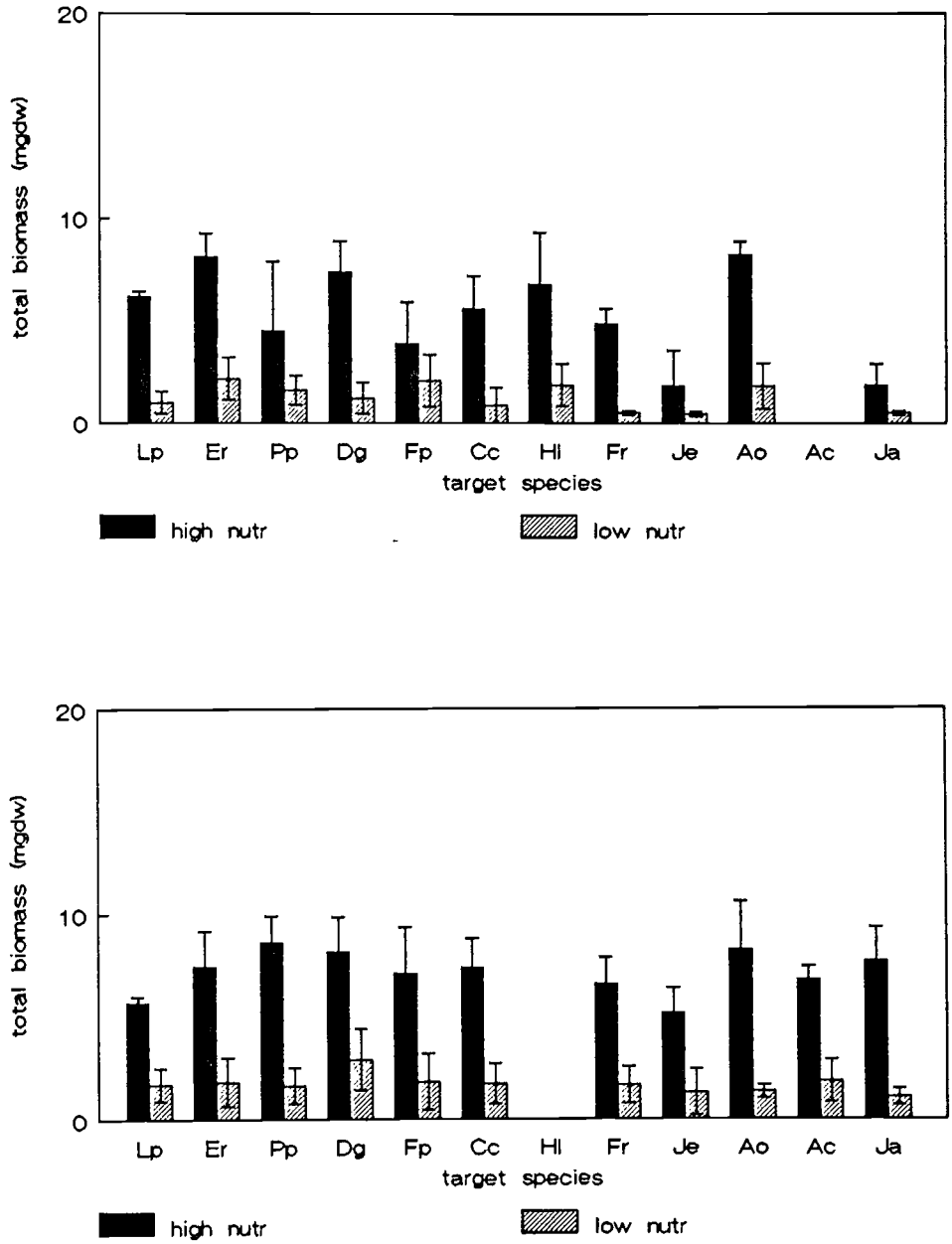
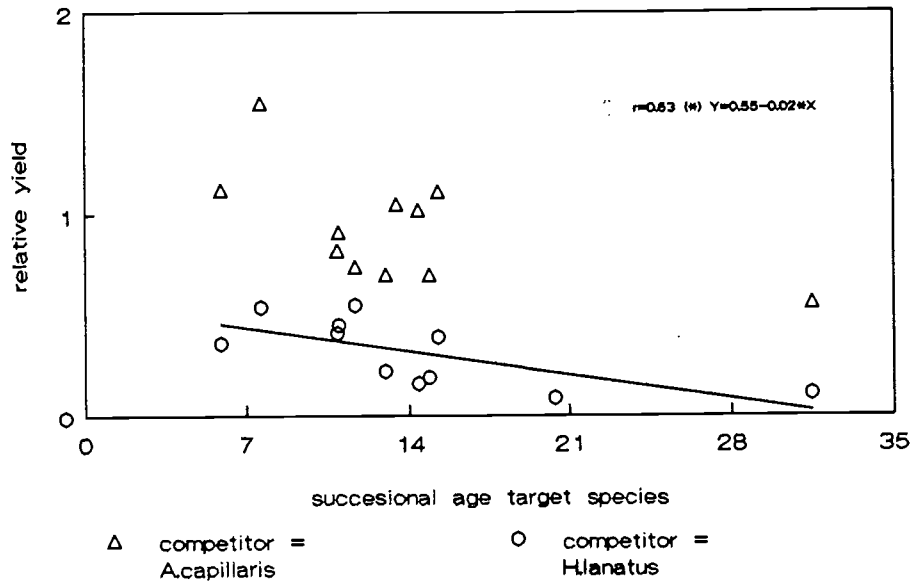


