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Nitrogen availability, local light regime and leaf rank effects on the amount and sources of N allocated within the foliage of young walnut (*Juglans nigra* × *regia*) trees

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Summary Early season leaf growth depends largely on nitrogen (N) provided by remobilization from storage, and many studies have tested the effect of N availability to roots on the amount of N provided for new leaf development by remobilization. Although it is well known that the light regime experienced by a leaf influences the amount of N per unit leaf area (LA), the effect of the local light regime on the amount of N derived either directly from root uptake or from remobilization for early season leaf growth has never been tested at an intracopy scale. The objective of this study was to quantify the relative importance of (1) N availability to roots, (2) local light regime experienced by the foliage (at the shoot scale) and (3) leaf rank along the shoot, on the total amount of N allocated to leaves and on the proportions of N provided by remobilization and root uptake. To quantify the importance of N uptake and remobilization as sources of leaf N, potted hybrid walnut trees (*Juglans nigra* L. × *regia* L.) were grown outdoors in sand and fed with a labeled (¹⁵N) nutrient solution. By removing the apical bud, the trees were manipulated to produce only two shoots. The experimental design had two factors: (1) high (HN; 8 mol N m⁻³) and low (LN; 2 mol N m⁻³) N availability; and (2) high (HL; 90% of incident photosynthetically active photon flux (PPF)) and low (LL; 10% of incident PPF) light.

Total leaf N per tree was unaffected by either N availability or irradiance. The HN treatment increased the amount of leaf N derived from root uptake at the whole-tree scale (typically around 8 and 2% in the HN and LN treatments, respectively). Nitrogen allocation within foliage of individual trees was controlled by the local light regime, which strongly affected individual leaf characteristics as leaf mass per unit LA and area-based amount of leaf N (N_a). Decreasing the light availability to a branch decreased the amount of N allocated to it, benefiting the less shaded branches. In contrast, shading of the lower

branch did not affect the fraction of total leaf N remobilized for either the lower, shaded branch or the upper, unshaded branch. The relevance of these findings for tree growth modeling is discussed.

Keywords: branch, leaf N, N allocation, N remobilization, N uptake, ¹⁵N, shading, shoot.

Introduction

Trees have to cope with spatial and temporal changes in soil nitrogen (N) availability during their growth (Vlassak et al. 1969, Le Tacon 1972, Bauzon et al. 1974, Gallardo et al. 2000). The N available for tree growth can be largely uncoupled from the immediate soil N supply because, while dormant, trees store N that is subsequently remobilized for growth (Chapin et al. 1990, Millard 1996), with N uptake over a number of years contributing to the pool of stored N (Weinbaum et al. 1987, Millard 1996, Weinbaum and Van Kessel 1998). In deciduous trees, remobilization can provide the majority of N for foliage growth (Millard and Proe 1991, Neilsen et al. 1997, Tagliavini et al. 1997, Weinbaum and Van Kessel 1998, Dyckmans and Flessa 2001, Frak et al. 2002a, Policarpo et al. 2002). However, the amount of leaf N derived by remobilization and its importance compared with the amount of leaf N obtained by root uptake depends on tree size and N availability. Nitrogen taken up by roots in spring and summer provides about 50% of total leaf N in small apple trees (Neilsen et al. 1997), but only 20–30% in mature pear trees (Sanchez et al. 1990), citrus (Feigenbaum et al. 1987) and almond trees (Weinbaum et al. 1984) and 40% in mature walnut (Weinbaum and Van Kessel 1998). The greater contribution of remobilization to leaf N in mature trees could be explained by their

larger pools of stored N (Millard 1996, Neilsen et al. 1997). Because N remobilization is source-driven (Millard et al. 2001), the N available from soil in any one year does not affect the amount of leaf N derived from remobilization (Millard and Proe 1991, Millard 1996). In contrast, N availability during the previous years affects the amount of stored N and consequently the amount of N that can be remobilized for leaf growth.

Previous studies have mainly quantified N uptake and remobilization fluxes on the whole-plant scale. Little is known about possible variations in the amount of leaf N derived from remobilization and the N remobilization/N uptake balance among leaves within tree crowns. The local light regime experienced by leaves affects leaf N per unit leaf area (LA) (DeJong and Doyle 1985, Le Roux et al. 1999), but its effect, if any, on the relative amount of N supplied for foliage growth by remobilization versus that supplied by root uptake is unknown. The relative importance of remobilization for foliage N supply generally decreases with time during the growing season (Neilsen et al. 1997). Thus, leaves produced during the early growing season are likely to depend more on N remobilization than leaves produced later.

