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Nitrogen and Sulfur Interaction Influences Net Photosynthesis and Vegetative Growth of Pecan

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Abstract. **Seedlings of pecan *[Carya illinoensis* (Wangenh.) C. Koch] grown in perlite culture were treated with N and S in a 5 x 5 factorial in a randomized complete block design to determine the effect of N, S, and N x S interaction on vegetative growth and photosynthesis. Nitrogen and S deficiency symptoms occurred when leaf N and S were < 25 and 1.4 mg·g^{-1} dry weight, respectively. Photosynthesis was reduced when combined leaf N and S exceeded 35 and 3.7 mg·g^{-1} dry weight, respectively; growth was reduced when leaf N and S were > 34 and 3.7 mg·g^{-1} dry weight, respectively. Photosynthesis and growth increased with N supply, but depended on leaf N : S ratio. In plants without visible N or S deficiency, a N: S ratio of ≈9 is proposed to be near the optimum for maximum growth. Comparison of leaf N, S, and the N : S ratio with similar analyses in selected orchards suggests that pecan productivity will increase from S application under field conditions. We conclude that the interaction" of N and S imposes stringent controls on leaf N and S, photosynthesis, and growth.**

In general, plant performance can be maximized by N application only if S is adequate and, similarly, maximum response from S application will occur only if N is sufficient. Studies using many herbaceous crops have demonstrated this N × S interaction on yield, nutrient uptake, and crop quality (Aulakh et al., 1980; Bolton et al., 1976; Hocking et al., 1987; Janzen and Bettany, 1984; Randall et al., 1981; Stewart and Porter, 1969). The N × S interaction is probably due to the interdependence of uptake and reduction of N and S (Clarkson et al., 1989; Reuveny et al., 1980) and that plants generally accumulate both N and S in amounts proportional to that incorporated into protein (Friedrich and Schrader, 1978).

Although the close relationship between N and S nutrition has been firmly established in herbaceous plants (Aulakh et al., 1980; Bolton et al., 1976; Clarkson et al, 1989; Hocking et al., 1987; Janzen and Bettany, 1984; Reuveny et al., 1980; Stewart and Porter, 1969), the inter-relationship of N and S in pecan is unknown and information for woody plants in general is rudimentary (Lambert, 1986). In a recent study, growth of pecan seedlings increased with leaf Sup to at least 2.7 mg·g^{-1} dry weight (Hu et al., 1991). Although the study did not examine a N and S interaction, growth was closely related to the leaf N: S ratio, which suggested a close N to S inter-relationship in pecan. Knowledge of the inter-relationship of N and S would allow a more complete interpretation of pecan leaf analysis, an improved N and S fertilizer recommendation to the grower, and, possibly, improved use of N. The objective of this study was to examine the N and S interaction effect on pecan photosynthesis and growth.

Materials and Methods

Stratified seeds (Sparks et al., 1974) of 'Curtis' pecan were planted (six per pot) on 31 Jan. 1990 into n-liter plastic pots filled with perlite and placed in the greenhouse. After germination, the seedlings were thinned to two plants per pot. Hoagland's solution (Hoagland and Arnon, 1950) without N or S was applied weekly from 31 Jan. until 9 Mar. At that time, the seedlings, which were ≈ 12 to 18 cm high, were divided into 10 replications with relatively uniform height within each replication. A treatment was randomly assigned to each pot within a replication. The treatments were factorial combinations of five levels of N (0, 3.5, 7.0, 14, and 28 mM) and five levels of S (0, 0.2, 0.8, 3.2, and 10 mM in a randomized complete block design. There were 20 seedlings per experimental unit or 500 total seedlings in the study. Nitrogen and S were applied weekly from 9 Mar. until 15 June. The basic N source was $Ca(NO_3)_2 \cdot 4H_2O$. In N treatments of 7 mM and higher, additional N was applied as KNO_3 and NH_4NO_3. Except for the 0 mM N, $(NH_4)_2SO_4$. was used to supplement N and S in the highest S treatment (10 mM) and the accompanying N combinations. The basic S source was $MgSO_4 \cdot 7H_2O$, which was supplemented, as necessary, with $CaSO_4$ and K_2SO_4. Additional S in 10 mM S treatment was supplied with Na_2SO_4. The differences in K, Mg, and Ca among different treatments were balanced with KCl, $MgCl_2 \cdot 6H_2O$, and $Ca(CH_3COO)_2 \cdot H_2O$. The highest concentration of Cl used was 285µg·g^{-1}. A separate experiment was conducted to determine if there was a difference between O and 285 µg Cl/g. Plant appearance and total dry weight (46 and 48 g/plant for O and 285 µg Cl/g, respectively) did not differ (P ≤ 0.05), indicating that the Cl level used had no detrimental effect.

On 4 to 13 July, leaf gas exchange measurements were made in the laboratory. Net CO_2 assimilation rate, air temperature, relative humidity, and photosynthetic photon flux (PPF) were measured with an ADC LCA-2 portable infrared gas analyzer, an air supply unit (flow rate = 400 cm^3·min^{-1}), and a Parkison broad-leaf chamber (aperture area = 6.25 cm^2) (Analytical Development Co., Hoddesdon, Herts, England). Outside ambient air from atop a four-story building was humidified before it entered the leaf chamber, so that a humidity of 45% to 50% was maintained in the chamber when no leaf was included. Metal halide electric discharge lamps (400 W) were used as the light source. The light passed through 1.5 cm of rapidly circulating water. All gas exchange measurements were made at 800 to 1000 µmol·m^{-2}·s^{-1} PPF.

An acclimation period was provided by transporting the plants from the greenhouse to the laboratory the night before the measurements were made. For each plant, gas exchange measurements were made on leaf 7 from the base of the trunk. However, plants in the 0-mM N and some plants in the 0-mM S treatment

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had fewer than seven leaves. In these plants, the most apical leaf with an area of more than 6.25 cm^2 was used. In all cases, leaf expansion was completed. The leaf was allowed to acclimate under the light for ≈ 1 h before measurement. The selected leaf on each plant was measured five times and the data averaged. Copper-constantan thermocouples were placed against the abaxial leaf surface to take leaf temperatures after photosynthetic measurements. Net photosynthesis was calculated according to Long and Hallgren (1985).

After photosynthesis determinations, each leaf measured on each plant. was washed with deionized water and dried for 72 h at 70C. Each leaf was ground, redried, and analyzed for N and S. Just before harvesting the plants, leaves per seedling, seedling height, and notations of visible N and S deficiency were recorded. Nitrogen and S deficiency symptoms were as previously described (Hu et al., 1991; Sparks, 1976). The plants were harvested, washed, dried for 72 h at 70C, and weighed.

Micro-Kjeldahl-N was analyzed according to McKenzie and Wallace (1954), except bromo-cresol green and methyl red were used as the mixed indicator. An analytically pure $(NH_4)_2SO_4$ solution and a pecan leaf standard were run simultaneously with the leaf samples to monitor precision of the analysis. Sulfur was analyzed (Jones and Isaac, 1972) with a Leco S analyzer (Leco Corp., St. Joseph, Mich.). Because methionine and cysteine comprise up to 90% of the total S on most plants (Giovanelli, 1987) and methionine is the major S amino acid in pecan leaves (Hu et al., 1991), purified commerical methionine was used as the standard for S analysis instead of oil (Jones and Isaac, 1972). Data were subjected to analysis of variance and regression (SAS Institute, 1987).

Leaf N, S, and the N : S ratio in the leaves from the greenhouse study were compared with those from 13 selected pecan orchards. Leaflet samples from orchards were collected according to standard procedures (Sparks, 1977) for sampling time (56 to 84 days after catkin fall) and for leaflet sampling (middle pair of leaflets from the leaf on the midportion of the shoot). Eleven orchards were located in Georgia, one in Texas, and one in New Mexico. The orchards were situated on a wide variety of soil types (sandy loam to clay) and varied in size from ≈24 to 243 ha.

Results and Discussion

Effect of N and S supply on leaf composition and plant appearance. When applied S was low (0 mM S), leaf N was substantially higher than when S was applied (Fig. 1). The effect became more pronounced with increasing N supply. This interaction of N and S on leaf N has been reported for other plant species (Aulakh et al., 1980; Hocking et al., 1987; Janzen and Bettany, 1984). The high leaf N associated with low S supply is characteristic of pecan and the elevated N is due to the accumulation of free amino acids, primarily arginine (Hu et al., 1991).

Leaf S increased with S supply, but the effect was modified by N supply (Fig. 2). When S was low (0.0 and 0.2 mM S) and the seedlings were visibly S-deficient (Table 1), N did not affect leaf S (Fig. 2). At intermediate levels of S (0.8 and 3.2 mM S), N application increased leaf S with a positive response to increasing N supply, but when S supply was high (10.0 mM S), addition of N initially increased leaf S, followed by a substantial decrease at the highest N supply. The interaction effect of N and S supply on leaf S has been reported for herbaceous plant species (Aulakh et al., 1980; Randall et al., 1981).

The N : S ratio in the leaf decreased with increased S supply

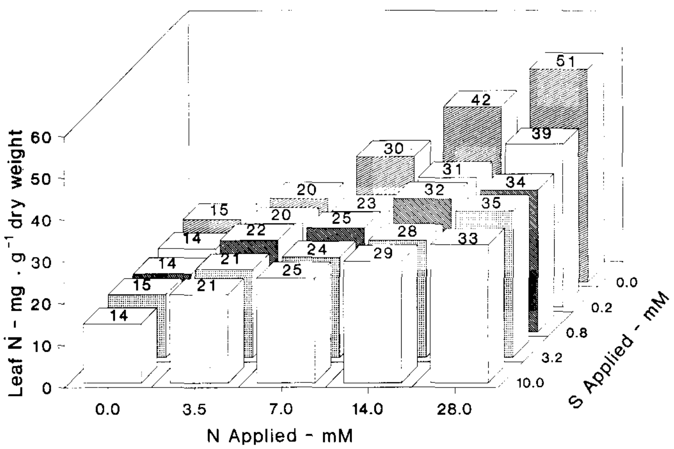

Fig. 1. Effect of N and S supply on leaf N of pecan seedlings. Nitrogen x S interactions, both linear and quadratic, are statistically significant ($P \leq 0.05$).

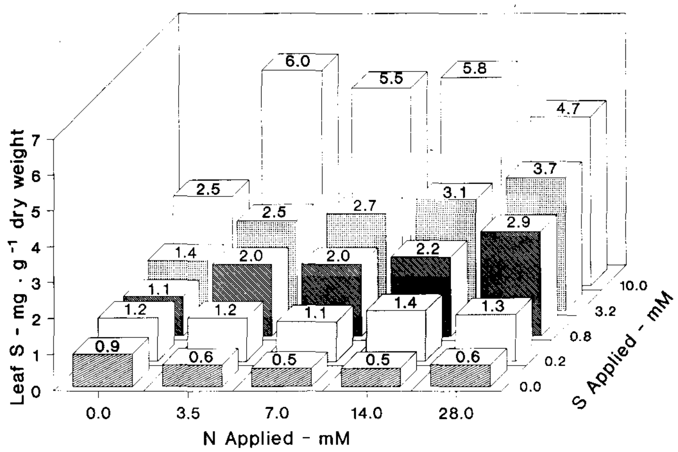

Fig. 2. Effect of N and S supply on leaf S of pecan seedlings. Nitrogen x S interactions, both linear and quadratic, are statistically significant ($P \leq 0.05$).

(Fig. 3). The ratio was affected by N supply only when the plants were showing S deficiency symptoms (0.0 and 0.2 mM S). Under S deficiency conditions, N application increased the N : S ratio, especially in the 0.0-mM S treatment. The ratio increased because, under S deficiency, N accumulates in the leaf (Hu et al., 1991).

Nitrogen deficiency symptoms occurred when leaf N was ≤25 $mg \cdot g^{-1}$ (Table 1, Fig. 1). This value is close to the critical deficiency value of 23 $mg \cdot g^{-1}$ previously reported for pecan (Alben, 1946; Sparks and Baker, 1975). Sulfur deficiency symptoms occurred when leaf S was ≤ 1.4 $mg \cdot g^{-1}$ (Table 1, Fig. 2). This value agrees closely with the 1.5 $mg \cdot g^{-1}$ found in another study of S nutrition of pecan (Hu et al., 1991). Visible S deficiency symptoms did not occur in plants treated with 0.0 mM N (Table 1). Similarly, Janzen and Bettany (1984) observed no S deficiency symptoms in rape *(Brassica napus* L.) when both N and S were low.

Severe S deficiency (0 mM S) was more detrimental to plant growth than severe N deficiency (0 mM N). Almost all the growing points died on plants treated with high N and no S. In contrast, shoots did not die in plants receiving no N, regardless of the amount of S applied. This difference was probably due to NH_4^+ toxicity when no S was applied, as NO_3^- reduction was not severely inhibited under S deficiency (Hu et al., 1991).

Table 1. Effect of applied N and S on deficiency symptoms in mature pecan leaves.

N applied (mM)	S applied (mM) 0.0	0.2	0.8	3.2	10.0
	N deficiency[z]				
0.0	Severe	Severe	Severe	Severe	Severe
3.5	Mild	Moderate	Moderate	Moderate	Moderate
7.0	None	Mild	Mild	Mild	Mild
14.0	None	None	None	None	None
28.0	None	None	None	None	None
	S deficiency[y]				
0.0	None	None	None	None	None
3.5	Severe	Mild	None	None	None
7.0	Severe	Moderate	None	None	None
14.0	Severe	Moderate	None	None	None
28.0	Very severe	Moderate	None	None	None

[z]Severe = uniform yellowing, apical leaves often with a reddish tinge; mild = pale yellow; moderate = light green.
[y]Very severe = golden yellow with apical leaves necrotic; severe = golden yellow with apical leaves cupped; mild = pale yellow, moderate = light green.

Effect of N and S supply on photosynthesis and growth. The effect of S on net photosynthesis was strongly dependent on N supply (Fig. 4). In the absence of applied N, application of 0.2 mM S increased photosynthesis slightly, followed by a small decrease with 10.0 mM S. When S was not applied, N application decreased photosynthesis slightly, but when S was applied, photosynthesis was greatly increased by N supply. Within a S treatment, the N effect was most pronounced when N was increased from 0.0 to 3.5 mM Above 3.5 mM N, photosynthesis was increased to a lesser degree, but linearly, with N supply. The effect of S on photosynthesis was maximized when S was 0.8 and 3.2 mM and decreased substantially with 10.0 mM S. Photosynthesis was reduced when leaf N and S in combination exceeded 35 and 3.7 mg·g[-1], respectively (Figs. 1, 2, and 4). Decreased photosynthesis under S stress has been reported before (Bouma et al., 1972; Dietz, 1989; Terry, 1976), as has the N effect (Boote et al., 1978; Evans, 1989; Field et al., 1983; Lugg and Sinclair, 1981), but we believe this to be the first report on the interactive effect of N and S.

Seedling growth was significantly affected by N and S (Fig. 5). Sulfur had no effect on plant dry weight when N was not supplied (Fig. 5), but when S was omitted, N increased dry weight slightly. The slight differential response to N and S application suggests that N in the medium and/or seed was more limiting than S. That is, there was enough residual and/or atmospheric S to use a portion of the applied N, but not enough

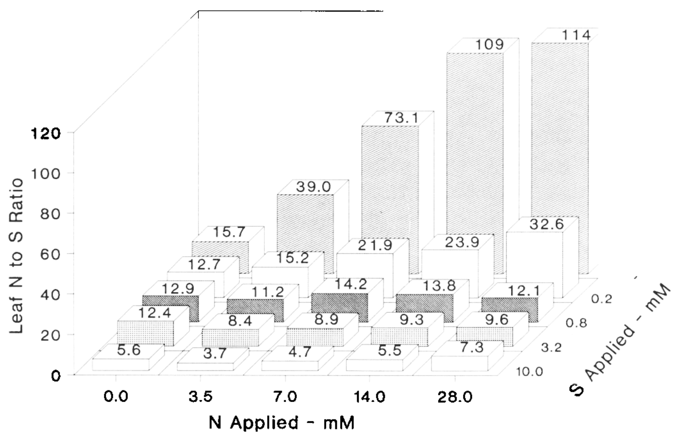

Fig. 3. Effect of applied N and S on the N : S ratio in leaves of pecan seedlings. Nitrogen x S interactions are statistically significant ($P \leq 0.05$).

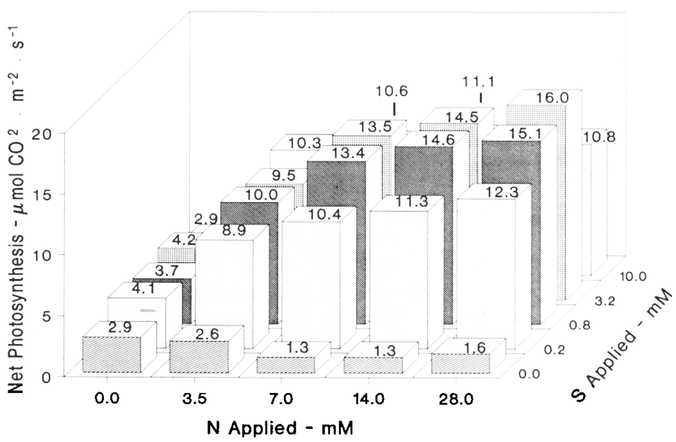

Fig. 4. Effect of N and S supply on net photosynthesis of seedling pecan leaves. Nitrogen x S interactions, both linear and quadratic, are statistically significant ($P \leq 0.05$).

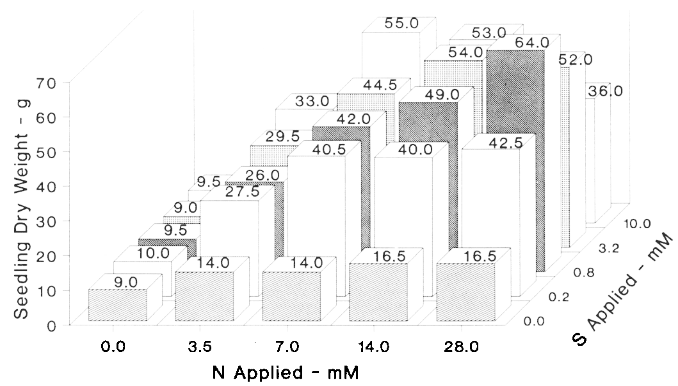

Fig. 5. Dry weight of pecan seedlings in response to N and S supply. Nitrogen × S interactions, both linear and quadratic, are statistically significant ($P \leq 0.05$).

residual N to result in a response to S application. With addition of S, growth increased with N supply, but the response was greatly dependent on S supply. At 0.2, 0.8, 3.2, and 10.0 mM S, maximum growth occurred when N was 28, 28, 14, and 7 mM, respectively. When N in the 10.0-mM S treatment exceeded 7.0 mM, growth was suppressed. The interactive effect of N and S on seedling height and leaves per plant was very similar to dry weight, except the number of leaves was more sensitive to higher levels of N and S (data not presented). Except with 0.0 mM S, leaf count was near maximum at 7.0 mM N, regardless of S supply. Dry weight was suppressed when combined leaf N and S exceeded 34 and 3.7 $mg \cdot g^{-1}$, respectively. (Figs. 1 and 2 vs. 5). The interaction of N and S on pecan growth is in agreement with results for herbaceous plant species (Bolton et al., 1976; Randall et al., 1981; Stewart and Porter, 1969).

When S supply was between 0.2 to 3.2 mM, growth (Fig. 5) and net photosynthesis (Fig. 4) were highly correlated (r^2 = 0.937). However, in the extreme treatments, 0.0 and 10.0 mM S, growth and photosynthesis were not similarly correlated. With 0.0 mM S, growth and photosynthesis were inversely related, and with 10.0 mM, photosynthesis was suppressed at a lower level of N than was dry weight. The lack of consistency was probably due to a growth response that occurred before the onset of severe S deficiency and toxicity in the 0.0 and 10.0-mM S treatments, respectively.

Relationship of photosynthesis and growth to leaf N and S. Photosynthesis (Fig. 4) and growth (Fig. 5) increased with N supply, but within a N supply, response depended on S supply. The interactive response suggests that pecan performance at a given N supply depends on the N : S ratio in the leaf. This contention is supported by data in Figs. 6 and 7 showing that photosynthesis (Fig. 6) and dry weight (Fig. 7) increased with N supply, but within a N level, response depended on the N :

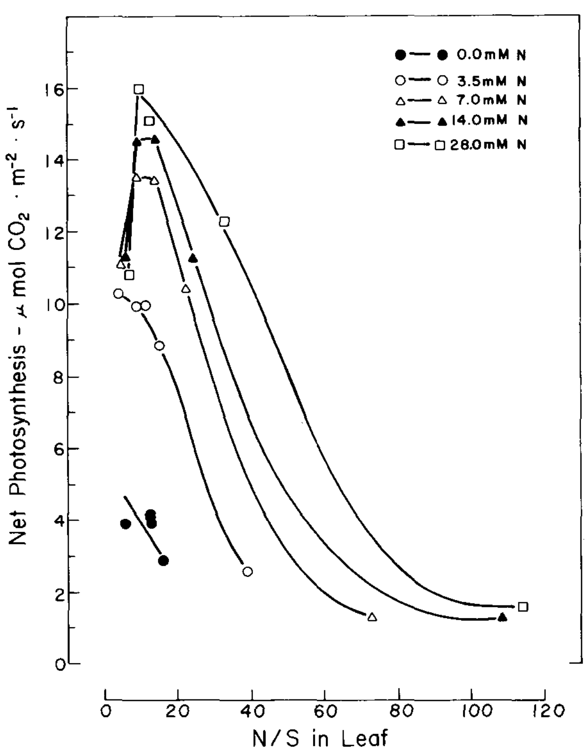

Fig. 6. Net photosynthesis of seedling pecan leaves as a function of N supply and the N : S ratio in the leaf.

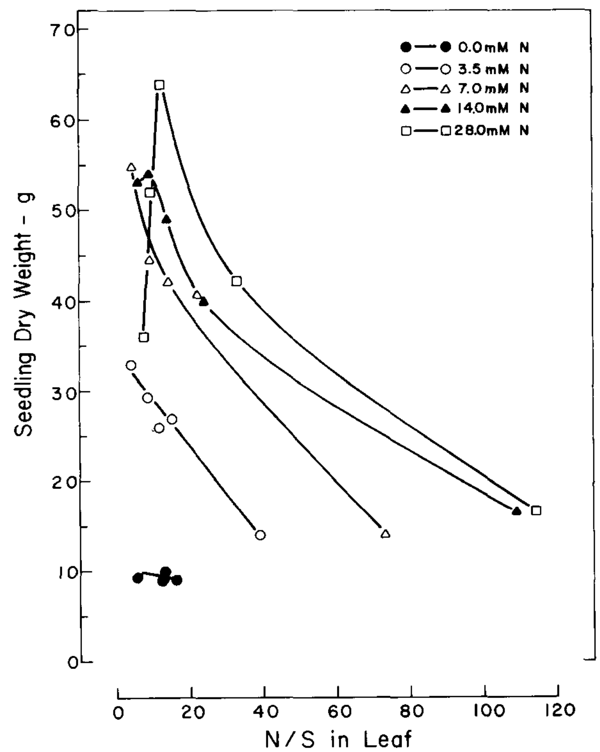

Fig. 7. Seedling dry weight vs. N supply and the N : S ratio in the leaf.

S ratio in the leaf. However, the N : S ratio likely is not the only ratio influencing N efficiency; the N : K ratio apparently is also a dominant factor (Sparks, 1985).

Net photosynthesis was at a maximum with 7, 14, and 28 mM N when the N : S ratio in the leaf was ≈ 9 (Fig. 6). In these treatments, net photosynthesis decreased at ratios less than ≈ 9. In contrast, with 3.5 mM N, photosynthesis continued to increase at ratios less than ≈ 9 and maximum photosynthesis occurred when the N : S ratio was at a minimum of ≈ 4. The decrease in net photosynthesis was associated with high N and S leaf concentrations and was not due to a low ratio.

Dry weight did not reach a definitive peak when the seedlings were visibly N-deficient (0.0, 3.5, and 7.0 mM N, Table 1 vs. Fig. 7). With 3.5 and 7.0 mM N, growth continued as the N : S ratio decreased to ≈ 4 and 5, respectively. In seedlings without N deficiency symptoms, growth was at a maximum when the N : S ratio was ≈ 9 (14 mM N) and 12 (28 mM N). The decrease in growth in these two treatments was associated with high N and S concentrations in the leaf and, as in the case of photosynthesis, the decrease was not due to a low ratio. The N values (33 to 35 $mg \cdot g^{-1}$) associated with 28 mM N are much higher than those that normally occur under field conditions (C.O. Plank, personal communications, 1990). Nitrogen contents associated with 14.0 mM N are most representative of nutrition in the field. Based on this reasoning, a N : S ratio of ≈ 9 is proposed to be near the optimum for maximum growth. This ratio is close to 10, which was associated with near maximum growth in another study with pecan (Hu et al., 1991). In that study, the N supply was 15 mM The leaf N level proposed for maximum growth of pecan is 27 to 29 $mg \cdot g^{-1}$ dry weight (Sparks and Baker, 1975). Based on a leaf N: S ratio of 9, the corresponding leaf S should be 3.0 to 3.2 $mg \cdot g^{-1}$ dry weight.

These results indicate that, at a given N supply, photosynthesis (Fig. 6) and plant growth (Fig. 7) can be expected to be at a maximum in normal plants when the leaf N: S ratio is ≈9. However, growth at a given ratio will vary depending on the N supply available to the plant (Fig. 8). In Fig. 8, the leaf N : S ratio of 12 was chosen because it is the minimum ratio not associated with suppressed growth that is common to all N treatments in Fig. 7.

Nitrogen and S status under orchard conditions. In all orchards, except No. 1, 8, and 13 (Table 2), N was within or above the range (2.7 to 2.9 mg·g^{-1} dry weight) required for optimum growth (Sparks and Baker, 1975). The N : S ratio higher than 9 indicates that all orchards, including the Texas and New Mexico orchards on calcareous soils, would be expetted to respond positively to S application. Field studies are needed for confirmation.

In summary, efficiency of N usage in pecan depends on the concentration of N to S in the leaf. Limited analyses from orchards indicate that pecans might respond favorably to S application because the N : S ratio was above the optimum range found in 'Curtis' seedlings in the present study.

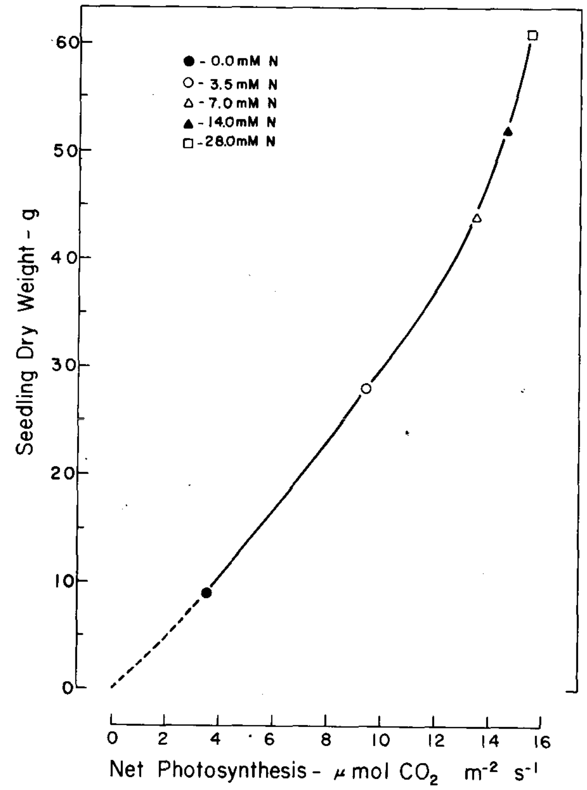

Fig. 8. Pecan seedling growth as a function of photosynthesis and N supply. Data were from Figs. 6 and 7 and at the point where the N : S ratio in the leaf was 12. Broken line is drawn to indicate intercept is near zero.

Table 2. Leaf N, S, and *N : S* ratio in selected pecan orchards.

Orchard location (county)[z]	Orchard no.	N (mg·g^{-1} dry wt)	S (mg·g^{-1} dry wt)	N : S
Zavala	1	26	2.2	11.9
Donaana	2	27	1.8	15.0
Dougherty	3	29	2.0	14.5
	4	33	1.9	17.4
	5	29	2.3	12.6
	6	28	2.2	12.7
Mitchell	7	29	2.1	13.8
Calhoun	8	26	2.3	11.3
	9	28	1.9	14.7
	10	31	2.3	13.5
	11	28	1.8	15.5
Houston	12	31	2.3	13.4
Morgan	13	26	1.9	13.7

[z]All counties are in Georgia, except Zavala and Donaana, which are in Texas and New Mexico, respectively.

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