Leaf nitrogen profiles in sunflower canopies during grain filling

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Summary. In vegetative canopies, the vertical gradient of lamina nitrogen concentration (NW) usually parallels the profile of light distribution. The light and NW profiles of sunflower crops were characterised during grain filling to evaluate the effects of grain demand for N on the pattern of NW distribution. Before the onset of N accumulation in grain, the pattern of NW was related to the distribution of light in the canopy. Afterwards, important changes in the profile of NW occurred that were unrelated to the light regime: NW declined simultaneously in leaves from all positions in the canopy and the rate of NW change was greater in leaves closer to the grain. The mechanisms involved in determining the distribution of leaf N in vegetative canopies, therefore, did not apply to sunflower during grain filling.

Introduction

Light distribution influences the actual profile of leaf N in vegetative canopies. These leaf N profiles are similar to the ones that, theoretically, maximise canopy photosynthesis (5). This paper evaluates the hypothesis that the presence of a strong sink for N, viz. growing grain, could affect the pattern of leaf N distribution described for vegetative canopies. Sunflower, with its oil- and protein-rich grain that may account for 60-75% of total shoot N at maturity (3) has been chosen for this investigation.

Materials and methods

The experiment was carried out at the Faculty of Agronomy, Buenos Aires. Hybrid sunflower cv. Prosol 35 was sown on 14 December 1991. Four treatments resulted from the factorial combination of two N levels (No = nil, and N50 = 50 kg N/ha, applied as urea) and two plant densities (d = 2.4, and D = 4.8 plants/m2). Treatments were established 21 days after emergence (DAE) and were arranged in a split-plot design with four replicates. N treatments and plant densities constituted the main plots and sub-plots, respectively. Crops were drip-irrigated twice-weekly. Crops reached first anthesis, last anthesis and physiological maturity at 49, 57 and 85 DAE. Profiles of leaf area, light, and lamina N concentration (NW, %) where measured weekly during the 'filling period' (from 53 to 85 DAE). Cumulative leaf area index above the level z (Li) was measured for nodes 10, 15, 20 and 25 from the plant base. NW for leaves at the same positions was determined by the microKjeldahl technique. PAR at any level z in the canopy (Id was calculated according to Beer's law using an extinction coefficient. K1 = 0.74, and measured irradiance at the top of the canopy.

Results and discussion

The combination of plant densities and N treatments generated the range of light profiles illustrated in Fig. I. At 53 DAE, L1 over node 10 ranged from 1.14 (treat. dNo) to 2.20 (treat. DN50) and the corresponding fractions of incident light at the level of node 10 were 0.44 and 0.26. Leaf area and light profiles above node 10 did not change from 53 to 78 DAE in the low density treatments. Leaf senescence and the corresponding changes in light profiles started earlier and were more marked in the high density treatments. At maturity, leaf senescence and changes in light penetration in the canopy were evident between nodes 10 and 20 at high density and between nodes 10 and 15 at low density.

Profiles of NW are shown in Fig. 2. Maximum NW of about 4% was found for leaves of the fertilised treatment. NW measured in completely senesced leaves (NW_{min}) was 0.96 % (s.e. = 0.06) in fertilised plants compared with 0.79 % (s.e. = 0.04) in unfertilised plants (P<0.025).

Crops reached last anthesis at 57 DAE and the onset of grain N accumulation, estimated as the x-intercept of the linear regression of grain N on time, between 54 DAE and 57 DAE. Hence. it can be

assumed that there was no effect of grain demand for N on NW distribution at 53 DAE and, in this sense, crops can be considered 'vegetative' at this stage. Thus, two stages are considered in the following analysis. First, profiles of NW and light distribution for 53 DAE are examined within the framework of the current knowledge for vegetative canopies. The changes in the pattern of NW is thus analysed for a second stage in which the relationship between sink (grain) demand and source (leaf) supply of N is established.
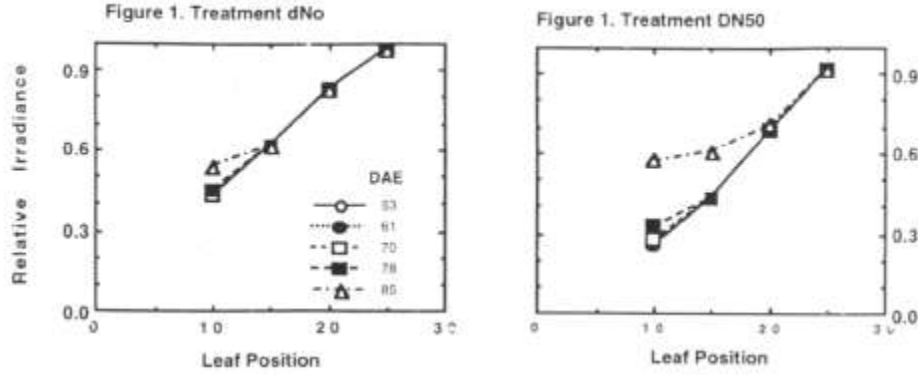