FIGURE 4: Mean shoot biomass (mgdw) of the second harvest (stem base excluded) per nutrient level for each target species.
a. Competition against A. capillaris.
b. Competition against H. lanatus..



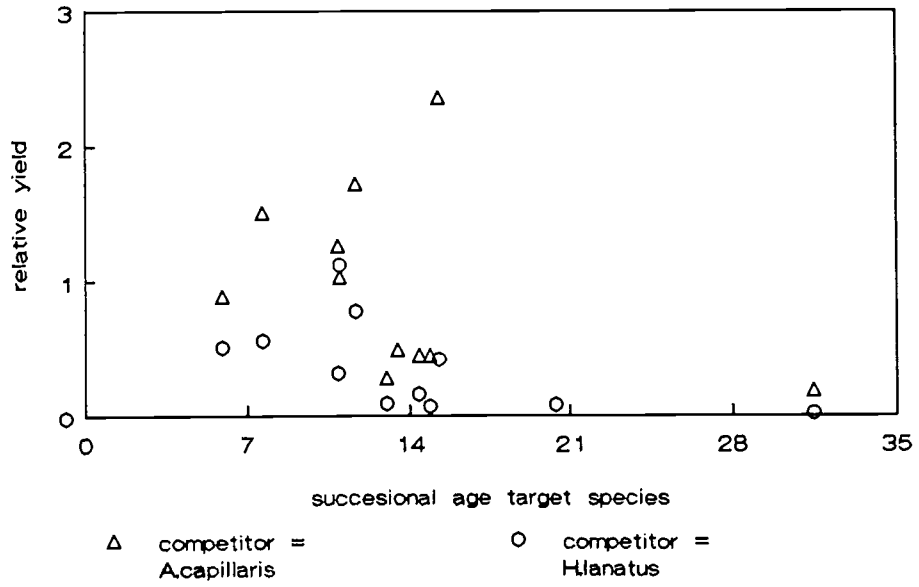
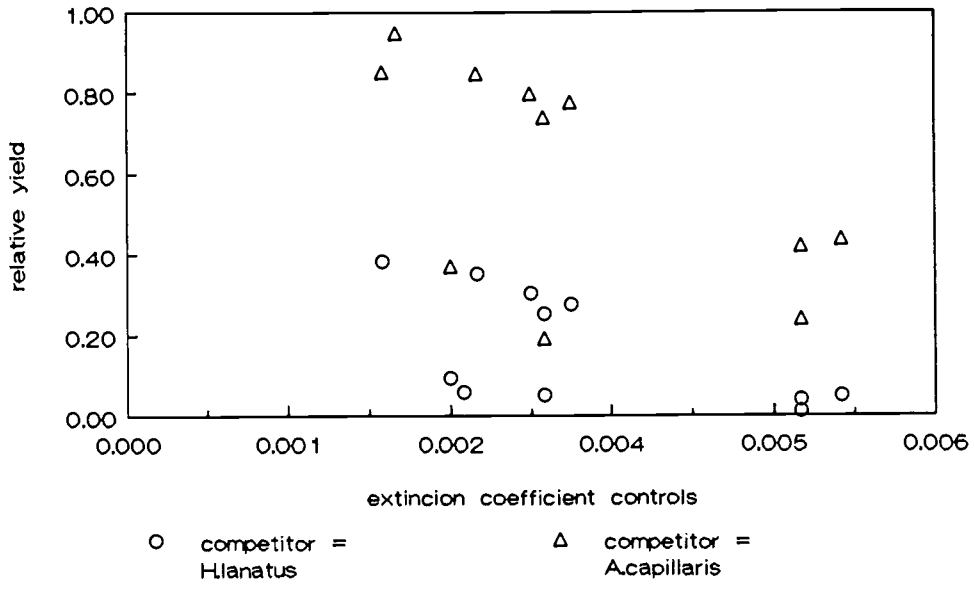


FIGURE 5: Mean relative shoot yield of target species as function of the successional age of target species at competition against A. capillaris and against H. lanatus for the second harvest.
a. High nutrients.
b. Low nutrients.