The objective of this study was to quantify the relative importance of: (1) N availability to roots; (2) local light regime experienced by the foliage (here at the shoot scale); and (3) leaf rank along the shoot, in determining the total amount of N allocated to leaves and the proportions of leaf N provided by remobilization and root uptake in hybrid walnut trees (*Juglans nigra* L. × *regia* L.).

Materials and methods

Plant material and growth conditions

In March 2000, 30 two-year-old hybrid walnut trees (*Juglans nigra* × *regia*, NG38, Payre Nursery, Vinay, France), bred for timber production, were planted in 35-dm³ pots filled with fine

sand. Plants were watered weekly and kept frost-free until bud break. In late April, trees were transferred outdoors. This walnut hybrid exhibits strong apical dominance, which generally prevents axillary bud growth. However, to ensure each tree had a suitable and similar shape, the apical bud and all but two axillary buds were removed before bud break (Table 1). Sixteen individuals exhibiting similar timing in bud break were selected. After bud break (beginning of May), each tree received 500 cm³ of a complete nutrient solution three times a week for 14 weeks. Half of the trees were fed with high N solution (HN; 8 mol N m⁻³) and half were fed with a low N solution (LN; 2 mol N m⁻³). Nitrogen was applied as ¹⁵NH₄¹⁵NO₃ enriched with ¹⁵N to 5.0 atom percent excess. At the end of the labeling period, trees in the HN and LN treatments had received a total N of 168 mmol and 42 mmol, respectively. The total labeled ¹⁵N supplied to the HN and LN treatments was 8.4 and 2.1 mmol, respectively. Other nutrients were supplied as described by Millard and Proe (1991). Depending on evaporative demand, the trees were watered automatically every other day.

To test the effect of contrasting light regimes for leaves of the same plant, the lower branch on each two-branch seedling was placed under controlled light conditions, whereas the upper branch remained in full sun. Immediately after bud burst, the lower branch was placed under acrylic screens (Altuglas, ALTUMAX, Cergy Pontoise, France) transmitting either 90% of incident photosynthetically active photon flux (PPF) (HL) or 10% of incident PPF (LL). The HL screens were neutral filters, whereas the LL screens induced green shade conditions mimicking natural shading within the canopy (for screen characteristics, see Frak et al. 2002b). Four trees were used in each of the HN-HL, LN-HL and LN-LL treatments, and three trees were used in the HN-LL treatment because one tree died. Plants were grown in the light treatments for 3 months until leaf expansion was complete. Incident radiation was recorded from late March to late August with a JYP 1000 sensor

Table 1. Number of buds removed per tree before bud break and morphological characteristics of 2-year-old walnut trees at harvest. The main effects of nitrogen (N) availability and light regime were tested by 2-way ANOVA. Abbreviations: HN = high N treatment; LN = low N treatment; HL = high light treatment; LL = low light treatment and ns = not significant ($P > 0.05$). Values are means ± SE. For HN-HL, LN-HL and LN-LL, $n = 4$ and for HN-LL, $n = 3$.

	Treatments				Main effects	
	HN-HL	HN-LL	LN-HL	LN-LL	N availability	Light regime
<i>Before bud break</i>						
No. of buds removed ¹	22.8 ± 0.85	20.0 ± 2.52	25.3 ± 0.75	20.5 ± 0.66	ns	–
<i>At harvest</i>						
Basal diameter (mm)	40.8 ± 2.3	43.7 ± 2.4	47.5 ± 7.1	43.0 ± 3.8	ns	ns
Tree height (m)	1.25 ± 0.06	1.39 ± 0.14	1.43 ± 0.04	1.24 ± 0.08	ns	ns
Total tree dry mass (g) ²	689 ± 35.7	699 ± 57.9	675 ± 84.0	627 ± 12.2	ns	ns
Total leaf dry mass (g)	87.6 ± 3.2	101.8 ± 3.5	83.8 ± 11.2	88.2 ± 4.2	ns	ns
Total no. of leaves	30.5 ± 0.87	32.3 ± 1.45	32.5 ± 0.96	32.0 ± 0.71	ns	ns
Total leaf area (m ²)	1.16 ± 0.04	1.31 ± 0.09	1.16 ± 0.16	1.22 ± 0.08	ns	ns

¹ In 2-year-old hybrid walnut trees, only one bud (generally the apical bud) develops and prevents the growth of any other shoots.

² Total tree dry mass corresponds to whole above- and belowground tree compartments.

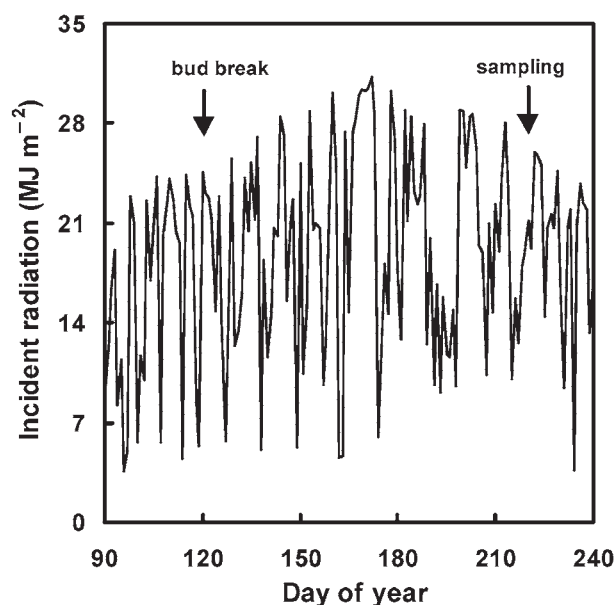


Figure 1. Time course of incident radiation from late March to late August 2000. Bud break and sampling periods are indicated.

(SDEC, Reignac sur Indre, France) (Figure 1). At sampling, no difference was observed between the four treatments in tree basal diameter, tree height, total dry mass, total leaf mass, total leaf number or total LA (Table 1).

Leaf harvesting and foliage dry mass, total N and ^{15}N contents

In early August, leaves from each branch of the two-branched trees were harvested and LA (m^2) was measured with an area meter (LI-3100, Li-Cor, Lincoln, NE). The other tree parts were freeze-dried and their dry masses (M ; g) measured. Leaves on the lower, shaded branch were sorted into three or four groups according to leaf rank along the branch (i.e., rank 1 contained the first four leaves in order of appearance, etc.), whereas leaves from the upper, unshaded branch were pooled. Leaf samples were freeze-dried, weighed to determine mass per unit LA (M_a ; g m^{-2}) and then milled. The amount of N per unit M (N_m ; %) and the ^{15}N abundance in each milled sample were determined with a Tracer Mat continuous flow mass spectrometer (Finningan MAT, Hemel Hempstead, UK). Total leaf N was expressed per unit area (N_a) as $(N_m \times M)/(\text{LA} \times 100)$. The recovery of ^{15}N in leaves was used to quantify the amount of leaf N derived from remobilization and from direct root uptake as described by Millard and Neilsen (1989).

Statistical analyses

The effects of soil N availability, light regime, and $\text{N} \times \text{light}$ interaction on the amounts of total N derived from root uptake and from remobilization were tested by two-way analysis of variance (ANOVA) (SPSS Version 9.0.1, SPSS, Chicago, IL).

Analysis of foliage N measured for the whole tree and for the lower and upper branches was adapted for the unbalanced data sets. The main effects of N availability and light regime on tree morphological characteristics and on individual leaf characteristics were analyzed by two-way ANOVA. The effects of N availability to roots, light regime experienced by the foliage, leaf rank, and the different corresponding interactions on the fraction of current-year leaf N provided by root uptake and by remobilization were tested by three-way ANOVA.

Results

N availability and light regime effects on the total leaf N

Nitrogen availability and light regime did not significantly influence total leaf N on the whole-tree scale (Table 2). Total leaf N in the upper branch was greater in the HN treatment than in the LN treatment (Figure 2, Table 2). Total leaf N in the lower branch was significantly higher in the HL treatment than in the LL treatment, whereas nutrient availability had no effect (Table 2, Figure 2).

N availability and light regime effects on the leaf N derived from root uptake

Nitrogen availability significantly influenced the amount of leaf N derived from root uptake on the whole-tree scale, whereas light regime had no effect (Table 2, Figure 3). More N was taken up by roots of trees grown with HN than with LN (0.2 and 0.025 g N tree^{-1} , respectively). In the lower branch, leaf N derived from root uptake was significantly higher in the

Table 2. Results (P values) of a 2-way ANOVA showing effects of nitrogen (N) availability, light regime and $\text{N} \times \text{light}$ interaction on total leaf N, leaf N derived from root uptake, from remobilization, and the fraction of total leaf N derived from remobilization as measured on whole-tree scale and branch scales. Values of P less than 0.05 indicate significant effects. Abbreviation: ns = not significant ($P > 0.05$).

	Leaf nitrogen			
	Total	Uptake	Remobilized	Remobilized/ total
<i>Tree scale</i>				
N availability	ns	< 0.0001	ns	< 0.0001
Light regime	ns	ns	ns	ns
$\text{N} \times \text{Light}$	ns	ns	ns	ns
<i>Upper branch</i>				
N availability	0.057	< 0.0001	ns	< 0.0001
Light regime	ns	ns	ns	ns
$\text{N} \times \text{Light}$	ns	ns	ns	ns
<i>Lower branch</i>				
N availability	ns	< 0.0001	ns	< 0.0001
Light regime	0.003	0.041	0.003	ns
$\text{N} \times \text{Light}$	ns	ns	ns	ns

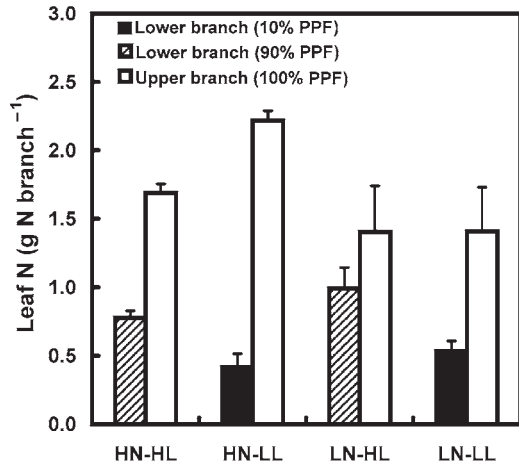


Figure 2. Total leaf nitrogen (N) content of lower and upper branches of walnut trees during the third year of growth. Abbreviations: PPF = photosynthetic photon flux; HN = high N treatment; LN = low N treatment; HL = high light treatment and LL = low light treatment. Bars are SE: $n = 4$ for HN-HL, LN-HL and LN-LL and $n = 3$ for HN-LL.

HN treatments than in the LN treatments. In addition, the overall light regime had a significant effect (Table 2).

N availability and light regime effects on the leaf N derived from remobilization

Nitrogen availability and light regime did not significantly affect the amount of leaf N derived from remobilization on the whole-tree scale (Table 2). The amount of N derived from remobilization ranged from 1.9 to 2.4 g N tree⁻¹. In LL, less N

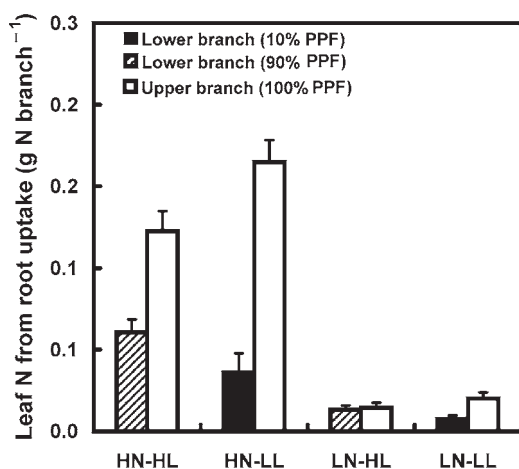


Figure 3. Amount of leaf nitrogen (N) provided by current-year root uptake measured on lower and upper branches of walnut trees during the third year of growth. Abbreviations: PPF = photosynthetic photon flux; HN = high N treatment; LN = low N treatment; HL = high light treatment and LL = low light treatment. Bars are SE: $n = 4$ for HN-HL, LN-HL and LN-LL and $n = 3$ for HN-LL. Note the difference in scale between Figures 3 and 4.

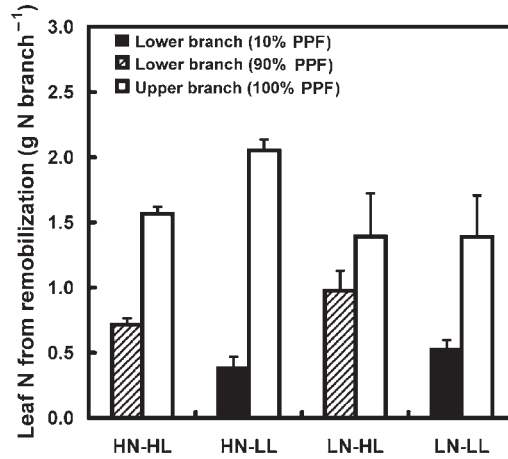


Figure 4. Amount of leaf nitrogen (N) derived from remobilization measured on lower and upper branches of walnut trees during the third year of growth. Abbreviations: PPF = photosynthetic photon flux; HN = high N treatment; LN = low N treatment; HL = high light treatment and LL = low light treatment. Bars are SE: $n = 4$ for HN-HL, LN-HL and LN-LL and $n = 3$ for HN-LL. Note the difference in scale between Figures 3 and 4.

was remobilized for leaf growth on the lower branches than in HL, whereas N supply had no effect (Table 2, Figure 4). The proportion of total leaf N from remobilization was affected by N availability but not by light regime (Table 2), varying from 92 to 98% of total leaf N in the HN and LN treatments, respectively (data not shown).

N availability and light regime effects on leaf number and individual leaf characteristics

On the whole-tree scale, the total number of leaves, individual LA and leaf M were unaffected by N availability or light regime (Table 1). However, in the LL treatments, the upper branch exhibited a significantly greater leaf number, M and M_a , and a lower leaf N_m than in the HL treatments. Light had no effect on the upper branch individual LA or N_a (Table 3). In HL, leaves on the lower branch always had significantly greater M , M_a and N_a than in LL, whereas leaf N_m , individual LA and leaf number were unaffected by local light regime (Table 3). Nitrogen availability had no observable effect on leaf number or on individual leaf characteristics (Table 3).

N availability, light regime and leaf rank effects on the sources of current-year leaf N

Nitrogen availability significantly influenced the fraction of leaf N derived from root uptake ($P < 0.001$), whereas leaf rank and light regime had no detectable effect. For each leaf rank, the fraction of total leaf N derived from root uptake was always greater in HN than in LN (about 8.5 and 1.2% of total leaf N, respectively; Figure 5). The fraction of total N derived from root uptake was similar among leaf ranks along the lower branch and values did not differ between leaves of the upper and lower branches (Figure 5).

Table 3. Effects of nitrogen (N) availability and light regime on leaf number per branch and individual leaf characteristics (mass-based N concentration (N_m), dry mass, area, mass-to-area ratio (M_a), and N on an area basis (N_a)). The main effects were tested by two-way ANOVA. Values of P less than 0.05 indicate significant effects. Abbreviations: HN = high N treatment; LN = low N treatment; HL = high light treatment; LL = low light treatment; and ns = not significant ($P > 0.05$).

	Treatments				Main effects	
	HN-HL	HN-LL	LN-HL	LN-LL	N availability	Light regime
<i>Upper branch</i>						
Leaf number	17.0 ± 0.71	20.0 ± 0.58	17.3 ± 0.63	19.5 ± 1.04	ns	0.007
N_m (%)	2.84 ± 0.09	2.60 ± 0.08	2.89 ± 0.10	2.60 ± 0.09	ns	0.02
Total leaf dry mass (g)	59.4 ± 1.82	85.3 ± 0.67	47.9 ± 10.0	69.8 ± 5.57	ns	0.003
Individual leaf area (cm ²)	425.2 ± 16.2	475.5 ± 17.3	343.0 ± 53.9	405.9 ± 32.6	ns	ns
M_a (g m ⁻²)	82.4 ± 0.70	89.9 ± 1.93	79.2 ± 1.95	88.7 ± 3.68	ns	0.005
N_a (g N m ⁻²)	2.34 ± 0.07	2.34 ± 0.12	2.29 ± 0.10	2.29 ± 0.02	ns	ns
<i>Lower branch</i>						
Leaf number	13.5 ± 0.29	12.3 ± 1.76	15.3 ± 0.95	12.5 ± 0.64	ns	ns
N_m (%)	2.70 ± 0.14	2.52 ± 0.13	2.70 ± 0.11	2.71 ± 0.07	ns	ns
Total leaf dry mass (g)	28.3 ± 1.94	16.5 ± 3.90	35.9 ± 5.5	18.4 ± 2.01	ns	0.002
Individual leaf area (cm ²)	313.1 ± 20.2	286.7 ± 27.9	352.1 ± 34.2	351.9 ± 44.9	ns	ns
M_a (g m ⁻²)	64.5 ± 1.71	44.9 ± 1.39	64.4 ± 1.04	42.7 ± 1.52	ns	< 0.0001
N_a (g N m ⁻²)	1.78 ± 0.11	1.12 ± 0.04	1.77 ± 0.07	1.22 ± 0.07	ns	< 0.0001

Discussion

N availability effect on total leaf N and on leaf N derived from remobilization and root uptake

Nitrogen availability did not influence the total amount of leaf N per individual walnut tree 3 months after bud burst, when the foliage was nearly fully developed. Nitrogen remobilized from storage provided about 95% of total leaf N and mainly supported leaf growth during spring and early summer. A previ-

ous study on 2-year-old walnut trees showed that N remobilization during the third year of growth (derived from N stored during the second year), provided 54% of the total leaf N, 3 months after bud burst (Frak et al. 2002a). This value was determined without accounting for remobilization of N stored during the first year of growth and, as suggested by the authors, presumably underestimated the importance of total remobilization for leaf N. Generally, remobilization to leaf N is expected to be greater in big trees than in small trees, because big trees have a larger pool of stored N (Millard 1996). The importance of remobilization as a source of leaf N, as observed in this study, is consistent with the results reported by Neilsen et al. (1997) for apple spur leaves (87% 2.5 months after bud burst). In contrast, Deng et al. (1989) and Weinbaum and Van Kessel (1998) found smaller percentages in field-grown mature walnut trees (47% of new shoot N 2 months after bud burst and 60% of total tree N demand over the whole year, respectively). The lower remobilization rates reported by other authors may reflect differences in experimental design. In the studies by Deng et al. (1989) and Weinbaum and Van Kessel (1998), labeled fertilizer was applied to soil to label N stored during the previous years, without accounting for the uptake of native soil N during the same period, thereby likely underestimating remobilization (cf. Millard 1996).

It could be argued that restricting the number of buds on the tree before bud break could alter the balance between bud number and N storage pool, leading to an overestimation of the importance of N remobilization for current-year foliage growth. This is the case when N remobilization is source driven rather than sink driven, so removing buds should result in more remobilized N per remaining bud (Millard et al. 2001). However, our hybrid walnut, which has been selected for timber production, normally exhibits strong apical dominance (Fady et al. 2003) and, as a result, only the apical, and possibly

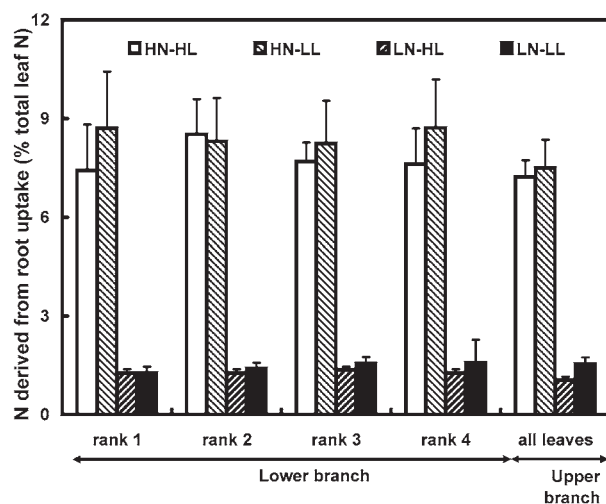


Figure 5. Percentage of total leaf nitrogen (N) derived from root uptake according to leaf rank along the lower branch and for all leaves from the upper branch. Abbreviations: HN = high N treatment; LN = low N treatment; HL = high light treatment and LL = low light treatment. Bars are SE: $n = 4$ for HN-HL, LN-HL and LN-LL and $n = 3$ for HN-LL.

one or two lateral buds, typically grow after bud break. Thus, selecting one apical and one lateral bud and removing all the other buds would not have greatly altered the natural source–sink balance and probably did not greatly alter the overall proportion of leaf N derived from remobilization in our trees.

