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Canopy structure and nitrogen distribution in dominant and subordinate plants in a dense stand of *Amaranthus dubius* L. with a size hierarchy of individuals

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Abstract The objective was to investigate how nitrogen allocation patterns in plants are affected by their vertical position in the vegetation (i.e. being either dominant or subordinate). A garden experiment was carried out with *Amaranthus dubius* L., grown from seed, in dense stands in which a size hierarchy of nearly equally aged individuals had developed. A small number of dominant plants had most of their leaf area in the highest layers of the canopy while a larger number of subordinate plants grew in the shade of their dominant neighbours. Canopy structure, vertical patterns of leaf nitrogen distribution and leaf photosynthetic characteristics were determined in both dominant and subordinate plants. The light distribution in the stands was also measured. Average N contents per unit leaf area (total canopy nitrogen divided by the total leaf area) were higher in the dominant than in the subordinate plants and this was explained by the higher average MPA (leaf dry mass per unit area) of the dominant plants. However, when expressed on a weight basis, average N contents (LNC_{av}; total canopy N divided by the total dry weight of leaves) were higher in the subordinate plants. It is possible that these higher LNC_{av} values reflect an imbalance between carbon and nitrogen assimilation with N uptake exceeding its metabolic requirement. Leaf N content per unit area decreased more strongly with decreasing relative photon flux density in the dominant than in the subordinate plants showing that this distribution pattern can be different for plants which occupy different positions in the light gradient in the canopy. The amount of N which is reallocated from the oldest to the younger, more illuminated leaves higher up in the vegetation may depend on the sink strength of the younger leaves for nitrogen. In the subordinate plants, constrained photosynthetic activity caused by shading might have reduced the sink intensity of these leaves.

Key words Canopy structure · Light · Nitrogen allocation · Photosynthesis · Size hierarchy of individuals

Introduction

The rate of leaf photosynthesis is positively related to the incident photon flux density (PFD) and to the nitrogen content per unit leaf area (n_L) (Field and Mooney 1986; Hirose and Werger 1987a; Evans 1989). The photosynthetic performance of a plant will therefore be affected by the light climate in which it is growing and by the way nitrogen is distributed over its leaves.

Plants growing in a dense stand are generally found to allocate leaf nitrogen in such a way that the leaves in the highest, most illuminated regions of the canopy have the highest n_L values (Field 1983; Hirose and Werger 1987a, 1994; Evans 1989; Pons and Pearcy 1994). For monospecific stands consisting of plants which are of approximately the same size, this results in an average nitrogen distribution which is parallel to the light climate in the canopy (Hirose and Werger 1987b; Hirose et al. 1988; Anten et al. 1995). Hirose and Werger (1987b) calculated that such a nitrogen distribution pattern, as compared to a more uniform N distribution, will contribute to increased photosynthetic nitrogen use efficiency (PNUE) at the canopy level. The non-uniformity of the N distribution (i.e. difference in n_L levels between the top and bottom of the canopy) was shown to increase with increasing leaf area index, F_T, (Hirose et al. 1988, 1989; Schieving et al. 1992a) and canopy extinction coefficient for light, K_L (Anten et al. 1995), and thus with decreasing PFD levels in the lowest layers of the canopy. Apparently, plants are able to perceive the light gradient which develops in a growing stand and react in

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an adaptive way by reallocation of N from shaded to more illuminated leaves (Pons et al. 1993). This export of N from shaded leaves may ultimately result in increased senescence and leaf death (Burkey and Wells 1991).

As mentioned, the studies discussed above were carried out with stands consisting of individuals of the same height. This implied that all plants in the stand experienced the same light climate and it had the advantage that the N distribution, which is a plant based characteristic, could be described at canopy level. However, uniformity of plant size is not generally found in natural plant communities (Weiner and Solbrig 1984). If plants in a stand differ in size, a stand can no longer be regarded as a simple summation of identical individuals and the N distribution will have to be described for individual plants or for groups of plants with the same height.

In dense stands of vegetation a skewed frequency distribution of individual plant size often develops, there being a large number of subordinate plants slightly smaller than the mean and a small number of dominant plants much greater than the mean (Ford 1975). Such distribution patterns are generally referred to as size hierarchy of individuals (Weiner and Solbrig 1984) and are caused, through variations in growth rate, by factors such as: competition, heterogeneity of resources, genetic variation and small differences in the rate of emergence (Ford 1975; Weiner and Solbrig 1984). Dominant plants, being taller, will be able to expand their leaves in the upper layer in the canopy where they receive high photon flux density (PFD) levels. Subordinate plants, on the other hand, will produce their leaves in the lower, more shaded regions of the canopy (Ford 1975; Hirose and Werger 1994).