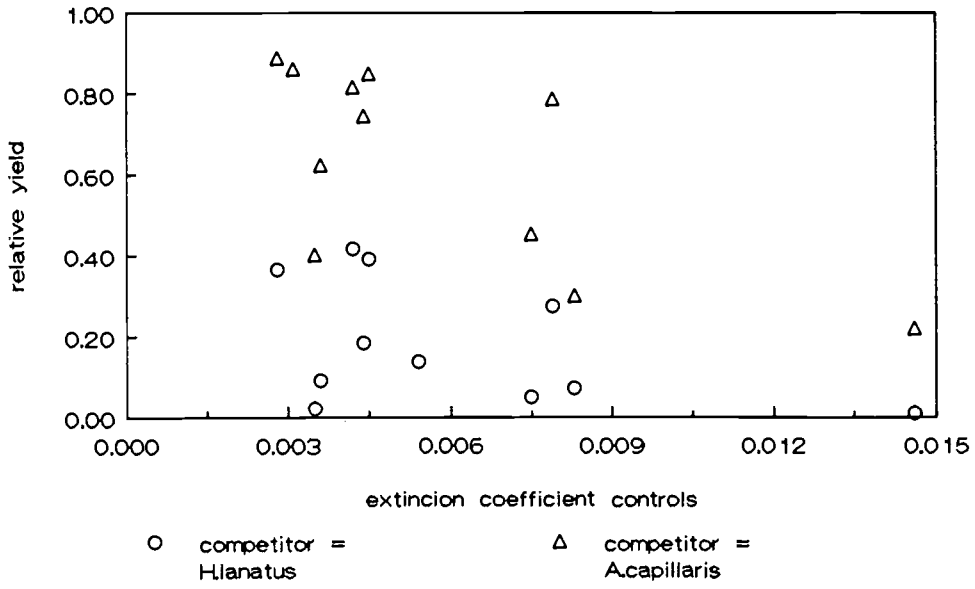
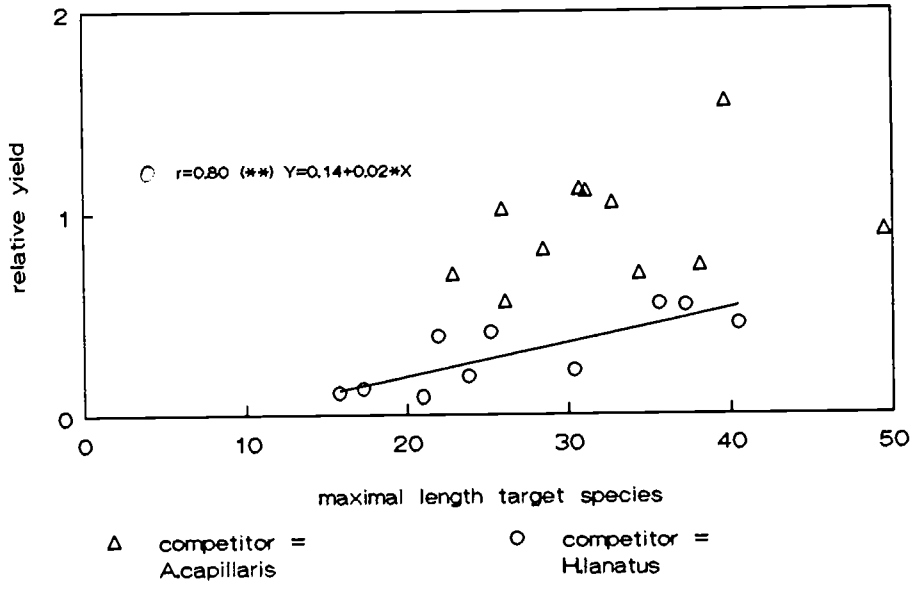


FIGURE 6: Mean relative shoot yield of target species at competition against A. capillaris and H. lanatus as function of the mean extinction coefficient of target species at controls for the second harvest.
a. High nutrients.
b. Low nutrients.