On the branch scale (for lower or upper branches), N availability significantly enhanced the amount of leaf N derived from root uptake but did not influence the amount of leaf N derived from remobilization. Thus, the N uptake:N remobilization ratio for each branch was higher in HN than in LN. In contrast, no change in the N uptake/N remobilization ratio was observed between branches, regardless of the light regime. This suggests a constant balance between the two leaf N sources in any location within the tree crown. This finding is of key importance for the extension of the recently proposed non-destructive method of quantifying N remobilization by coupling sap flow velocity or whole-tree transpiration and amino acid concentration in large trees in the field (Frak et al. 2002a, Grassi et al. 2002).

Light regime effect on total leaf N and leaf N derived from remobilization and root uptake

Total foliage N measured on the whole-tree scale was unaffected by light availability. Even if the apical bud was removed, the upper branch developing from the highest remaining bud maintained a clear dominance over the lower branch, and always had a greater N content, irrespective of the light regime. Walnut leaves are preformed in the bud and their number per bud decreases from the top to the bottom of the stem (Sabatier and Barthélémy 2001), although a second flush of newly formed leaves can occur on vigorous shoots. This biological trait can explain the higher number of leaves on the upper branches and thus, the greater amount of foliage N measured in upper branches compared with lower branches. As the number of preformed leaves was higher in the upper branches than in the lower branches, the upper branches responded to shading of the lower branches by developing new leaves. This trait explains why different degrees of shading (10 or 90% of PPF) imposed on lower branches did not influence leaf number but changed leaf number of the upper branches. Consequently, differences in the amount of foliage N measured in lower branches in the HL and LL treatments resulted from changes in the amount of N per leaf and not in leaf number. These changes were caused by alterations in individual leaf M_a , because LA and N_m were unaffected by light availability. The observed, light-induced changes in N_a (i.e., higher values in HL than in LL) were consistent with results reported for mature walnut trees (Weinbaum et al. 1994, Le Roux et al. 1999), and with the optimal N allocation theory (Hirose and Werger 1987, Hollinger 1996). The amount of shade (10 or 90% PPF) imposed on individual lower branches also changed the pattern of total N allocation between lower and upper branches. Decreasing the irradiance experienced by the lower branch (LL treatments) always enhanced N allocation to the upper branch, partly because of the increase in leaf number and, to a lesser extent, N_m of the upper branch. Thus, N allocation within the foliage of an individual tree is influenced by the lo-

cal light regime experienced by leaves, and decreasing the light availability for a given tree branch decreases the amount of N allocated to this branch, benefitting the less shaded branch(es). This is consistent with the results of Vos and van der Putten (2001) who showed that shading of the primary axis changed N allocation between axes and increased sink strength for N of non-shaded apical branches in *Solanum tuberosum* L.

In contrast, the local light regime experienced by the lower branches did not affect the fraction of total leaf N derived from remobilization. However, the amount of N allocated to lower branches that was derived from both remobilization and from current root uptake was lower in LL than in HL.

Leaf rank effect on the balance between N provided by root uptake and remobilization for current-year foliage growth

The relative importance of root uptake and remobilization as sources of N for current-year foliage did not depend on leaf rank along the shoot, perhaps because of the short duration of foliage growth in walnut (around 50 days; Frak et al. 2002a). We speculate that, in plant species with a continuous growth pattern or with several flushes of leaf growth each summer, the relative importance of root uptake and remobilization could change with the period of leaf growth. In particular, late-season growth could depend more on N provided by root uptake and retranslocation from other leaves than on N stored in previous years (Millard and Proe 1992, Wendler et al. 1995, Stephens et al. 2001, Grelet et al. 2003). Thus, our results cannot be generalized from walnut, which has a single flush of leaf growth, to species with an indeterminate growth pattern.

In conclusion, we showed that, in young walnut trees over a 3-month period after bud break, leaf growth relies largely on N stored from root uptake in previous years. We also demonstrated that the light regime experienced by shoots influences the amount of N derived from remobilization and, more generally, that it drives the allocation of total N within the foliage by affecting shoot sink strength but has no effect on the balance between N uptake and N remobilization. Because our study was conducted on manipulated, two-branch trees, generalization of our results would require additional studies in more complex canopies (e.g., big tree crowns). However, our results are consistent with the hypothesis of simple plant growth models, where leaf N allocation is driven by sink strength, which is modulated by irradiance (Thornley 1998) or photosynthesis (Dewar et al. 1998).

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