Anten et al. (1995) hypothesized that the distribution of leaf nitrogen is strictly determined by the PFD gradient across the leaves of a plant and that it is independent of the absolute PFD level incident on the highest most-illuminated leaves. This implies that this allocation pattern is independent of plant height and position in the light gradient in the canopy. If this hypothesis holds for stands with a size hierarchy of individuals, we would expect patterns of N distribution in dominant and subordinate plants to be similarly related to the differences in relative PFD incident on the leaves.

In the present study, we investigated this in dense stands of the erect dicotyledonous herb *Amaranthus dubius* L. in which a clear size hierarchy of individuals had developed. We measured the PFD gradient in the canopy and separately determined patterns of N distribution in the dominant and subordinate plants. By comparing the results for these groups of plants we could investigate how the N distribution in a plant is affected by its size and position in the light gradient in the canopy.

Materials and methods

Calculations

Light factors

Light attenuation in the canopy can be described by Beer's law (Monsi and Saeki 1953):

$$I = I_o \exp(-K_L f_h) \qquad (1)$$

where I_o and I are the PFD on a horizontal plane above the canopy and within the canopy at depth h, respectively, and K_L is the canopy extinction coefficient for light. K_L is determined from the slope in the linear regression of I/I_o after logarithmic transformation on f_h. The variable f_h denotes the total cumulative leaf area index from the top until depth h and is given as:

$$f_h = f_{hs} + f_{hd} \qquad (2)$$

where the subscripts s and d refer to the subordinate and dominant components of the canopy, respectively. The mean PFD incident on a leaf at depth h (I_L) can be given as:

$$I_L = \frac{I_o K_L}{(1-t_L)} \exp(-K_L f_h) \qquad (3)$$

where t_L is the transmission coefficient (Hirose and Werger 1987b). Note that the assumption of a single K_L value in Eqs. 1 and 3 holds only if the dominant and subordinate plants have similar foliage structure (i.e. leaf angles) and t_L values.

A non-rectangular hyperbola was used to fit the light response of net leaf photosynthesis (P_n):

$$P_n = \frac{[(P_m + \Phi I_L) - \{(P_m + \Phi I_L)^2 - 4P_m \Phi \theta I_L\}^{1/2}]}{2\theta} - R_d \qquad (4)$$

where P_m is light-saturated photosynthesis, R_d the dark respiration and Φ and θ the quantum yield and curvature factor, respectively (Hirose and Werger 1987a). The variables P_m and R_d were assumed to be linearly related to the nitrogen content per unit leaf area n_L (Hirose and Werger 1987a):

$$P_m = a_p(n_L - n_b) \qquad (5a)$$

$$R_d = a_r(n_L - n_b) + b_r \qquad (5b)$$

with a_p and n_b the slope and x intercept of the $P_m - n_L$ relation, a_r the slope of the $R_d - n_L$ relation and b_r the R_d for a leaf with $n_L = n_b$. The values of Φ and θ were assumed to be independent of n_L (Schieving et al. 1992b).

Nitrogen distribution in the canopy

The measured nitrogen distributions were fitted to an exponential function of the total cumulated leaf area index f_h (Anten et al. 1995):

$$n_{Li} - n_{bi} = (n_{oi} - n_{bi}) \exp(-K_{ni} f_h) \qquad (6)$$

where K_n is the N allocation coefficient, n_o is the n_L value at the top of the canopy ($f_h = 0$). The subscript i refers to individuals plants or groups of equally sized plants and in the present study it stands for either group of dominant (d) or subordinate (s) plants. K_n is estimated from the slope in the linear regression of ($n_L - n_b$) after logarithmic transformation on f_h. The value of K_n increases with increasing non-uniformity of the N distribution (increasing difference between the n_L levels of leaves in the top and the bottom of the canopy). For K_n values close to zero Eq. 6 will tend to the uniform distribution (i.e. the n_L level of all the leaves equals the mean). The relation between leaf N content (n_L) and the relative

PFD (I/I_o) can be found by eliminating f_h from Eqs. 1 and 6.

$$n_{Li} - n_{bi} = (n_{oi} - n_{bi})(I/I_o)^{K_{ni}/K_L} \quad (7)$$

Hence, the nitrogen distribution in both dominant and subordinate plants is described as a function of the light distribution in the canopy. From Eq. 7 it can be seen that if the N distribution in dominant and subordinate plants is similarly related to I/I_o, then we should expect to find similar K_n values in both groups of plants.