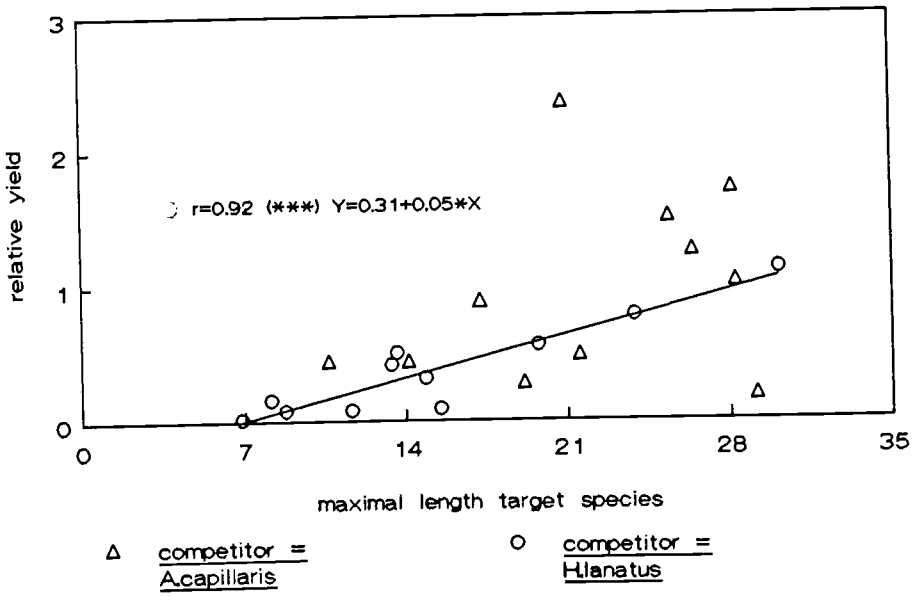
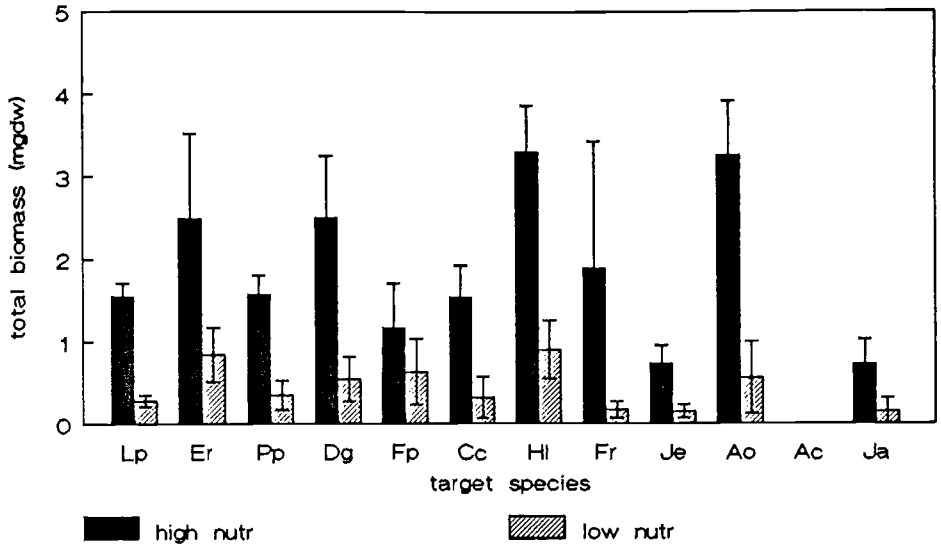


FIGURE 7: Mean relative shoot yield of target species as function of the maximal plant length of target species at competition afainst A. capillaris and H. lanatus for the second harvest.
a. High nutrients.
b. Low nutrients.