Fig. 1. Profiles of relative irradiance. Standard error of differences between means (s.e.d.) were: 0.024 for comparisons between dates, 0.014 for comparisons between N and plant density treatments, and 0.021 for comparisons between leaf positions.
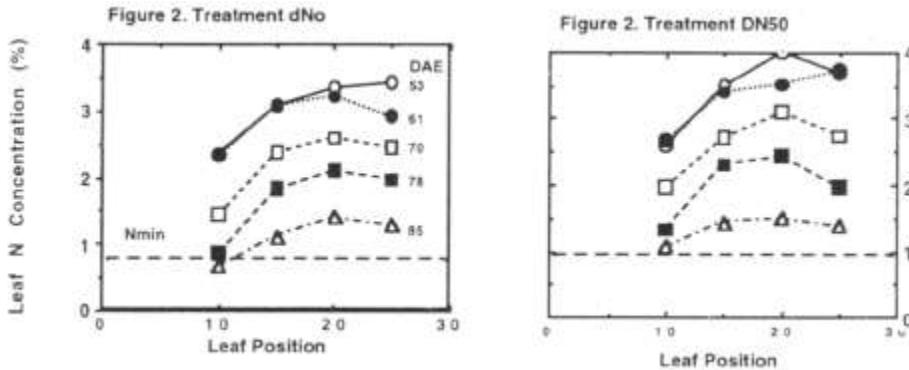

Fig. 2. Profiles of NW. Symbols for dates arc as in Fig. 1. s.e.d. were: 0.061 for comparisons between dates, 0.038 for comparisons between and plant density treatments, and 0.054 for comparisons between leaf positions.

Leaf N profiles before the onset of grain N accumulation.

To test the association between NW and light, as found in vegetative canopies of other species, the model of Hirose *et al.* (2) was fitted to the data for 53 DAE:

$$RN = c\,RI^d \text{ (eq. 1)}$$

where RI is relative irradiance at depth z within the canopy (I_z/I_0), RN is relative NW (RN = N_zW_0),

and *c* and *d* are empirical coefficients. RN and RI were significantly correlated (Fig. 3). Parameter *c* was close to I. indicating that maximum NW corresponded to leaves exposed to maximum irradiance (Fig. 3). Parameter *d* is related to the coefficient of N allocation, K_a., (1). K_a depends on total L (L_0) and quantifies

the distribution of N between leaves, i.e. it increases with increasing non-uniformity in N distribution. Estimated K_a for the crops in the present experiment indicates that leaf N response to irradiance of sunflower was quantitatively similar to that of other species including *Solidago ahissitna* (I), *Lvsimachia vulgaris* (2) and *Medicago saliva* (4) (not shown).

Leaf N profiles during the period of grain N accumulation

Central to this study is the concept that sink /source interactions may affect the pattern of leaf N distribution. To investigate this relationship, changes in the amount of N (g N m^{-2}) for lamina (Δ_{leaf},<0)
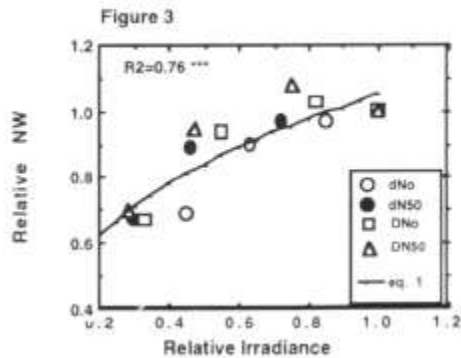

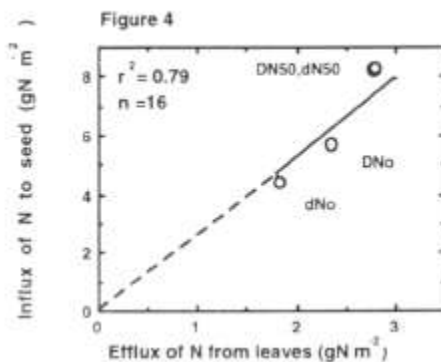**Fig. 3. RN vs RI at 53 DAE. The fitted curve is eq. (I) with parameters $c = 1.06$ and $d = 0.32$.**