Plant material and growth of stands

Amaranthus dubius L. is an annual dicotyledonous species with the C_4 photosynthetic pathway. It grows at open fertile sites and in northern South America it is regarded as an important agricultural weed.

A garden experiment was carried out at the Fondo Nacional de Investigaciones Agropecuarias research station in Maracay, Venezuela (10 °15'N 67 °45'W; altitude 400 m) on a sandy loam soil. Stands of *A. dubius* were grown from seed, sown on 8 October 1992 in rows placed 8 cm apart and 150 seeds m^{-1} in each row. Plants were fertilized with nitrogen (120 kg N ha^{-1} as urea) and phosphorus (50 kg P ha^{-1} as triple superphosphate). There were four replicate plots each 2.3 × 2 m.

Seedlings emerged between 5 and 9 days after sowing (DAS). Generally the plants which had emerged first rapidly grew taller than those which had emerged later. From 12 to 34 DAS we regularly thinned the stands, generally removing the smallest plants. After the thinning about 24 plants per row remained (300 plants m^{-2}). Towards the end of the experiment (as from 34 DAS), two distinct size classes of plants had developed. One size class was composed of a relatively small number of tall plants (± 50 plants m^{-2}) which dominated the top of the canopy, while the second consisted of a large number of short plants (± 250 plants m^{-2}) which grew in the shade of their larger neighbours. In the remainder of this paper these two groups will be referred to as "dominant" and "subordinate" plants, respectively. The thinning process had been carried out in such a way that the plants within each size class were reasonably uniform in size and that tall and small plants were homogeneously distributed in all plots.

Stand structure

Canopy structure and light distribution were determined shortly before flowering (54 DAS) basically following the method described in Hirose and Werger (1987a). In each plot a 0.8 × 0.5 m quadrat was established. PFD (400–700 nm) was measured at height increments of 10 cm for six replicates, using an SF80 line sensor (Decagon Devices Ltd., UK) under an overcast sky. Reference PFD at the top of the canopy was measured after each reading. Leaf angles were measured with a protractor.

After the measurement of PFD all plants in each quadrat were cut at soil level, sealed in plastic bags and brought to the laboratory. Here plant length from the base to the youngest developing leaf was measured. Plants which were taller than 80 cm (dominant plants) were separated from the others (subordinate plants). All plants were clipped every 10 cm in height from the base and divided into leaves and stems. Leaf area was measured with a leaf area meter (LI3100, LiCor, USA) and dry weights were determined after oven drying at 70 °C for 3 days. Organic nitrogen content was determined with a continuous flow analyzer (SKALAR, The Netherlands) after Kjeldahl digestion.

Gas exchange measurements

Photosynthesis and dark respiration were measured with a portable open gas exchange system using an infra-red gas analyzer (IRGA: LCA2, Analytical Development Co. Ltd., UK). The IRGA was calibrated by drawing air from a compressed air cylinder with known CO_2 concentration (349 ppm; Matheson Gas Products Inc.). The humidity sensor in the LCA2 was calibrated using a column (30 cm long and 5 cm diameter) filled with $FeSO_4 \cdot 7H_2O$. The quantum sensor was checked against a newly calibrated sensor (LI190SA, LiCor). A Parkinson leaf chamber with an 11-cm^2 window area was connected to the instrument.

Within 2 days after harvesting, photosynthesis measurements were conducted on attached leaves (30 per plant size class) from different heights on plants near the gap which had been created by the removal of harvested plants. The light response of photosynthesis was measured by interposing neutral density light filters and thus reducing the PFD level from approximately 1800 to 25 μmol m^{-2} s^{-1} using a clear sky as a light source. Dark respiration was determined for leaves (15 per plant size class) on plants which had been placed in the dark for about 1 h. Leaf temperature as calculated from an energy balance equation averaged 31.6 °C (± 2.0 °C) which was close to the ambient temperature. The gas exchange data and stomatal conductance were calculated from the raw data according to von Caemmerer and Farquhar (1981). After the gas exchange measurements leaves were dried and their organic nitrogen content was determined as described above.