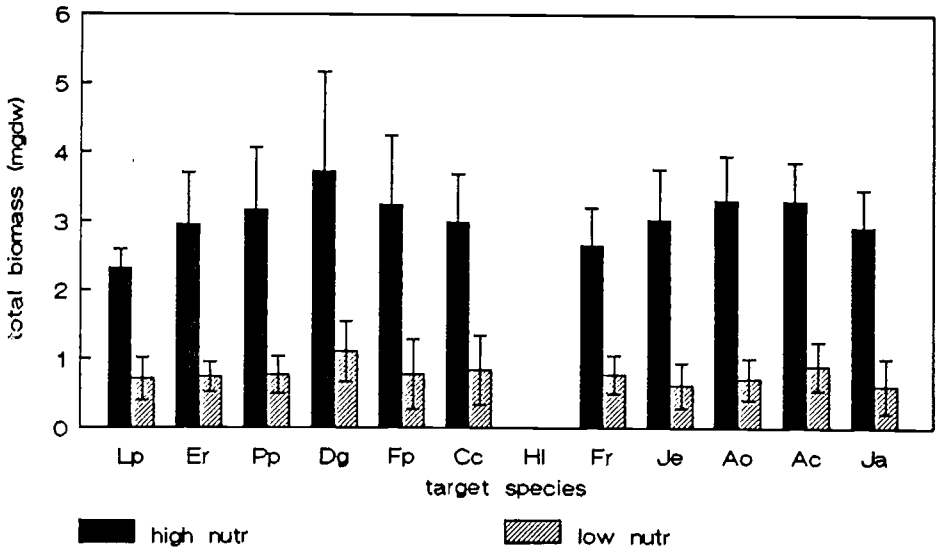
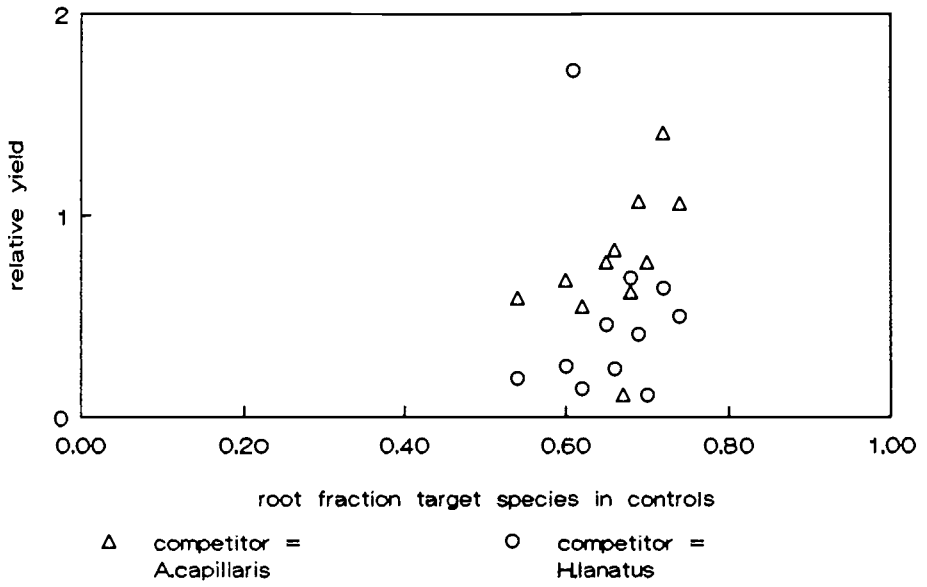


FIGURE 8: Mean shoot biomass (mgdw) (stem base excluded) of the third harvest per nutrient level for each target species.
a. Competition against A. capillaris.
b. Competition against H.lanatus.



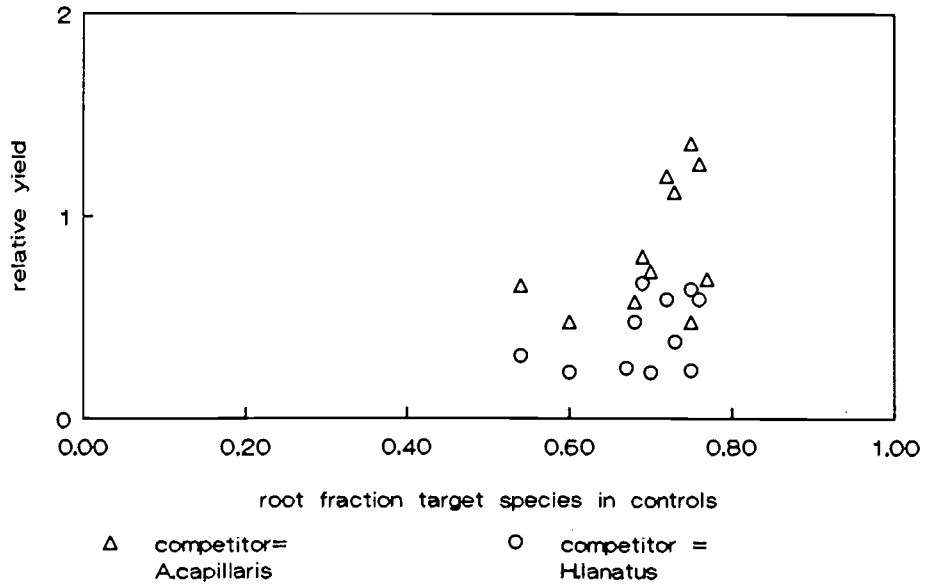


FIGURE 9: Mean relative total yield of target species at competition against A. capillaris and H. lanatus as function of the root fraction of target species in controls.
a. High nutrients.
b. Low nutrients.