Fig. 4. ΔN_{grain} vs ΔN_{leaf}. S.e.d. appropriate for comparisons between N and plant density treatments, were: 0.5r for ΔN_{leaf} and 1.26 for ΔN_{grain} leaf

and grain (ΔN_{grain} ,>0) during the tilling period were calculated. Influx of N to grain was closely related to the efflux of N from leaves (Fig. 4). The substantial amount of N in the mature grain that resulted from mobilisation of leaf N (= 40%) together with the correlation shown in Fig. 4 indicates that grain demand for N and source activity (efflux of N from leaves) were closely related. A causal relationship between these variables, however, cannot be elucidated from these data.

Lemaire *et al.* (4) found that eq. (1) fitted the data for vegetative alfalfa canopies irrespective of plant age. In contrast, we found quite large deviations from this model for the successive observations as grain filling progressed (not shown). In fact, during most of the filling period, important variations in the distribution of N among leaves (Fig. 2) occurred with little or no change in the profiles of light (Fig. 1).

After discarding the idea that light influenced the distribution of leaf N during the grain-filling phase, the changes in NW were analysed further. It was apparent that NW started to decline earlier from apical leaf positions (Fig. 2); means across treatments showed no significant change between 53 and 61 DAE in NW for leaves 10 (2.43 vs 2.54 %) and 15 (3.28 vs 3.22%) whereas NW decreased significantly (P<0.05) for leaves 20 (3.62 vs 3.38%) and 25 (3.56 vs 3.34%). After 61 DAL NW decreased in leaves from all canopy positions. The rate of change of NW (for NW > NW_{min}) was fairly constant during grain filling. as indicated by significant linear relationships of NW with time (0.60 r^2 0.89, P<0.001). The rate of change of NW correlated significantly (P<0.001) with initial NW, viz:. actual NW at 53 DAE (Fig. 5A). However, initial NW was also correlated with leaf position (r^2 = 0.64. P<0.001) and, consequently, the rate of change of NW increased with leaf position (Fig. 5B). This caused the marked gradient of NW established in the vegetative phase to level out as grain filling progressed (Fig. 2). There are at least two explanations for the pattern of change in leaf N observed during grain filling in sunflower. On the one hand, it can be proposed a concentration-dependent mechanism by which N is depleted faster from the leaves where it is more concentrated. On the other hand, a position-dependent mechanism can be postulated by which N is depleted faster from the leaves closer to the grain.
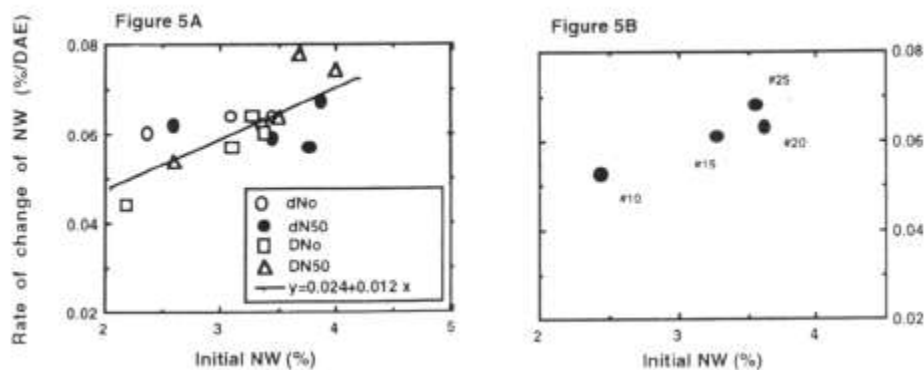

Fig. 5. Rate of change of NW during the filling period vs initial NW (NW at 53 DAE). (A) Each data point is mean of four replicates and variation within treatment is due to leaf position. (B) Averages across treatments for leaf positions 10, 15, 20, and 25.

Summarising, the distribution of leaf N followed contrasting patterns during the 'vegetative' and grain-tilling stages in sunflower. Before the onset of N accumulation in grain, the pattern of NW was similar to that described for other species and it was related to the distribution of light in the canopy. Afterwards, important changes in the profile of NW occurred that did not appear to be associated with the light regime. The concentration of N in leaves close to the infructescence at the beginning of grain filling might facilitate the supply of N to the highly-demanding growing grain. This hypothesis and those related to the control of N depletion during grain filling warrant further investigation. It is concluded that the mechanisms involved in determining the distribution of leaf N in vegetative canopies did not apply to sunflower during grain filling.

References

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