Nodule Distribution among Root Morphological Components of Field-grown Cowpeas

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Abstract. Field experiments were conducted in 1985 at Fort Pierce, Fla., and Bixby, Okla., to quantify and describe the distribution of nodules among root morphological components of cowpea (Vigna unguiculata (L.) Walp.). Plants of ‘Knuckle Purplehull’, ‘Mississippi Cream’, and ‘White Acre’ were sampled by cultivar on separate dates at three stages of ontogeny, especially for nodules from taproots. Although 70% of the root mass was in the taproot and its associated laterals at both locations, the taproot per se was generally located on the basal and lateral roots. When percentage distribution of total nodule weight was examined, neither growth stage nor cultivar was found to

Materials and Methods

Three cowpea cultivars (‘Knuckle Purplehull’, ‘Mississippi Cream’, and ‘White Acre’) from the same seed lots were grown at Fort Pierce, Fla., and Bixby, Okla., using a commercial cultural system of double rows. Double-row plots, with 0.46 m between the two rows within each plot and 1.64 m between the rows of adjacent plots, were used at both locations. The plots were on raised beds (1.09 m wide and 0.15 m high) in Florida and on the flat in Oklahoma. Plots were hand planted at 20 seeds per meter of row and thinned to 10 plants per meter of row shortly after emergence at both locations.

Cultural practices--Fort Pierce, Fla. The experiment was conducted at the Agricultural Research and Education Center during Spring 1985. The soil was an Oldsmar fine sand (sandy, siliceous, hyperthermic Alfic Arenic Hapludalfs). Preplant fertilization consisted of 94N–62P–195K (kg–ha−1) as a band application in the center of each bed. The rates reflected the leaching potential at Fort Pierce due to sandy soils and high seasonal rainfall. Seeds were planted on 28 Feb. Plots were 3.0 m long. No Rhizobium inoculants were used, since previous studies with cowpea at Fort Pierce had shown that native Rhizobia populations provided extensive nodulation. Seeds were dusted with the fungicide 3a,4,7a-tetrahydro-2-[trichloromethyl]thio]-1-H-isouindole-1,3(2 H)-dione (captan) before planting. Pentachloron-
Weights of root mass components increased between the PA and lateral roots, and taproots also increased between the PA and SI stages. Weights of basal roots, test at significant growth stages and SI stages in Florida, then either remained unchanged or decreased between the SI and H stages. Weights of nodules from lateral roots and from taproots declined between the PA and SI stages in Oklahoma, but further increases occurred between the SI and H stages.

Plants of ‘Mississippi Cream’ usually had lower shoot weights (data not presented) and total root weights than plants of ‘Knuckle Purplehull’ and ‘White Acre’ (Table 2). However, cultivar differences in total root weight were not always consistent over growth stages, as evidenced by the growth stage × cultivar interactions at both locations.

The percentage distribution of total root weight among the four root morphological components was little affected by cultivar, growth stage, or location (data not presented). Grand means were: adventitious roots, 3.5%; basal roots, 24%; lateral roots, 27.5%; and taproots, 45%.

Neither cultivar nor growth stage affected weights of nodules from adventitious roots (Table 3). ‘Knuckle Purplehull’ had higher weights of nodules from basal roots, lateral roots, and taproots than the other two cultivars in Florida. Fewer differences were evident among cultivars in Oklahoma. Weights of nodules from basal and lateral roots were unaffected by growth stage in Florida, while weights of nodules from taproots declined between the SI and H stages. Weights of nodules from lateral roots and from taproots declined between the PA and SI stages in Oklahoma, then did not change between the SI and H stages.

‘Knuckle Purplehull’ had a higher total nodule weight than the other two cultivars in Florida, but not in Oklahoma (Table 3). Total nodule weights did not differ between the PA and SI stages in Florida, but were greater at the SI stage than at the H stage. In contrast, total nodule weights were highest at the PA stage in Oklahoma and did not differ between the SI and H stages.

The percentage distribution of total nodule weight among the four root morphological components was calculated, based on the data in Table 3 (percentages not presented). Differences among cultivars were present only for nodules from adventitious roots and from taproots. ‘White Acre’ had a relatively low percentage (9%) of its nodule weight located on taproots at both locations. In Oklahoma, a greater percentage of the total nodule weight was located on taproots at the PA stage than at the SI and H stages, with a reciprocal trend evident for nodules from adventitious roots. A similar effect of growth stage on nodules from taproots was observed in Florida, but growth stage did not significantly affect nodule distribution among adventitious roots, basal roots, or lateral roots. On average, ≈50% of the total nodule mass was associated with lateral roots in Florida, with another 31% associated with basal roots. About 60% of the total nodule mass was associated with nodules from lateral roots plus nodules from basal roots in Oklahoma.