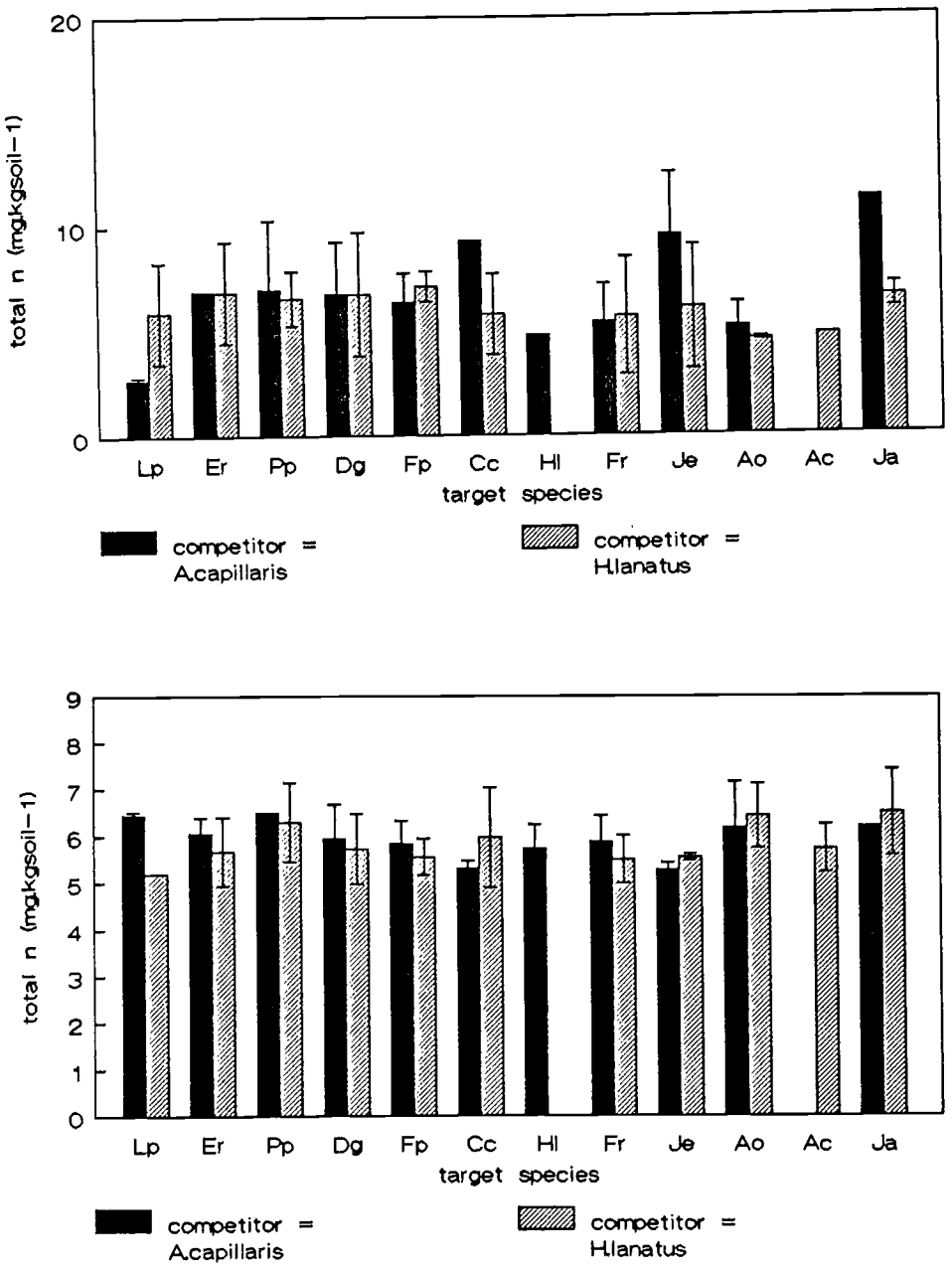
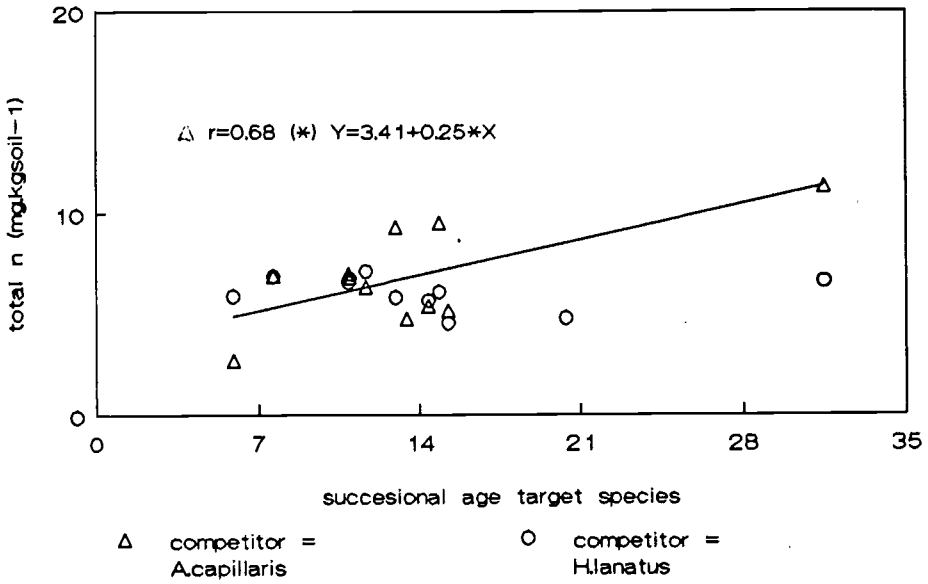


FIGURE 10: Mean total extractable N (NO3- + NH4+) (mg.kg soil^{-1}) at the end of the experiment per target species per competitor per nutrient levels.
a. High nutrients.
b. Low nutrients.



