

Legume Growth and Nitrogen Fixation as Affected by Plant Competition for Light and for Soil Nitrogen¹

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ABSTRACT

Since the legume responses to environmental factors may be different in grass mixtures than in pure stands, a pot experiment was conducted to evaluate the effects of plant top and root competition on the growth and N fixation of *Desmodium intortum*, cv. 'Greenleaf' grown in association with *Setaria anceps*, cv. 'Nandi'. The plants were grown in deep, narrow pots which provided for \pm top competition (set close together or far apart) and \pm root competition (roots in same or different half sections of the pot). All treatments were grown with and without an initial application of 60 kg N/ha.

Greenleaf was a better competitor for light than Nandi in spite of the taller height of Nandi. However in contrast with Nandi, Greenleaf yields and leaf areas were reduced by root competition, especially in the minus-N treatments. There were no significant differences in acetylene reduction activity due to either N levels or competition treatment. Nodule numbers were depressed by both top and root competition at both N levels, but the plants were able to compensate to various degrees by increases in nodule size and to a greater extent by increases in acetylene reduction activity per unit of nodule weight.

Additional index words. *Setaria anceps*, *Desmodium intortum*, Leaf area, Plant height, Nodulation.

THE effects of environmental factors such as light intensity, temperature, soil water, and soil N on legume growth and symbiotic N₂-fixation have been studied extensively for legumes grown alone (Bethlenfalvay and Phillips, 1977; Waughman, 1977; Sprent, 1972; Kitamura and Nishimura, 1977; Lie, 1974). However, such results may not apply to legumes grown in mixtures with grasses because the competing grass plants moderate the effects of environmental factors such as light (Stern and Donald, 1962), water, and soil nutrients (Blaser and Brady, 1950).

An experiment was therefore conducted in Hawaii to evaluate the interactions between environmental factors and grass competition on legume growth and symbiotic N₂-fixation.

MATERIALS AND METHODS

A pot experiment was conducted in the greenhouse of the NifTAL Project, University of Hawaii, commencing on 2 Feb. 1977, using *Desmodium intortum*, cv. 'Greenleaf' and *Setaria anceps*, cv. 'Nandi', hereafter termed Greenleaf and Nandi, respectively. Average day temperature during the experimental period was 25 to 30 C which is near the optimum temperature

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for this legume. Maximum radiation levels in the greenhouse were approximately 55% of outside levels or approximately 200 cal cm⁻² day⁻¹. Greenleaf was inoculated with *Rhizobium* TAL 282, a NifTAL Project selection.

Polyvinyl pipes of 10 cm diameter were cut into 30 cm lengths and used as pots. Each pot was divided into two sections using a vertical glass partition which provided equal surface area and volume in each section.

This grass-legume combination was grown with or without N application (+N or -N), with or without plant top competition, and with or without plant root competition in all factorial combinations for a total of eight treatments. Treatments were replicated five times.

Each half-section of pot was sown with Greenleaf and/or Nandi so as to provide four plants in each half-section. Greenleaf and Nandi were then grown in the same half-section (to give root competition) or in opposite half-sections (no root competition) as per Snaydon (1971). Competition for light by the plant tops was created by setting the pots contiguous to each other or eliminated by setting the pots far apart (50 cm between pots). Pots set far apart were insulated with styrofoam to avoid higher soil temperatures. Contiguous pots were surrounded by border pots on all sides.

A well aggregated soil (Humoxic Tropohumult) was passed through a 5-mm sieve, and the pH was adjusted to 6.0 with CaCO₃. The pots were filled with soil; and triple superphosphate and muriate of potash were applied at rates of 200 kg P and 150 kg K/ha, respectively. Urea was applied at the rate of 60 kg N/ha in the +N pots. Other essential nutrients were provided as a single application of 50 ml of 50X strength minus N Hoagland solution/pot.

Plants were harvested 45 days after seeding, and separated into leaf, stem, and root. Leaf area was measured by photocopying the leaf surface, cutting out the leaf images, weighing the paper, and converting the weight into surface area. Stem numbers (total tillers/pot) were counted at harvest time for Nandi. Roots were separated from the upper one-third of soil volume in each vertical half-section, and incubated in a polyethylene container for acetylene reduction assay, using a modification of the method of Hardy et al. (1968). Roots were washed with tap water, and separated into Greenleaf and Nandi fractions. The root nodules of Greenleaf were then separated from the roots. The lower two-thirds of the soil volume contained no nodules and only total dry weights of the grass, legume, or combined roots were determined. All tissue samples were dried at 60 C to constant weight. Treatment means were compared using the Bayes L.S.D. test (Duncan, 1965).

RESULTS AND DISCUSSION

Dry Matter Yields

Total dry matter yields of Greenleaf plus Nandi tops were greater when urea was applied and there was no significant interaction between N application and root or top competition (Fig. 1A). Compared with no competition total dry matter yields of the plant tops (grass plus legume) tended to increase with competition, but the effect was significant only with combined top and root competition. Total root weights were greatest with root competition and least under top competition.

The effects of competition on the top and root weights of the individual species are shown in Fig. 1C and 1D. Nandi was the dominant component of the mixture in all cases.

There was a tendency for suppression of Nandi top and root growth in the top-only competition treatment. Although the effect was not significant, this observation is reinforced by the significant depression in leaf area (Fig. 1E) in the minus-N series. In contrast to Nandi, however, Greenleaf top growth was significantly increased by top competition, indicating that Greenleaf was a better competitor for light than Nandi. Greenleaf root growth was reduced under top competition, probably because top growth required most of the available assimilates under conditions of competition for light.

Under conditions of root-only competition, the Nandi roots were able to exploit the entire pot volume (i.e. both half-volumes). Nandi roots were thus able to obtain sufficient N and other nutrients to develop a large leaf area (Fig. 1E). Since this large leaf area had an abundance of sunlight (no border pots), the roots received sufficient assimilates to support maximum growth. Greenleaf responded very differently to root competition; top growth was severely depressed

under root competition even though root growth was similar to the control. We therefore conclude that Greenleaf roots were not able to compete effectively for nutrients when Nandi roots were growing in the same volume of soil.

When both top and root competition were applied (the normal situation in pasture), Nandi top growth was further stimulated, although the plants were somewhat etiolated (Table 1). Root growth, however, was restricted due to the shading effect of border pots and the increased demands of stems and leaves for available assimilates.

Yields of Greenleaf tops and roots were both severely depressed under conditions of top-plus-root competition. Since the effect on Greenleaf top growth was similar to root competition alone, we conclude that competition for nutrients was the main factor limiting Greenleaf yields. Additionally, the depression in Greenleaf root growth was similar to the top-only competition, indicating that reductions in leaf irradiance also caused availability of assimilates for root growth.

Leaf Area, Plant Height, and Stem Number

Leaf areas were generally correlated with dry weights with several notable exceptions. Nandi leaf area was depressed by top competition in the minus-N series only and increased by root competition (including top plus root competition) in the plus-N series only (Fig. 1E). This interaction with N level ($P < 0.01$) suggests that N application greatly enhances the capacity of Nandi to compensate for the competition or to exploit the benefits of a greater rooting volume. Another exception occurred in the Greenleaf plus-N series; whereas DM yields were depressed by both root and top plus root competition, leaf area was depressed only by root competition. This suggests that N-fertilized Greenleaf subjected to root competition produces more leaf area per unit of DM when grown in the partial share of Nandi.

Average leaf areas per unit of top dry weight (leaf plus stem) were 40% higher for Greenleaf ($= 240 \text{ cm}^2 \text{ g}^{-1}$) than for Nandi ($= 170 \text{ cm}^2 \text{ g}^{-1}$). Conversely, specific leaf weights (SLW) were somewhat higher for Nandi. SLW values were generally increased by N application in both species, but there was no consistent pattern of SLW response to competition treatments (data not presented).

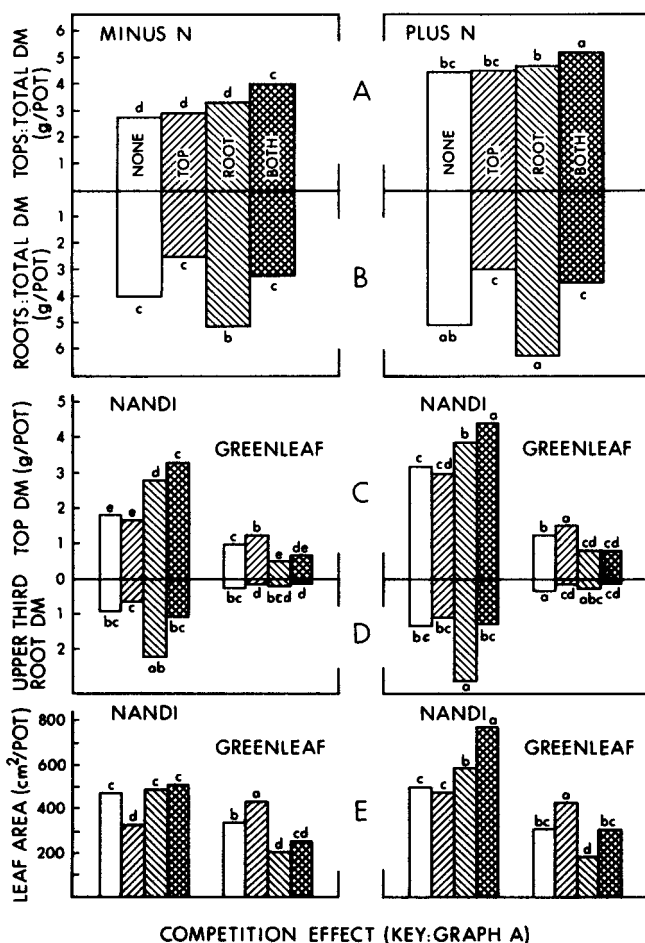


Fig. 1. Influence of top and/or root competition and starter N fertilization on dry matter yields of tops and roots and on leaf areas of Greenleaf and Nandi mixtures. Bars in graphs A and B not followed by the same letters are different at approximately the 5% level of significance (Bayes' L.S.D.). Significant differences in graphs C, D, and E are shown similarly except that letters apply to only one species at both levels of N.

Table 1. Competition and N effects on some plant characters of Nandi and Greenleaf.*

Treatment effects	Height		Stem no.	Nodule no.
	Nandi	Greenleaf	Nandi	Greenleaf
N-fertilizer effects				
-N	65.0	17.5	6.8	105 n.s.
+N	78.4***	21.3***	8.0 n.s.	95
Competition effects				
None	58.7 c	7.6 c	7.8 a	155 a
Top	76.9 b	35.7 a	5.5 b	95 b
Root	60.0 c	6.2 c	9.5 a	97 b
Both	91.1 a	28.2 b	6.6 b	52 c

* All competition effects significant at $P < 0.001$ except Nandi stem number ($P < 0.01$). Interaction term significant only for height of Greenleaf. All means within columns not followed by the same letters are significantly different at approximately the 5% level (Bayes L.S.D.).

Nitrogen application significantly ($P < 0.001$) increased the height of both Nandi and Greenleaf (Table 1). In contrast to dry matter yields, plant heights were increased primarily by top competition and were unaffected or decreased by root competition. However, Nandi and Greenleaf reacted differently to top plus root competition; the vigorous growth of Nandi (compared to top competition alone) resulted in increased plant height, whereas the opposite occurred in the case of Greenleaf where both top growth and plant height were less than in the top competition alone treatment.

Stem numbers per pot of Nandi (Table 1) were reduced under top competition compared with no competition or root competition at both N levels. There was no effect of N application on stem numbers. Apparently Nandi stem numbers were reduced by top competition (border pots) just as root growth was reduced in these treatments. There were no effects of N or competition treatments on Greenleaf stem numbers.

At both N levels, the top weights and leaf areas of Greenleaf increased with top competition, whereas with Nandi these characters remained the same or decreased with top competition. Both species responded to top competition by increased plant height, but Greenleaf heights increased four to six times whereas Nandi height only increased 1.3 to 1.6 times. These results are consistent with the explanations advanced by other workers that plants which possess long petioles and broad horizontal leaves are more competitive for light (Black, 1960), and that legumes can maintain relatively higher dry matter productivity than grasses under lower light intensity (Blackman and Templeman, 1938).

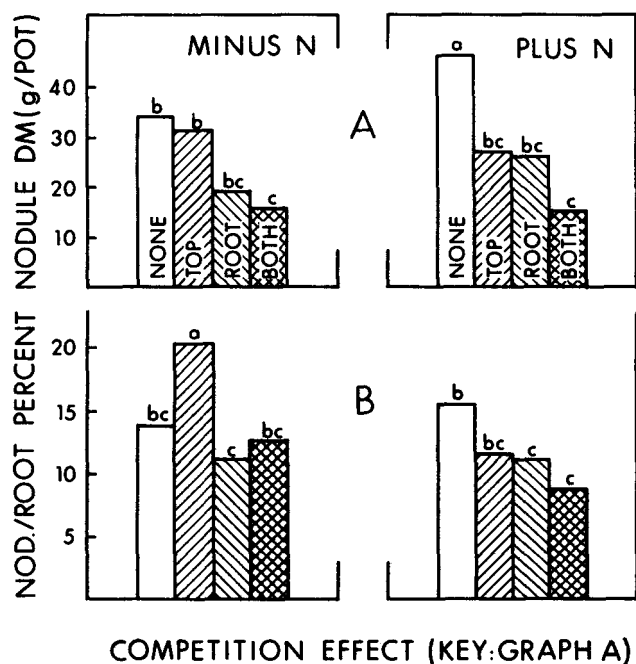


Fig. 2. Influence of top and/or root competition and starter N fertilization on nodule weights and proportions of nodules as a percentage of root weight. Bars within each graph not followed by the same letter are different at approximately the 5% level of significance (Bayes' L.S.D.).

The effect of the root competition treatment was also different for the two species: beneficial for Nandi but detrimental for Greenleaf. This was probably due to more rapid root development by Nandi which would allow it to extract nutrients from a greater soil volume than Greenleaf (Stevenson, 1967) and to deplete the soil nutrients to levels insufficient for optimum growth of Greenleaf (Blaser and Brady, 1950). We thus conclude that Nandi is more competitive for soil nutrients than Greenleaf.

Nodule Formation and Nitrogen Fixation

Nitrogen fixation activity as estimated by acetylene reduction activity was not significantly affected at harvest time by either N level or competition effects. However, there was a suggestion of depressed nodule activity due to root competition (including root plus top competition) in the minus-N series, which may be related to the reduced leaf areas in these treatments. It must, however, be inferred that total nodule activity during the course of the experiment must have been higher in the control and top-competition treatments, since top yields were approximately double those where root competition occurred, and percentage of N in the tissues would not vary greatly between treatments (Eriksen, 1978).

Total nodule numbers (Table 1) and nodule weights (Fig. 2) were reduced by both top and root competition at both N levels, with the exception that nodule weights were not significantly reduced by top competition in the minus-N series. The reductions in nodule number were compensated to some extent by increases in weight per nodule (Fig. 3). At both N levels the plants also compensated for reduced nodule weight by achieving greater acetylene reduction per unit of nodule weight (Fig. 4). Thus the plants were able to compensate for fewer nodules by two methods: larger nodules and increased specific activity, both resulting in greater activity per nodule.

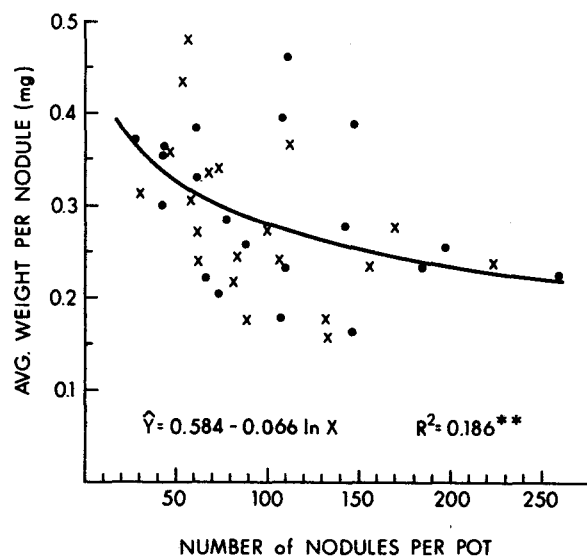


Fig. 3. Number of nodules per pot versus average weight per nodule of Greenleaf (x = minus-N treatments; • = plus-N treatments).

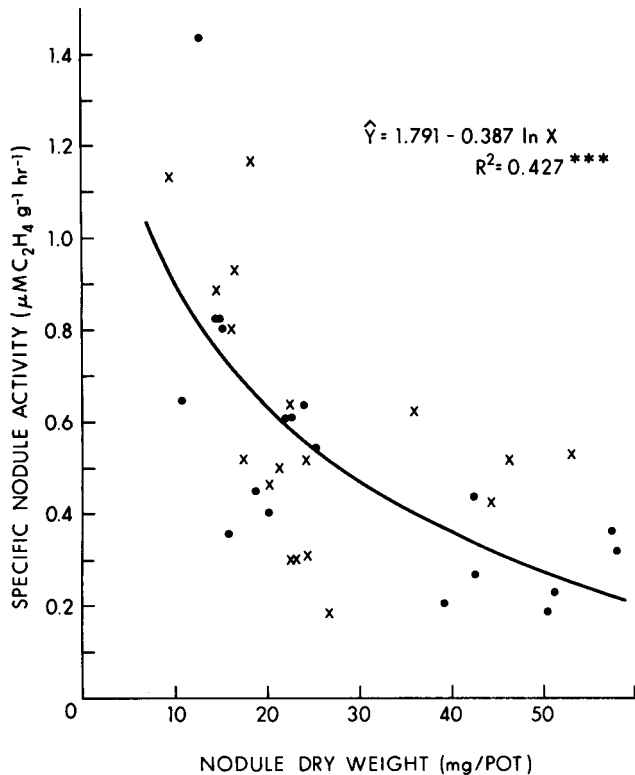


Fig. 4. Nodule weight per pot versus specific nodule activity of Greenleaf grown under different competition treatments (x = minus-N treatments; ● = plus-N treatments).

Nodule numbers were probably set some time prior to sampling, and the plants subsequently were able to compensate for top and root competition when the sink strength of the nodules for available assimilates became fully expressed.

CONCLUSIONS

By subjecting Greenleaf and Nandi to top and root competition (individually and in combination) it was possible to draw conclusions regarding their relative ability to compete for available light and to obtain nutrients from the same rooting volume. The results indicate that Greenleaf is a better competitor for light, probably due to its thin horizontal leaves which probably have lower light compensation levels than Nandi. However, Greenleaf yields were reduced and Nandi yields were increased when the two species shared a common rooting volume, indicating that Greenleaf was a poor competitor for nutrients. Nodulation of Greenleaf was reduced by both top and root competition, but the plants were apparently able to compen

sate for reduced nodule numbers by increased weight per nodule and increased specific activity once nodule sink strength was fully developed.

Root development was restricted by top competition, more so in Greenleaf than Nandi. This suggests that although Greenleaf is a better competitor for light than Nandi in terms of top growth, Greenleaf would probably require at least moderate radiation levels and a lenient management regime to avoid depletion of root reserves and subsequent further reduction in its ability to compete with an associated grass.

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