**Discussion**

Changes in root weights during ontogeny were similar to those previously reported (Kahn and Stoffella, 1987). Root growth may have ceased before harvest in Florida. Others have reported decreases in total root weight during late podfill in cowpeas (Minchin et al., 1980; Ryle et al., 1979).

Nodule counts were not recorded in our studies. Nodules sometimes were lobed, making differentiation difficult. Also, field studies have indicated that nodule weight is more relevant to N fixation in cowpea than is absolute number of nodules (Miller et al., 1982, 1986). Strong linear relationships between total nodule fresh weight and quantity of N fixed have been reported (Miller et al., 1982; Wadisirisuk and Weaver, 1985). Lawn and Bushby (1982) also suggested that nodule fresh weight was a better indicator of effects of different root and shoot
genotypes on N\textsubscript{2} fixation than was either specific or total nodule activity.

Cowpea nodule weights usually are highest from about anthesis to mid-pod fill (Eaglesham et al., 1977; Minchin et al., 1980; Summerfield et al., 1977), but apparently functional nodules have been observed even at final harvest (Dart et al., 1977). In our studies, nodule weights usually were lower at harvest than at earlier stages of ontogeny, especially in Oklahoma (Table 3). The decline in weight was especially noteworthy for nodules from taproots (Table 3). Others (Minchin and Summerfield, 1978; Minchin et al., 1980) had identified two distinct nodule populations in growth-chamber-grown cowpeas. Nodules in "crown" positions on the main taproot and on earlier-formed secondary roots near the junction with the taproot predominated during vegetative growth. After anthesis, these nodules generally senesced and sloughed off, and "secondary" nodules (located on secondary, tertiary, and higher-order roots away from the primary root) became dominant. In one study, these secondary nodules accounted for more than 50\% of total nodule dry weight at the time the first pods were maturing (Minchin et al., 1980). Our data indicate that while some nodules were present on the taproot following anthesis, the taproot was

Table 1. Dry weights (grams/plant) of root mass components for three cowpea cultivars at three growth stages grown at two locations.\textsuperscript{a}

| Main effects | Adventitious roots | Basal roots | Lateral roots | Taproots |
|--------------|------------------|-------------|---------------|----------|
|              | FL | OK | FL | OK | FL | OK | FL | OK |
| Cultivar     |     |    |    |    |    |    |    |    |
| Knuckle Purplehull | 0.05 b | 0.02 b | 0.47 a | 0.30 a | 0.46 a | 0.26 a | 0.57 a | 0.53 a |
| Mississippi Cream | 0.02 b | 0.01 b | 0.18 b | 0.10 c | 0.24 b | 0.15 b | 0.34 b | 0.23 b |
| White Acre | 0.08 a | 0.04 a | 0.40 a | 0.20 b | 0.39 a | 0.25 a | 0.56 a | 0.57 a |
| Growth stage |    |    |    |    |    |    |    |    |
| PA | 0.02 b | 0.01 b | 0.13 b | 0.11 c | 0.15 c | 0.13 c | 0.22 b | 0.28 c |
| SI | 0.06 a | 0.03 ab | 0.51 a | 0.20 b | 0.53 a | 0.22 b | 0.57 a | 0.43 b |
| H | 0.07 a | 0.04 a | 0.41 a | 0.28 a | 0.40 b | 0.30 a | 0.67 a | 0.62 a |
| CV | 60.5 | 70.0 | 37.9 | 47.0 | 40.2 | 27.7 | 38.4 | 43.9 |

\textsuperscript{a}Locations: FL = Fort Pierce, Fla; OK = Bixby, Okla. All growth stage \times cultivar interactions were nonsignificant at P = 0.05. Mean separation in columns and among growth stages or among cultivars by Duncan's multiple range test, P = 0.05.

Table 2. Total dry weights of roots (grams/plant) at three growth stages for three cowpea cultivars grown at two locations.

| Cultivar     | Fort Pierce, Fla. | Bixby, Okla. |
|--------------|-------------------|--------------|
|              | Growth stage      |              | Growth stage |
|              | PA    | SI    | H    | X    | PA    | SI    | H    | X    |
| Knuckle Purplehull | 0.77 | 2.03 | 1.83 | 1.55 | 0.64 | 1.10 | 1.57 | 1.10 |
| Mississippi Cream | 0.43 | 0.87 | 1.01 | 0.77 | 0.30 | 0.52 | 0.65 | 0.49 |
| White Acre | 0.36 | 2.09 | 1.84 | 1.43 | 0.66 | 1.01 | 1.50 | 1.06 |
| X | 0.52 | 1.66 | 1.56 | 1.25 | 0.54 | 0.88 | 1.24 | 0.88 |
| Interaction LSD\textsuperscript{a} | 0.56 | 0.56 | 0.56 | 0.56 |
| CV | 29.9 | 18.0 | 18.0 | 18.0 |

\textsuperscript{a}Growth stage \times cultivar interactions significant at P = 0.05.