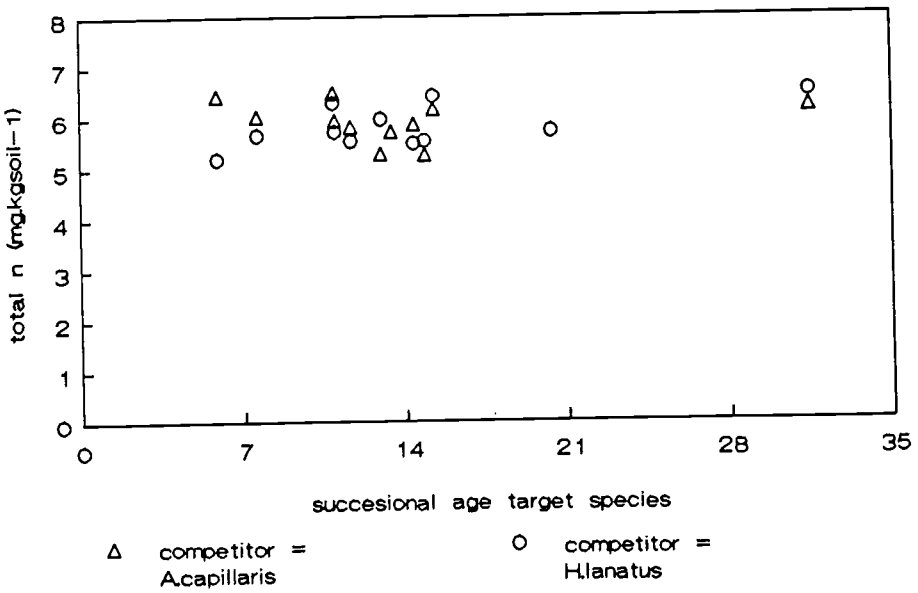


FIGURE 11: Mean total extractable N (NO3- + NH4+) at the end of the experiment as function of the successional age of the target species at competition against A.capillaris and H. lanatus.
a. High nutrients
b. Low nutrients.

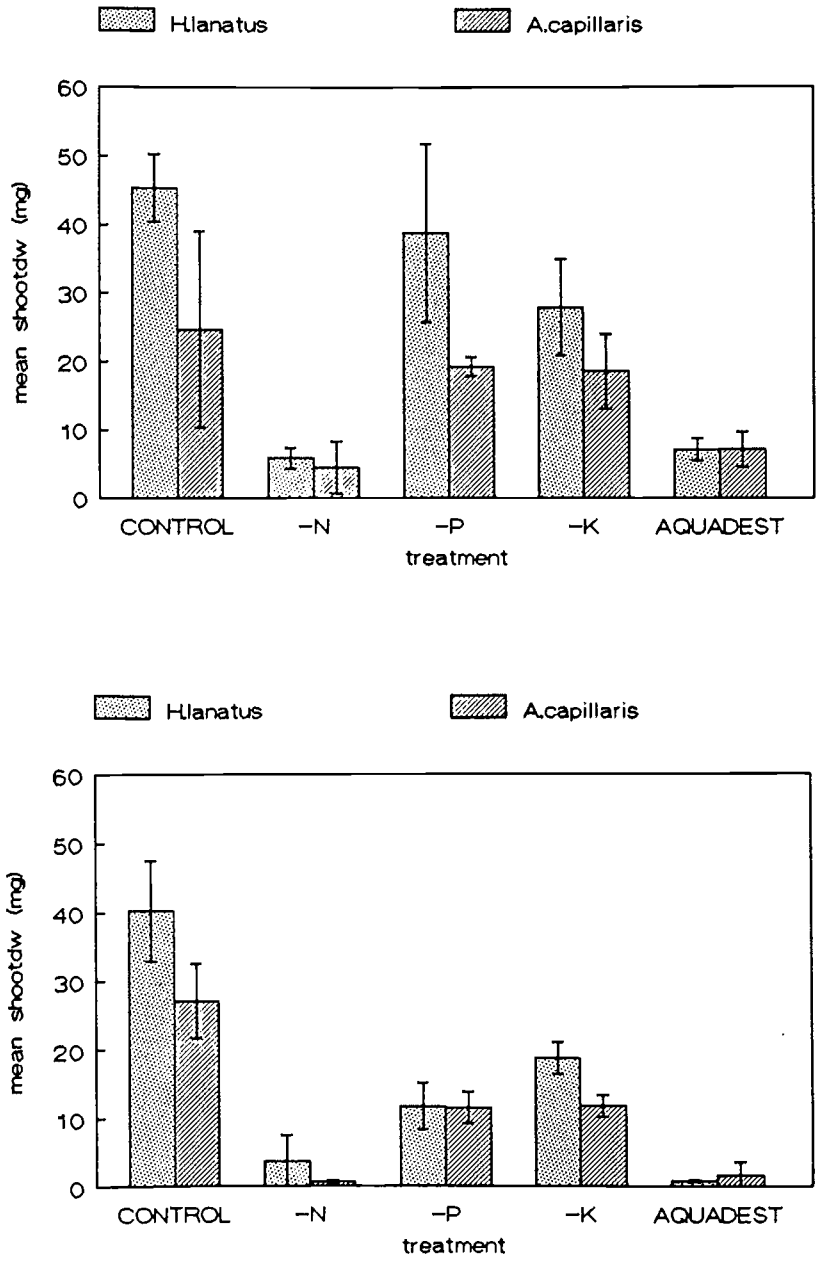
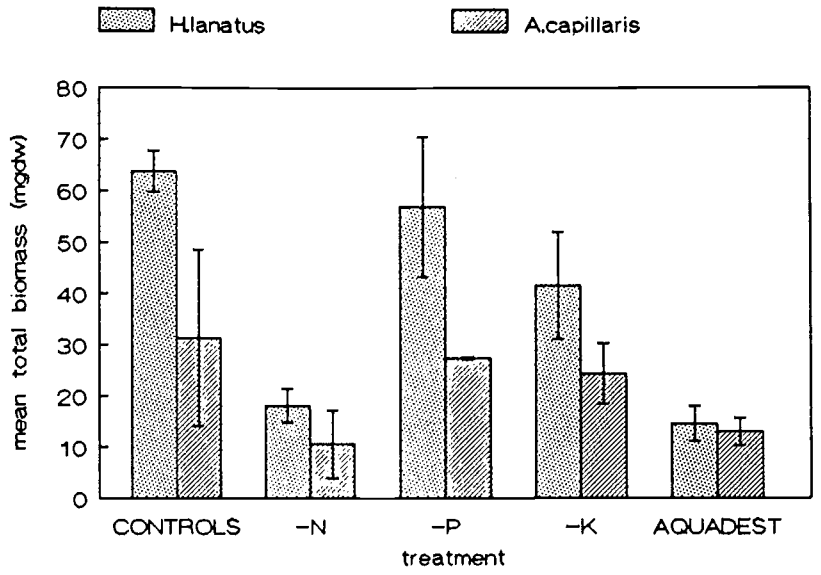


FIGURE 12: Fytometric determination of the relative defficiencies of minerals of aerated soils: mean shootdw (mg) of A. capillaris and H. lanatus at high and low nutrient levels.
a. High nutrients
b. Low nutrients.



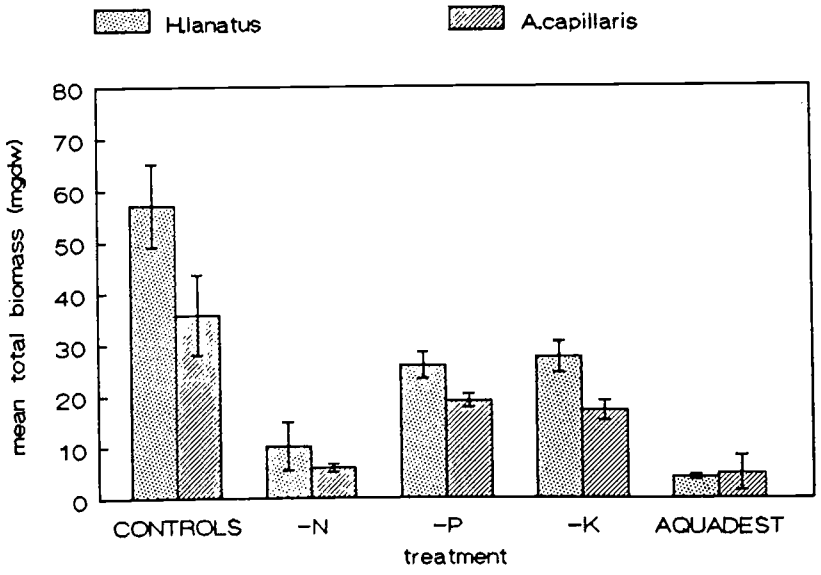


FIGURE 13: Fytometric determination of the relative defficiencies of minerals of aerated soils: total dw (mg) of A. capillaris and H. lanatus at high and low nutrient levels.
a. High nutrients.
b. Low nutrients.