Results

Canopy structure and light distribution

The total above ground biomass of the dominant plant group (approximately 50 plants m^{-2}) was about twice that of the subordinate plant group (approximately 250 plants m^{-2}) (Table 1). The subordinate plants on the other hand produced significantly more leaf area per unit biomass (LAR; Table 1) than the dominant ones. The leaf area indices (F_T) of both groups in the stand were approximately equal. Both dominant and subordinate plants had a leaf weight ratio of about 0.5 (Table 1). However, the leaf area per unit mass (SLA) of the subordinate plants was almost twice that of the dominant ones.

Average heights of the subordinate and dominant plants were 56.1 (± 2.16 SE, $n = 4$) and 98.7 (± 2.84, $n = 4$) cm, respectively. Approximately 78% of the subordinate plants were 45–65 cm tall while 1.5% were taller than 75 cm and 4.5% shorter than 40 cm. About 80% of the dominant plants were 90–110 cm in length; 3% were shorter than 90 cm and 1.5% taller than 115 cm.

The vertical distributions of the leaf area index with height in the vegetation is presented in Fig. 1A. The dominant plants had most of their leaf area between 50 and 100 cm above soil surface with 50% close to the top of the vegetation (80–100 cm). The subordinate plants had spread their leaves more evenly along the length of their stems with most of the leaf area between 20 and 70 cm above the soil surface (Fig. 1A).

PFD decreased exponentially with increasing cumulated leaf area from the top of the canopy (f_h) (Fig. 2). Note that f_h refers to the total cumulated leaf area; i.e. the leaf area indices of dominant and subordinate plants together (Eq. 2). There was a strong linear rela-

Table 1 Canopy characteristics, allocation coefficients and nitrogen contents of dominant and subordinate plants in an *Amaranthus dubius* stand. Data are means with 1 SE in parentheses. Superscripts denote the differences between the two plant groups based on a studentized *t*-test; ^{s}significant $P < 0.05$; ^{ns}not significant. A single extinction coefficient (K_L) was calculated for the whole canopy

	Dominant	Subordinate
Dry weights (g m^{-2})		
Leaves	101.2 (7.13)	55.1 (3.46)^{s}
Stems	105.4 (3.42)	65.0 (7.03)^{s}
Total	206.6 (10.47)	120.1 (9.79)^{s}
Ratios^{a}		
LAI (m^2 m^{-2})	2.76 (0.145)	2.29 (0.165)^{ns}
LAR (m^2 kg^{-1})	13.37 (0.274)	19.36 (1.431)^{s}
LWR (kg kg^{-1})	0.489 (0.0097)	0.464 (0.0223)^{ns}
SLA (m^2 kg^{-1})	27.39 (0.887)	41.56 (1.314)^{s}
Canopy extinction coefficient		
K_L (Eq. 1)	0.744 (0.023)	
Nitrogen contents		
Total canopy N (mmol N m^{-2})	308.7 (15.94)	202.7 (12.69)^{s}
Average leaf N (mmol N m^{-2})	111.8 (0.988)	89.1 (1.701)^{s}
Average leaf N (mmol N g^{-1})	3.065 (0.124)	3.69 (0.062)^{s}
Nitrogen allocation coefficients		
K_n (Eq. 6)	0.388 (0.025)	0.162 (0.018)^{s}
K_n/K_L (Eq. 7)	0.517 (0.026)	0.249 (0.028)^{s}

[a] Ratios determined on basis of aboveground biomass

tion between log transformed values of relative PFD and f_h ($r^2 = 0.929$; Fig. 2, Table 1) indicating a constant value of the extinction coefficient for light (K_L) which was about 0.73 (Table 1). Based on the vertical leaf area distribution of both plant groups and the value of K_L, it can be calculated that the highest leaves of the subordinate plants (those which were at about 70 cm above the soil) received approximately 25% of the PFD incident at the top of the canopy. Average leaf inclination angles were 24.7° and 27.9° in the subordinate and dominant plants, respectively. Within each group of plants leaf angles were constant with height in the canopy.

Gas exchange characteristics

In both size classes rates of light-saturated photosynthesis (P_m) were found to increase linearly with leaf N content (n_L) (Fig. 3). The slope value of the P_m – n_L relation (a_p) was higher in the dominant than in the subordinate plants while the x intercepts, n_b, of this

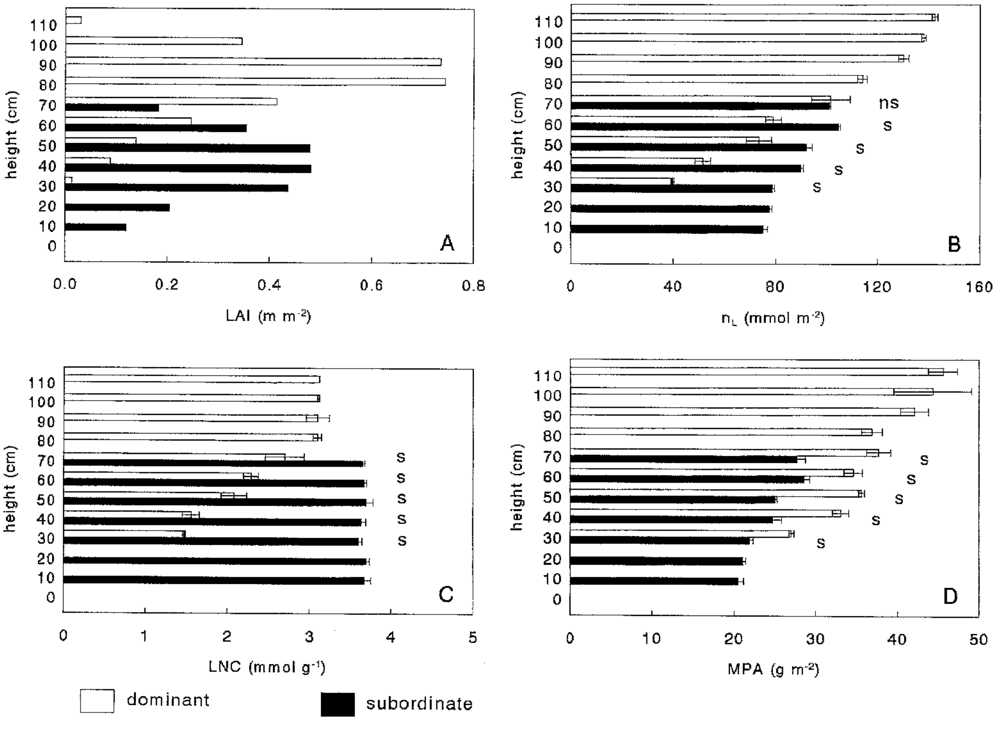

Fig. 1A–D Vertical distribution of **A** leaf area index (LAI), **B** leaf nitrogen content per unit leaf area (n_L), **C** leaf N content per unit weight (LNC) and **D** mass per area (MPA) in dominant and subordinate plants in a dense stand of *Amaranthus dubius*; ^{s} and ^{ns} denote significant and non-significant differences between dominant and subordinate plants based on a studentized *t*-test ($P > 0.05$)

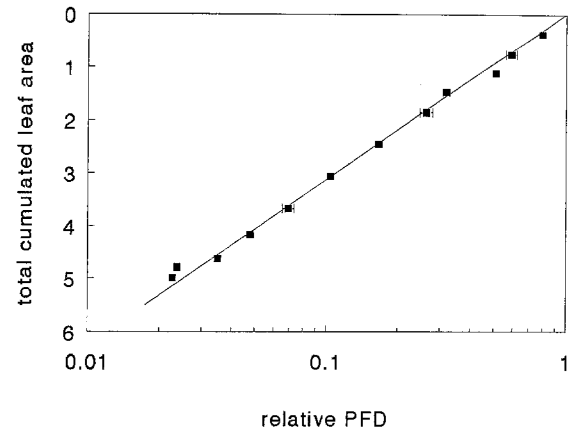

Fig. 2 Relative photon flux density (PFD) against cumulative leaf area index in a dense stand of *A. dubius*. Fits were made with Eq. 1 and the regression coefficient is given in Table 1. *Bars* denote SEs ($n = 4$)