Table 3. Fresh weights (grams/plant) of nodules from four root mass components for three cowpea cultivars at three growth stages grown in two locations.\textsuperscript{a}

| Cultivar     | Adventitious roots | Basal roots | Lateral roots | Taproots |
|--------------|------------------|-------------|---------------|----------|
|              | FL | OK | FL | OK | FL | OK | FL | OK |
| Knuckle Purplehull | 0.05 | 0.02 | 1.08 a | 0.11 a | 1.35 a | 0.09 a | 0.32 a | 0.07 a | 2.80 a | 0.30 |
| Mississippi Cream | 0.06 | 0.03 | 0.37 b | 0.05 b | 0.72 b | 0.05 b | 0.22 b | 0.07 b | 1.37 b | 0.20 |
| White Acre | 0.09 | 0.08 | 0.25 b | 0.06 b | 0.46 b | 0.06 ab | 0.08 c | 0.02 a | 0.88 b | 0.22 |
| Growth stage |    |    |    |    |    |    |    |    |    |
| PA | 0.07 | 0.02 | 0.47 | 0.11 | 0.88 | 0.11 a | 0.28 a | 0.12 a | 1.70 ab | 0.37 a |
| SI | 0.05 | 0.07 | 0.89 | 0.06 | 0.99 | 0.05 b | 0.24 a | 0.03 b | 2.18 a | 0.21 b |
| H | 0.07 | 0.04 | 0.35 | 0.06 | 0.65 | 0.03 b | 0.10 b | 0.01 b | 1.18 b | 0.14 b |
| CV | 109.8 | 140.7 | 56.5 | 63.1 | 47.8 | 58.6 | 46.6 | 96.4 | 35.5 | 48.6 |

\textsuperscript{a}Locations: FL = Fort Pierce, Fla; OK = Bixby, Okla. All growth stage \times cultivar interactions were nonsignificant at P = 0.05. Mean separation in columns and among growth stages or among cultivars by Duncan's multiple range test, P = 0.05. Mean separation letters do not appear when main effects were nonsignificant (F test) at P = 0.05.
proportionally less important as a locus of nodulation at the SI and H stages than the PA stage.

Dart and Wildon (1970) reported that many more nodules formed on “secondary roots” of cowpea than on the primary root (taproot). This pattern of nodulation may reflect the physical distribution of the root system in the soil. The taproot is a single structure growing in essentially one plane. In contrast, each plant has several basal and lateral roots (Kahn and Stoffella, 1987) that can extend in many directions, thereby providing more potential sites for infection by *Rhizobium*.

Adventitious roots accounted for only 4% of the total root weight in Florida and 3% in Oklahoma. However, nodules from adventitious roots accounted for ≈ 21% of the total nodule weight in Oklahoma, compared to ≈6% in Florida (based on data in Table 3). This difference may have reflected soil differences between the two locations. A more likely explanation, however, is the presence of rhizobial inoculant. Kamicker and Brill (1987) found that inoculant added to the seed furrow (as was done in Oklahoma) produced nodules mainly in the upper region of the soybean [*Glycine max* (L.) Merr.] root system, while inoculant tilled into the soil produced nodules primarily in the lower region of the root system. Whatever the explanation, adventitious roots were important as loci for nodulation in Oklahoma, particularly for ‘White Ace’.

No consistent linear correlations were evident between the variables in Tables 1 through 3 (correlations not presented). Most values of *r* were below 0.50. Thus, no linear correlation was found between the weight of a particular root morphological component and the nodule weight associated with that component. Total root weight and total nodule weight also were not strongly correlated (*r* = −0.35 in Oklahoma, significant at *P* = 0.05; *r* = 0.15 in Florida, not significant at *P* = 0.05). Rosas and Bliss (1986) obtained a low correlation between root dry weight and nodule dry weight in field-grown common bean (*r* = 0.38, significant at *P* = 0.01). Genotypic effects on determinants of N<sub>2</sub> fixation are known to be complex. Lawn et al. (1974) suggested that the control of soybean nodule initiation occurs primarily in the root itself, but the control of nodule fresh weight occurs solely in the shoot and is related to the supply of assimilates.

These studies confirmed a previous report (Kahn and Stoffella, 1987) that the majority of the root mass in cowpea occurs in the taproot and its associated laterals. The taproot per se, however, was not the primary locus of nodulation, particularly after anthesis. Instead, most nodules generally were located on the basal and lateral roots. