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Plant Growth Analysis of Field-grown Cowpeas

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Abstract. **Plant growth aspects of field-grown cowpea [*Vigna unguiculata* (L.) Walp.] were investigated under four N regimes: No N, rhizobial inoculation (cowpea "EL" inoculum), 100 kg fertilizer N/ha (NO_3-N) at planting, and inoculation + 50 kg fertilizer N/ha at flowering. Five indeterminate cultivars, Brown Crowder, California Blackeye No. 5, Mississippi Silver, Tennessee White Crowder, and Lady, and one determinate cultivar, Bush Purple Hull, were compared. Plant growth variables were measured biweekly starting at the 4th week. Dry matter and leaf area per plant reached maximum at 56 days after planting in all five indeterminate cultivars, and 1 week later in the determinate cultivar. Large-seeded cultivars, California Blackeye No. 5, Mississippi Silver, Brown Crowder, and Tennessee White Crowder, generally produced larger leaves throughout the season than did 'Bush Purple Hull' and 'Lady'. The relative growth rate (RGR) declined linearly with harvest time, irrespective of N treatment. The RGR of 'Bush Purple Hull' was lower than that of the indeterminate cultivars throughout the growth period. The net assimilation rate (NAR) of the indeterminate cultivars declined slowly from maximum values at 4 weeks and became negative during pod development. However, 'Bush Purple Hull' NAR increased during pod development, but declined very rapidly during late pod development. The leaf area ratio (LAR) declined curvilinearly with time in all N treatments and cultivars. The LAR values were lowest for the determinate cultivar, and the differences among indeterminate cultivars were not significant. Total dry matter, leaf area per plant, and average leaf size of inoculated and N-fertilized plants were greater than the uninoculated and unfertilized control. Nitrogen treatments did not affect physiological components RGR, NAR, and LAR.**

Seed yield of cowpea depends not only on adequate production of photosynthetic assimilates but also on adequate storage capacity of photosynthates, and is influenced by a combination of genetic and environmental factors. Cowpeas usually are grown in low-fertility soils, and N deficiency during different growth stages limits the expression of genetic yield potential (4). Rhizobial inoculation can increase seed yield to a level equivalent to N fertilized (100 kg·ha^{-1}) plants (3). A thorough knowledge of the physiological basis for this yield increase can assist in selection for high seed yield.

Techniques used in plant growth analysis have been reviewed in detail (8) and used to study the physiological basis for variation in crop yield (9), but few attempts have been made to apply these techniques to cowpea. The objective of this investigation was to determine the role of several plant growth variables on total dry matter production of field-grown cowpeas under different N regimes.

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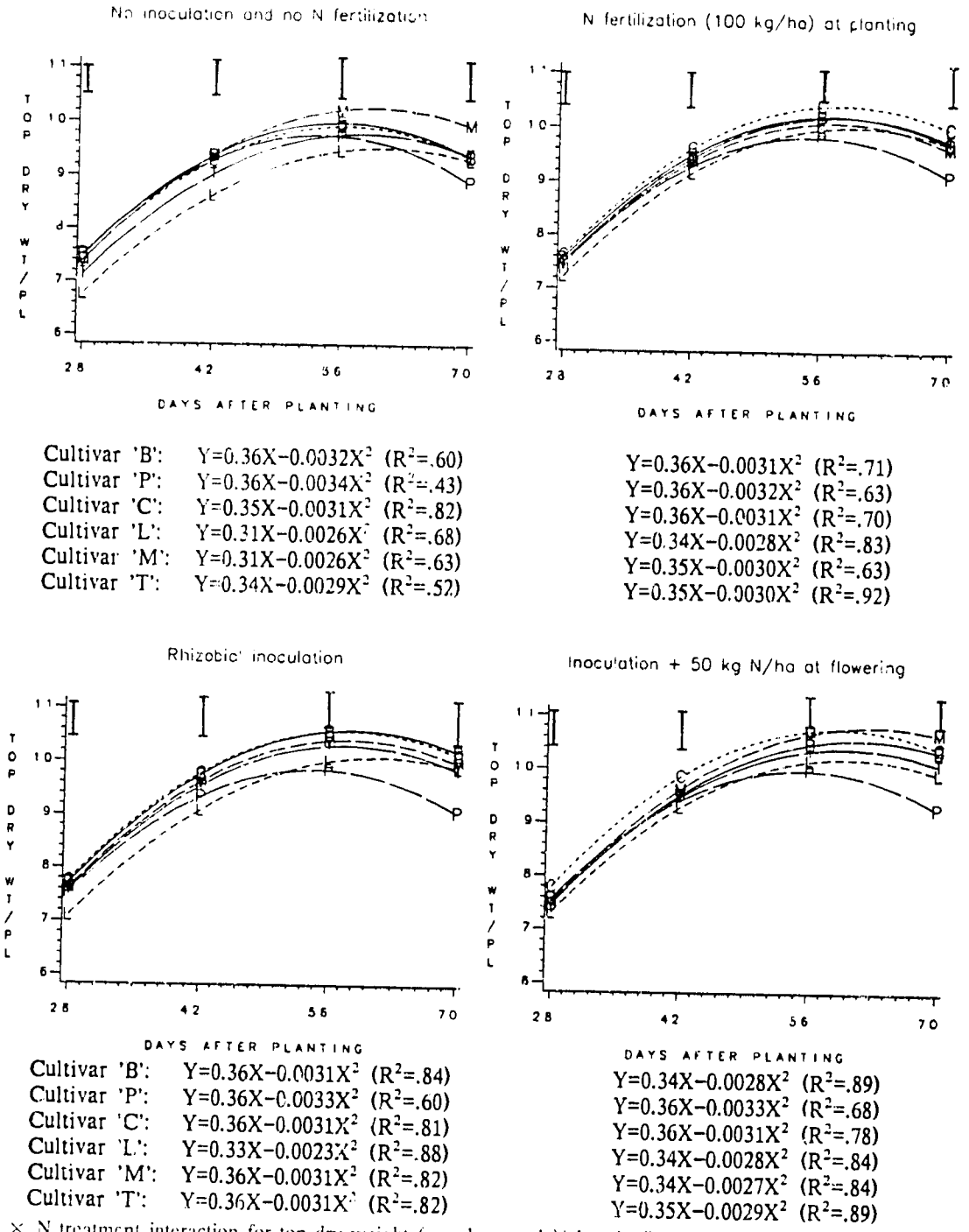


Fig. 1. Cultivar × N treatment interaction for top dry weight (mg, $\log_e$ scale)/plant in field-grown cowpea. B = 'Brown Crowder', P = Bush Purple Hull', C = California Blackeye', L = 'Lady', M = 'Mississippi Silver', T = 'Tennessee White Crowder'.

Table 1. Significance levels of treatment combinations for variables tested in the field study.

Treatment	Variables[z]					
	W	A	LS	LAR	LWR	SLA
Cultivar	0.0001[y]	0.0001	0.0001	0.0001	0.0001	0.06
Treatment	0.0001	0.0001	0.0001	0.13	0.004	0.12
Cultivar × treatment	0.0227	0.0278	0.80	0.22	0.22	0.06
Harvest time	0.0001	0.0001	0.0001	0.0001	0.0001	0.04
Treatment × harvest	0.004	0.0074	0.77	0.0116	0.73	0.46
Cultivar × harvest	0.0001	0.0001	0.0001	0.0001	0.0001	0.04
Treatment × cultivar × harvest	0.57	0.59	0.10	0.16	0.64	0.78

[z]W = Top dry weight ($\log_e$ scale)/plant, A = Leaf area ($\log_e$ scale)/plant, LS = Leaf area/leaf, LAR = Leaf area ratio, LWR = Leaf weight ratio, SLA = specific leaf area.
[y]Probability ≥ F.

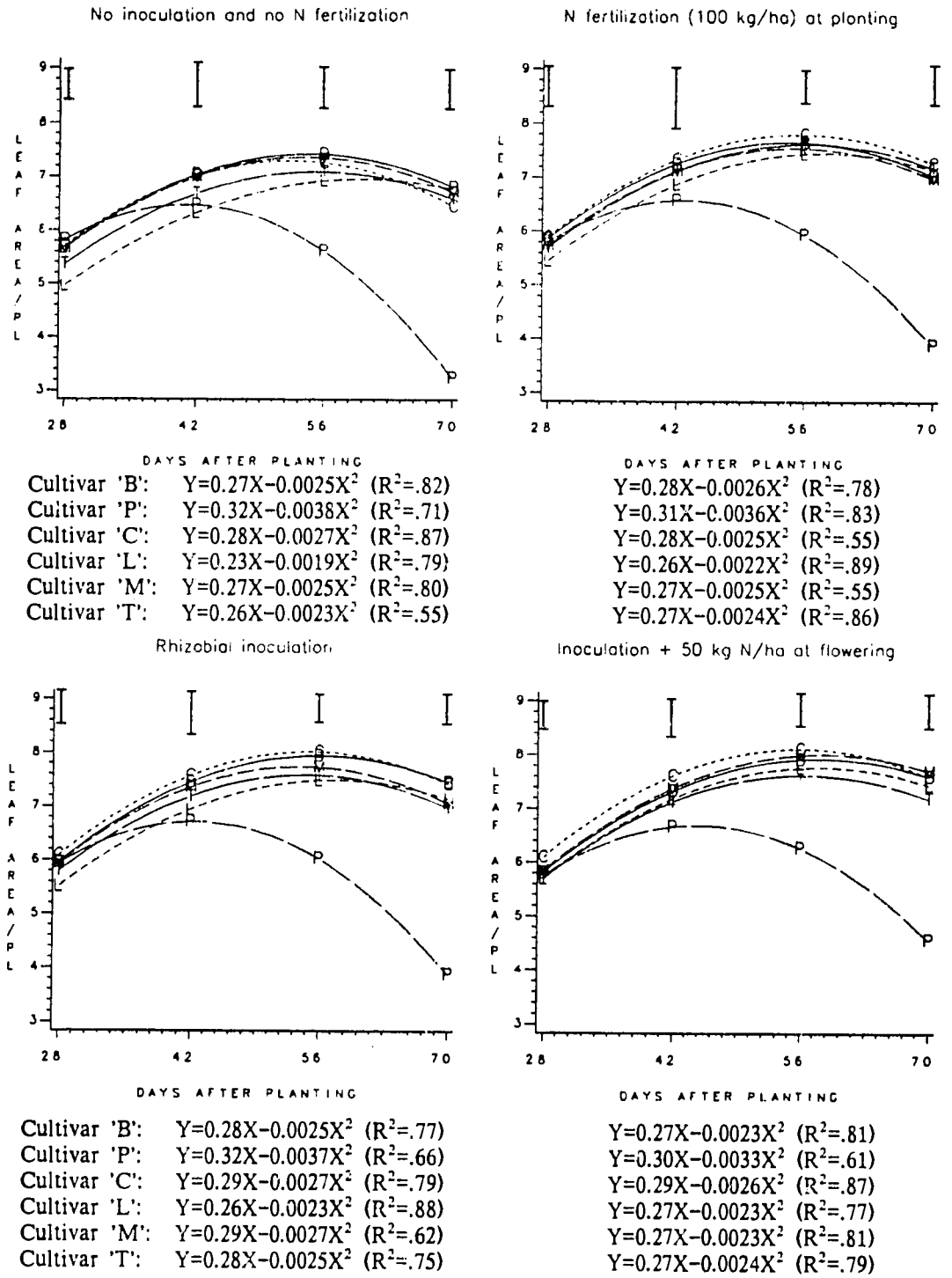


Fig. 2. Cultivar × N treatment interaction for leaf area (cm^2, log_e scale)/plant in field-grown cowpea. B = 'Brown Crowder', P = 'Bush Purple Hull', C = 'California Blackeye', L = 'Lady', M = 'Mississippi Silver', T = 'Tennessee White Crowder'.

Materials and Methods

The study was conducted in the field at College Station, Texas during Summer 1984 on a vertic albaqualf, fine, montmorillonitic, thermal soil at pH 6.7. A 5-cm layer of sawdust was applied evenly to the experimental site 3 months before planting and thoroughly incorporated to reduce soil N (NO_3) to 0.5 ppm at planting. To control the native *Rhizobium*, the experimental site was fumigated with methyl bromide (a.i. = 100%) at a rate of 436 $kg \cdot ha^{-1}$, 1 month before planting.

Four main plot treatments, no inoculation or N fertilization, inoculation with cowpea commercial "EL" innoculant, N fertilization with 100 kg N/ha ($CaNO_3$, 15.5% N) at planting, and inoculation + 50 kg N/ha at flowering, were randomized in a 4 × 4 Latin square. Five indeterminate cultivars, Brown Crowder, California Blackeye No. 5, Mississippi Silver, Tennessee White Crowder, and Lady, and one determinate cultivar, Bush Purple Hull, were randomized within each main plot. Prior to planting, $Ca(NO_3)_2$ was banded by hand and incorporated to a depth of 12 cm in those plots receiving N fertilizer treatment. In *Rhizobium*-inoculated plots, seeds were treated with a peat-based cowpea "EL" commercial inoculum at the rate of 1 g/hole. The plots were irrigated as needed.

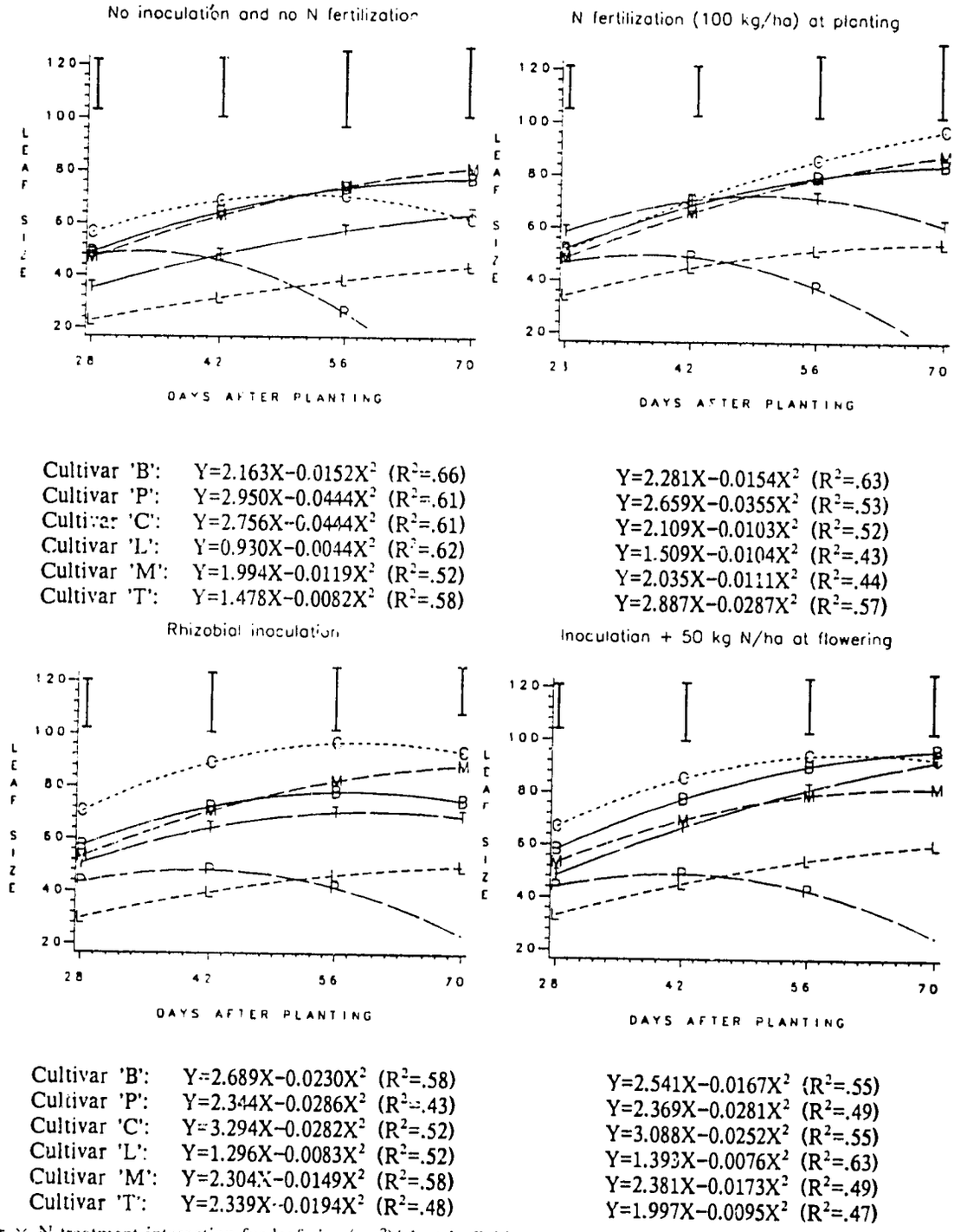


Fig. 3. Cultivar × N treatment interaction for leaf size (cm^2)/plant in field-grown cowpea. B = 'Brown Crowder', P = 'Eush Purple Hull', C = California Blackeye', L = 'Lady', M = 'Mississippi Silver', T = 'Tennessee White Crowder'.

Fumigation effectively controlled weeds. Plot size was 4 × 1 m. Three seeds per hill were planted at an 8-cm spacing on 4-m rows, 1 m apart on 5 June, 1984. Two weeks after emergence, plants were thinned to one plant per hill to establish a population of 120,000 plants/ha.

Four harvests of three random plants were taken biweekly from each plot, starting from the 4th week. Leaves and pods were separated from the plant, and number of leaves (LN) and leaf area (A) per plant were measured using a LI-COR (Model 3000) leaf area meter. Plant parts were dried in a forced-air oven at 70°C for 72 hr and dry weights of leaves (LW), stems (SW), and pods (PW) were measured separately.

Logarithmic transformations (natural log) of primary data, top dry weight (W), and A were made, rendering the variability more nearly homogeneous over time. Following Hunt (6), the transformed data were fitted to an exponential model in the form of: $Y = \beta_0 + \beta_1 t + \beta_2 t^2$; where $Y = \log_e W$ or $\log_e A$ and t = time in days after emergence. Using this exponential model, the following plant growth variables were measured as described by Hunt (6): a) relative growth rate (RGR) = $1/W \cdot dw/dt$ b) net assimilation rate (NAR) = $1/L \cdot dw/dt$; c) leaf area ratio (LAR) = L/W; d) leaf weight ratio (LWR) = LW/W; e) specific leaf area (SLA) = A/LW; and f) average leaf size (LS) = A/LN.

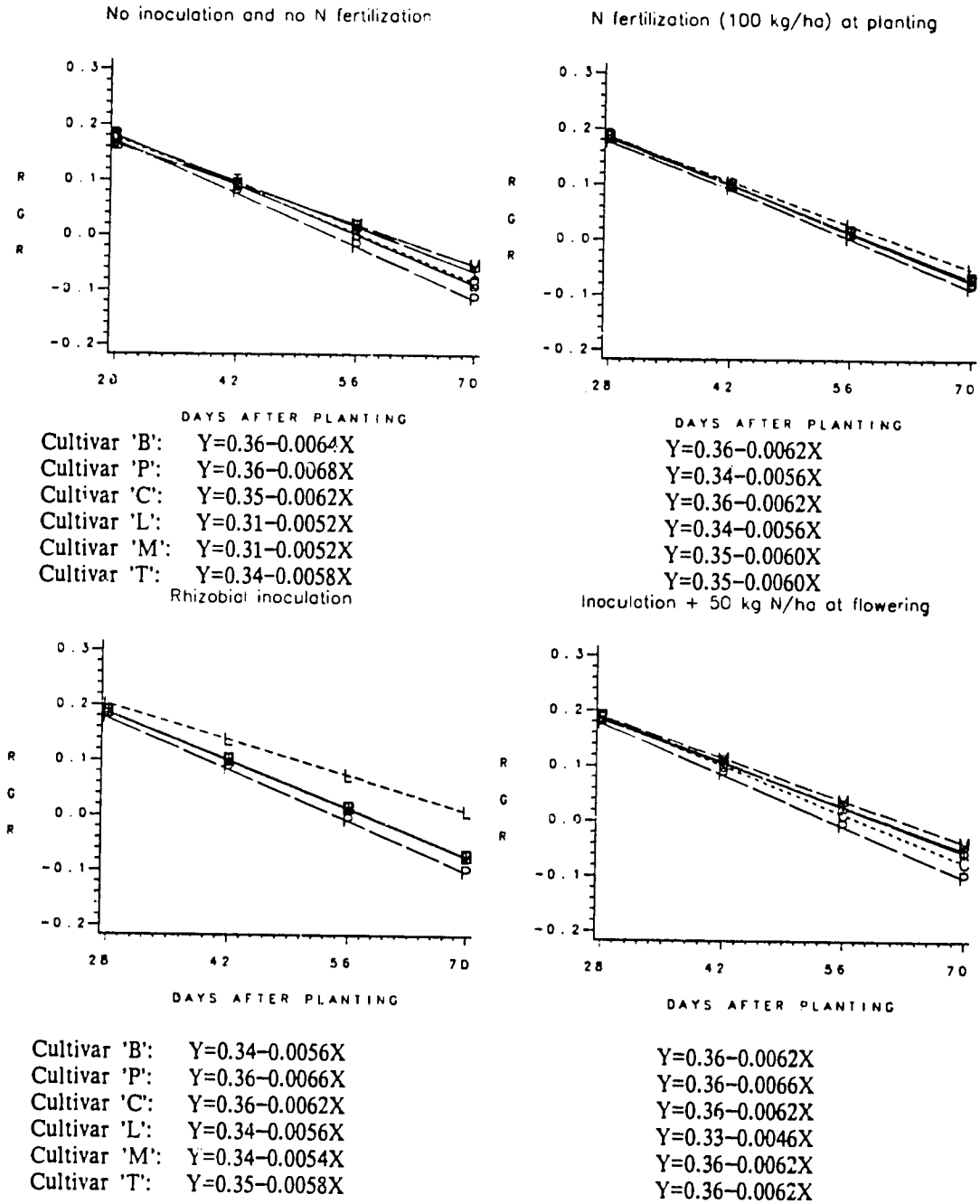
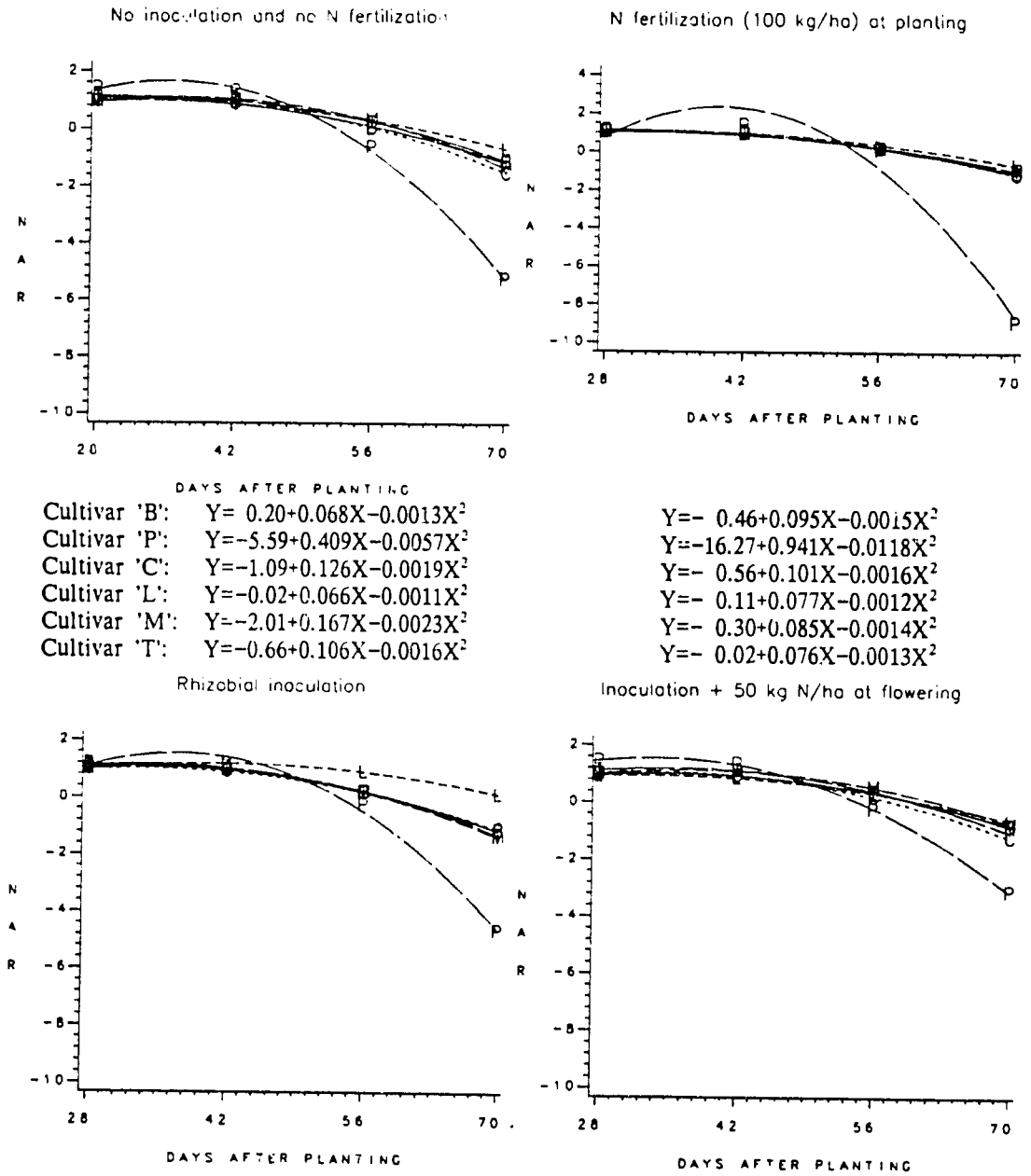


Fig. 4. Cultivar × N treatment interaction for relative growth rate (RGR) (per day) in field-grown cowpea. B = 'Brown Crowder', P = 'Bush Purple Hull', C = 'California Blackeye', L = 'Lady', M = 'Mississippi Silver', T = 'Tennessee White Crowder'.

Results and Discussion

Summary of test statistics. Cultivar effects were highly significant for all variables except SLA, whereas N treatments influenced all variables except LAR and SLA (Table 1). The interactions between cultivar and N treatment were significant for W and A. Within a cultivar, all growth variables were influenced by the growth stages expressed at harvest time. Differential growth responses were not observed for LS, LAR, and LWR in the cultivar × N treatment interaction. Plant growth variables W, A, and LAR changed differentially under different N treatments as growth progressed. The SLA was stable among cultivars and N treatments; however, only growth stage influenced SLA.

Dry matter accumulation reached maximum at 56 days in all five indeterminate cultivars and 49 days for the determinate cultivar (Bush Purple Hull) with inoculation (Fig. 1). However, in the uninoculated treatments, the maximum dry matter accumulation of 'Bush Purple Hull' was delayed by 4 to 7 days (Fig. 1). In all N treatments, maximum leaf area was reached at 56 days in the indeterminate cultivars and 42 days in 'Bush Purple Hull' (Fig. 2). During pod development, 'Bush Purple Hull' and 'Lady' accumulated less dry matter than other cultivars. These results confirm our previous finding that 'Bush Purple Hull' and 'Lady' yielded less than the other cultivars (3, 4) and suggest that increased dry matter accumulation during pod development increased seed yield. Similar findings also were reported in soybean (5). The rates of dry matter accumulation were higher in the inoculated and N-fertilized treatment than in the control, especially in 'Lady' and 'Tennessee White Crowder' (Fig. 1).



Cultivar 'B':	$Y= 0.20+0.068X-0.0013X^2$	$Y=- 0.46+0.095X-0.0015X^2$
Cultivar 'P':	$Y=-5.59+0.409X-0.0057X^2$	$Y=-16.27+0.941X-0.0118X^2$
Cultivar 'C':	$Y=-1.09+0.126X-0.0019X^2$	$Y=- 0.56+0.101X-0.0016X^2$
Cultivar 'L':	$Y=-0.02+0.066X-0.0011X^2$	$Y=- 0.11+0.077X-0.0012X^2$
Cultivar 'M':	$Y=-2.01+0.167X-0.0023X^2$	$Y=- 0.30+0.085X-0.0014X^2$
Cultivar 'T':	$Y=-0.66+0.106X-0.0016X^2$	$Y=- 0.02+0.076X-0.0013X^2$

Cultivar 'B':	$Y=-0.55+0.103X-0.0016X^2$	$Y= 0.74+0.101X-0.0015X^2$
Cultivar 'P':	$Y=-6.19+0.417X-0.0056X^2$	$Y=- 2.51+0.241X-0.0036X^2$
Cultivar 'C':	$Y=-0.59+0.099X-0.0015X^2$	$Y=- 0.83+0.113X-0.0017X^2$
Cultivar 'L':	$Y=-0.83+0.099X-0.0012X^2$	$Y=- 0.17+0.071X-0.0011X^2$
Cultivar 'M':	$Y=-1.24+0.133X-0.0019X^2$	$Y=- 0.13+0.129X-0.0017X^2$
Cultivar 'T':	$Y=-0.88+0.122X-0.0018X^2$	$Y=- 1.05+0.127X-0.0018X^2$

Fig. 5. Cultivar × N treatment interaction for net assimilation rate ($mg \cdot cm^{-2} \cdot day^{-1}$) in field-grown cowpea. B = 'Brown Crowder', P = 'Bush Purple Hull', C = 'California Blackeye', L = 'Lady', M = 'Mississippi Silver', T = 'Tennessee White Crowder'.

Leaf area declined very rapidly in 'Bush Purple Hull' as compared to the indeterminate cultivars. 'Bush Purple Hull' appeared to remobilize dry matter into the pods and shed its leaves at the end of pod development, whereas the indeterminate cultivars maintained leaf area by replacing mature leaves with young, actively photosynthesizing leaves. Thus, the high harvest index reported for 'Bush Purple Hull' (3) can be attributed, at least in part, to its rapid leaf senescence rate

Average leaf size was influenced greatly by treatment, cultivar, and plant growth stage (Fig. 3). The LS was lower in the control than in the other treatments. Large-seeded cultivars (California Blackeye No. 5, Mississippi Silver, Brown Crowder, and Tennessee White Crowder) produced larger leaves throughout the season than 'Bush Purple Hull' and 'Lady', where seed size was medium and small, respectively (3). During the vegetative growth period, leaf size of 'Bush Purple Hull' was larger than 'Lady'; however, as leaves began to senesce after 42 days in 'Bush Purple Hull', average leaf size declined rapidly. The close association between leaf size and seed size also has been reported in common bean (2).

Relative growth rate is a complex physiological component of dry matter accumulation and is equivalent to the slope of the

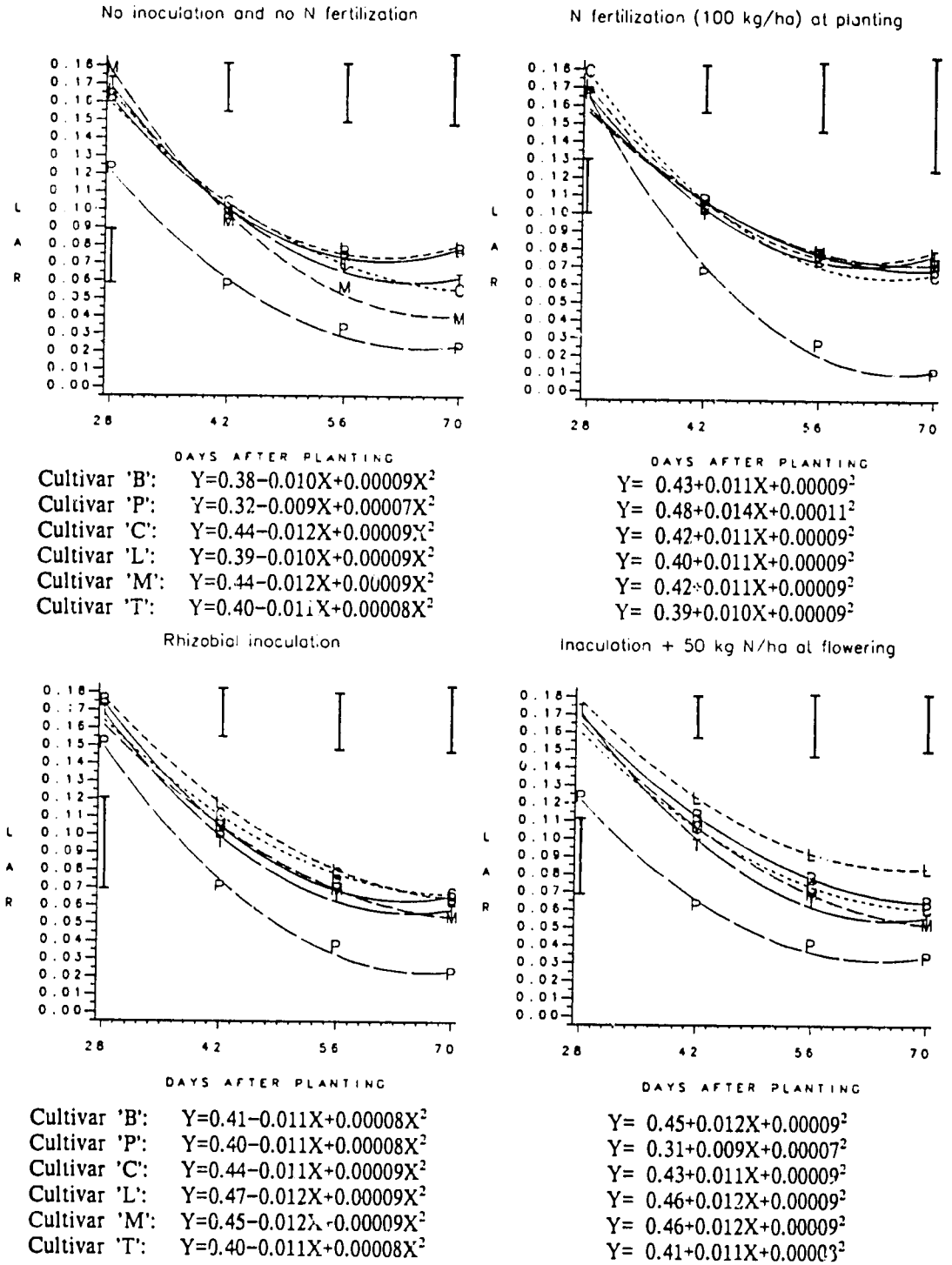


Fig. 6. Cultivar × N treatment interaction for leaf area ratio ($cm^2 \cdot mg^{-1}$) in field-grown cowpea. B = 'Brown Crowder', P = 'Bush Purple Hull', C = 'California Blackeye', L = 'Lady', M = 'Mississippi Silver', T = 'Tennessee White Crowder'.

curve between the $\log_e$ of W and sampling times (6). It is specific to the given time and therefore is known as instantaneous RGR. In this study, RGR declined linearly with sampling time, irrespective of N treatment or cultivar (Fig. 4). The RGR of 'Bush Purple Hull' was lower than that of the indeterminate cultivars, although not pronounced.

The RGR is equivalent to the product of its physiological components, LAR and NAR (8). The efficiency of dry matter assimilation is expressed as NAR, while LAR is the ratio of photosynthesizing to respiring tissues in the plant (6, 8). In this study, NAR declined slowly from maximum values at the beginning of sampling and became negative during the late growth period. However, the differences among N treatments or indeterminate cultivars for NAR were not pronounced (Fig. 5). In 'Bush Purple Hull', NAR increased to a level that was slightly greater than the indeterminate cultivars during vegetative growth and declined rapidly following pod development (Fig. 5). The decline in RGR and NAR with sampling time is attributed to both ontogenetic and environmental factors (1, 7). Nutrient availability, mutual leaf shading, and leaf senescence as the season progressed were probably the major causes for the rapid decline in RGR and NAR with time.

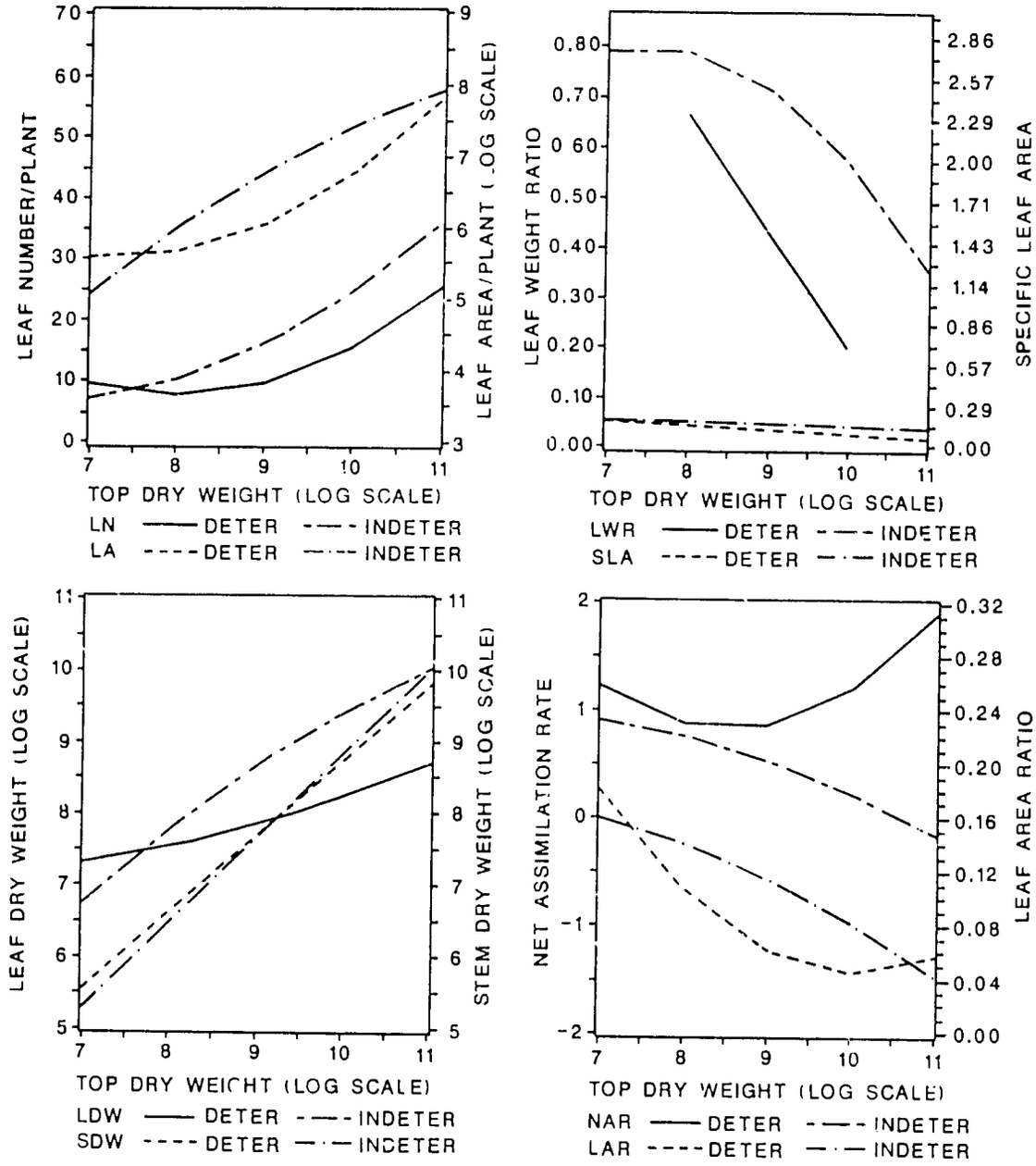


Fig. 7. Relationships between dry weight and plant growth variables in determinate and indeterminate cowpea cultivars.

Leaf area ratio declined curvilinearly with sampling time in all N treatments and cultivars (Fig. 6). The ratio of leaf area to total dry matter was highest during the vegetative growth period and, when pods developed and leaves senesced, LAR became small. The LAR was lowest for 'Bush Purple Hull', and the differences among indeterminate cultivars were not significant. The effects of N treatments on LAR were not evident in the indeterminate cultivars. However, in 'Bush Purple Hull', LAR of N-fertilized plants (100 kg·ha^{-1} at planting) was relatively larger than in the other treatments (Fig. 6). Thus, N fertilization produced more leaf area than inoculation in the low-N_2-fixing 'Bush Purple Hull' (3) at the early growth stage.

Number of leaves per plant, leaf area per plant, and leaf and stem dry weights per plant increased linearly with an increase in total dry weight, both in determinate and indeterminate cultivars (Fig. 7). In the determinate cultivar, because of rapid leaf senescence, a unit increase in total dry matter was accompanied by a relatively smaller increase in leaf area than in the indeterminate cultivars. However, the relationship between stem and total dry weight was similar in both determinate and indeterminate cultivars. High W also was associated with increasing and higher values of NAR in 'Bush Purple Hull' than in the indeterminate cultivars (Fig. 7). These results suggest that the determinate cultivar, Bush Purple Hull, synthesized and mobilized dry matter from leaf tissue to pods more efficiently than did the indeterminate cultivars.

The relationships between LAR and W were negatively curvilinear in the determinate and indeterminate cultivars (Fig. 7). In 'Bush Purple Hull', rapid leaf senescence rate was accompanied by increasing dry matter accumulation in the pods. Thus, the slope of the LAR curve was greater in the determinate cultivar than in the indeterminate cultivars. LAR is the product of two components, namely, leaf weight ratio (LWR), which measures the differential distribution of photosynthetic products between leaves and other plant parts, and specific leaf area (SLA), a measure of leaf thickness. Of these two components, only

LWR showed a relationship similar to that between LAR and W (Fig. 7). In the determinate and indeterminate cultivars, SLA did not respond to the changes in W, indicating that average leaf thickness was stable during plant growth and was not influenced by the different N regimes in the six cultivars studied.

Although N fertilization and rhizobial inoculation increased total dry matter accumulation and leaf area, the physiological components of plant growth were less influenced by N treatment. Among the cultivars studied, the major distinction in total dry matter accumulation, total leaf area development, and physiological components was found between the determinate and five indeterminate cultivars. The observed differences in the physiological components within the indeterminate cultivars were not significant.

Total leaf area and dry matter accumulation were greater in the indeterminate cultivars than in 'Bush Purple Hull'. Although RGR was higher for the indeterminate cultivars than for the determinate cultivar during vegetative growth and early pod development, NAR was higher in the determinate cultivar than in the indeterminate cultivars. Large values of NAR during vegetative growth and small LAR in 'Bush Purple Hull' could be associated with efficient remobilization of dry matter, thereby increasing harvest index, as reported elsewhere (3). Leaf weight ratio influenced LAR more than specific leaf area (SLA). Thus, dry matter accumulation and leaf area development during the vegetative and pod-development stages were large enough to cause differences in yield among N treatments and cultivars. A clear relationship between physiological components of plant growth and yield potential of the cultivars was not evident; however, there was a relationship between harvest index and the physiological components. In grain legumes, relatively large amounts of metabolites are used to synthesize proteins and oil-rich storage products, which contain more energy per unit of dry matter. Thus, in grain legumes, physiological components based on dry matter accumulation probably do not adequately reflect the efficiency of dry matter use. Plant growth measurements computed in energy units might be more informative than dry matter accumulation in evaluating assimilation efficiency of grain legumes.

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