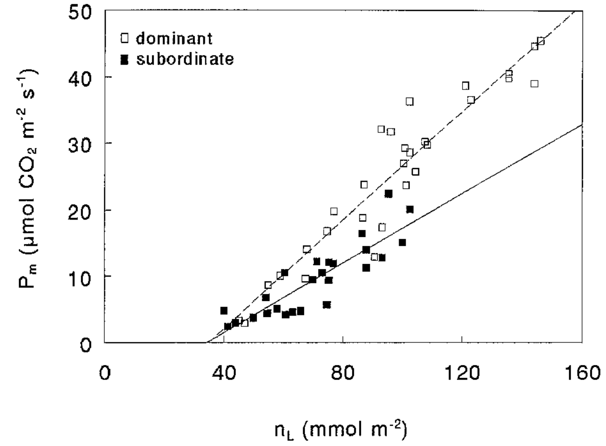

Fig. 3 Light-saturated rates of photosynthesis (P_m) of leaves from dominant and subordinate plants of *A. dubius* as a function of leaf nitrogen content (n_L). Fits were made using Eq. 5a and regression coefficients are shown in Table 2

relation were similar (Table 2). Thus, for a given n_L value above the minimum n_b, dominant plants were found to have higher P_m values than subordinate plants. In the dominant plants, there was a significant positive correlation between dark respiration (R_d) and n_L. In the subordinate plants such a correlation between R_d and n_L was not found (Table 2). R_d varied between 0.3 and 1 µmol $CO_2\,m^{-2}s^{-1}$ in the subordinate and between 0.3 and 2.2 µmol $CO_2\,m^{-2}s^{-1}$ in the dominant plants.

Leaf nitrogen contents

The total amount of leaf nitrogen expressed per unit soil area (N_T) was higher in the dominant than in the subordinate plants (Table 1). Since both components of the stand had about the same leaf area index (F_T), the average nitrogen content per unit leaf area (n_{Lav}) was also higher in the dominant plants. On the other hand, the average leaf N content on a dry mass basis (LNC_{av}) was higher in the subordinate plants.

Table 2 The slopes (a_p, a_r mmol CO_2 mol^{-1} N s^{-1}) of the relations between light-saturated gross photosynthesis (P_m µmol CO_2 m^{-2} s^{-1}) and dark respiration (R_d µmol m^{-2} s^{-1}) and leaf nitrogen content (n_L mmol N m^{-2}), the *x* intercept (n_b mmol N m^{-2}) of the $P_m - n_L$ relation, the R_d value for $n_L = n_b$ (b_r), the quantum yield (Φ µmol CO_2 $µmol^{-1}$) and the curvature factor (Θ dimensionless) for dominant and subordinate plants of *A. dubius*

	Dominant	Subordinate
$P_m = a_p\,(n_L - n_b)$ Eq. 5a		
a_p	0.407	0.261
n_b	35.5	33.9
r^2 ($P <$)	0.895 (0.001)	0.764 (0.001)
$R_d = a_r\,(n_L - n_b) + b_r$ Eq. 5b		
a_r	0.0098	0.0034
b_r	0.491	0.422
r^2 ($P <$)	0.528 (0.001)	0.060 (0.225)
Φ	0.0479	0.0487
SEM ($n = 30$)	0.0052	0.0067
Θ	0.675	0.789
SEM ($n = 30$)	0.075	0.048

Figure 1B shows the vertical distribution of leaf N content on an area basis (n_L). In both groups of plants n_L declined with decreasing height but this effect was much stronger in dominant than in subordinate plants. In the canopy layers between 30 and 70 cm above the soil which were shared by both groups, the n_L values of the dominant plants were significantly lower than those of the subordinate ones (Fig. 1B), even though the dominant plants had higher average n_L values (n_{Lav}). The distribution of n_L as a function of total cumulative leaf area index (f_h, given by Eq. 2) is presented in Fig. 4A. The nitrogen allocation coefficient (K_n; Eq. 6) was higher in the dominant than in the subordinate plants (Table 1). In Fig. 4B, n_L values were plotted against relative PFD (I/I_o). The data show that n_L declined more strongly with decreasing relative PFD in the dominant than in the subordinate plants. Fitting the data with Eq. 7 yielded K_n/K_L values of about 0.5 and 0.2 in the dominant and subordinate plants, respectively (Table 1).

In the dominant plants, n_L of the leaves lowest in the canopy was about 40 mmol N m^{-2} compared to 75 mmol N m^{-2} in those of the subordinate plants at equal height in the canopy. A considerable amount of senescent leaves were observed lower down on the dominant plants but not on the subordinate plants. The nitrogen contents (n_L) of yellow and of dead leaves were 25.3 (± 2.5) and 15.7 (± 1.3) mmol N m^{-2}. In view of the fact that n_L in the dominant plants may be more than 120 mmol m^{-2}, this suggests that during senescence about 90% of leaf N was withdrawn before leaf abscission.

In the dominant plants both dry mass per unit leaf area (MPA) and leaf nitrogen content per unit dry

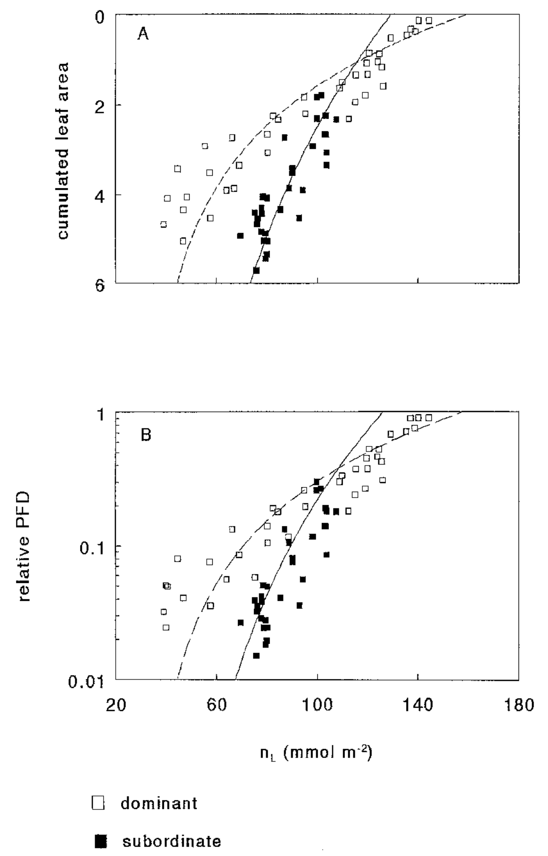

Fig. 4A, B Leaf nitrogen content (n_L) as a function of **A** cumulative leaf area index and **B** relative photon flux density (PFD) in dominant and subordinate plants in a dense stand of *Amaranthus dubius*. In **A** fits were made with Eq. 6 and in **B** with Eq. 7. The respective values of K_n and K_n/K_L are shown in Table 1

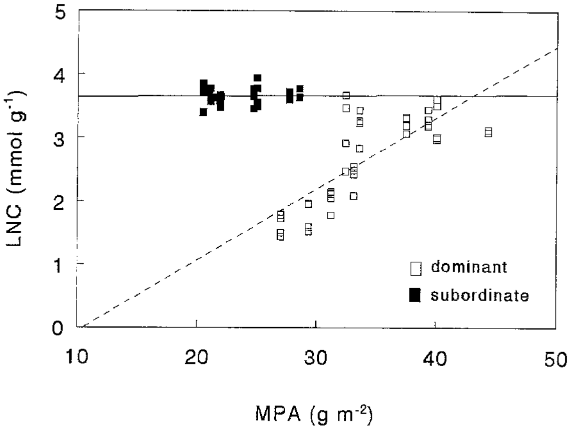

Fig. 5 Relationship between leaf nitrogen concentration (LNC) and mass per area (MPA) in dominant and subordinate plants in a dense stand of *A. dubius*. *Lines* denote linear regressions (dominant plants $r^2 = 0.590$; subordinate plants $r^2 < 0.001$)

weight (LNC) increased with height in the canopy while in the subordinate plants only MPA increased and LNC remained constant (Fig. 1C, D). In the canopy layers which were shared by both groups (30–70 cm), the dominant plants had significantly higher MPA but significantly lower LNC values than the subordinate ones.

Leaf nitrogen per unit area (n_L) is the product of the MPA and the LNC. The effects of MPA and LNC on n_L are best examined by plotting LNC against MPA (Fig. 5). Clearly, there was a strong correlation between LNC and MPA in the dominant but no correlation in the subordinate plants with LNC in the subordinate plants being constant (Fig. 1C). Thus, in the dominant plants variation in n_L was the result of variation in MPA and LNC while in the subordinate plants it resulted only from variation in MPA.

Discussion

Nitrogen contents and mass per area

Subordinate plants produced leaves with higher average nitrogen concentrations (LNC$_{av}$) but lower amounts of dry mass per unit area (MPA) and average N contents per unit area (n_{Lav}) than dominant plants (Table 1). These differences can be attributed to differences in light availability. Plants growing under shaded conditions are often found to have lower MPA (Walters and Field 1987; Pons and Pearcy 1994; Reich and Walters 1994) and sometimes higher LNC values (Dale and Causton 1992; Reich and Walters 1994) than those grown under high light conditions. Dale and Causton (1992) suggested the higher LNC values found in plants grown under shaded conditions to signify an imbalance between nitrogen metabolism and carbon fixation with N uptake exceeding its metabolic requirement. A restricted assimilate supply caused by shading appears to have a relatively small effect on the active absorption of nutrients (Crapo and Ketlapper 1981) thus leading to increased nitrogen concentrations in the plant (Dale and Causton 1992).

Photosynthesis nitrogen relationship

Dominant plants were found to have higher photosynthetic capacities (P_m) per unit n_L than subordinate plants (Fig. 3). From Figs. 1B and 4B it can be seen that the leaves of dominant plants generally received higher PFD levels than those of subordinate plants with the same n_L. Acclimation of the photosynthetic apparatus to low light levels leads to a greater proportional investment of n_L in the light harvesting complex at the expense of electron transport and Calvin cycle capacities (Burkey and Wells 1991; Evans 1989, 1993; Pons and Pearcy 1994) which may result in a lower slope of the $P_m - n_L$ relation (Evans 1989). Thus, it appears that the lower P_m per unit n_L of the subordinate plants may be attributed to the lower relative PFD levels to which their leaves are exposed.

Vertical distribution patterns of nitrogen and leaf area in the canopy

In both dominant and subordinate plants leaf N content (n_L) was found to decrease with increasing depth h in the canopy (Fig. 1B) and thus with increasing cumulative LAI and decreasing relative PFD levels (I/I_o; Fig. 4). However, this gradient in n_L was considerably stronger in the dominant than in the subordinate plants (Figs. 1B and 4) with the dominant plants having a higher N allocation coefficient (K_n, Eq. 6; Table 1). Apparently, dominant plants responded more strongly to the PFD gradient in the canopy by reallocating larger amounts of N from the most shaded to the most illuminated leaves. These data indicate that in stands of plants of different heights, the distribution of leaf nitrogen in a plant is strongly influenced by the absolute PFD level incident on its highest, most-illuminated leaves and thus by the vertical position which the plant occupies in the canopy.

The question arises why the relation between n_L and I/I_o is not as steep in subordinate as in dominant plants. During canopy development, redistribution of nitrogen takes place from the most shaded leaves lower down to the more illuminated ones higher up in the canopy (Hirose and Werger 1987b; Schieving et al. 1992a, b; Pons et al. 1993). This indicates that the leaves higher up in the canopy act as nitrogen sinks and those lower down as nitrogen sources. The rate of N loss from nitrogen exporting leaves is regulated by the presence and strength of the nitrogen sink (Stoddart and Thomas 1982; Khanna-Chopra and Reddy 1988). In the subordinate plants the absolute PFD level incident on the most illuminated leaves at the top of the plants was on average only 25% of that incident on the top of the stands. As mentioned above, N uptake by the subordinate plants appeared to exceed its metabolic requirement. It can thus be argued that photosynthesis in the most illuminated leaves of these plants was strongly limited by light and not by nitrogen. This might have reduced the sink strength of these leaves for nitrogen (Dale and Causton 1992) and this could restrict the redistribution of leaf nitrogen in the subordinate plants.

The subordinate plants had their leaf area spread along most of the length of the stems while in the dominant plants it was amassed close to the top of the plants (Fig. 1A). Werger and Hirose (1988) showed that plants growing in dense stands concentrate their leaf area more in the highest layers of the canopy than plants growing in open stands and suggested that this resulted from increased light competition in dense stands. Since light availability decreases exponentially with increasing cumulated leaf area above a given point in the canopy (Eq. 1; Fig. 2), the absolute decline in PFD levels with decreasing height will be strongest in the upper layers of the vegetation. For dominant plants which can harvest high incident PFD levels, it will therefore be important to form new leaves continuously at the top of the vegetation to keep receiving full irradiance. To maintain this production, large amounts of nitrogen have to be redistributed from the older leaves lower down in the canopy to those newly formed at the top. Leaves lowest down in the canopy eventually become N starved, senesce and die. The canopy of dominant plants is thus gradually lifted upwards. In subordinate plants on the other hand, formation of new leaf area is probably restricted by assimilate supply. Because of the apparent lack of a strong N sink in the top-most leaves, less N is redistributed from older to newly formed leaves higher up in the canopy and the oldest leaves are maintained on the plant resulting in a more even distribution of leaf area along the stem.

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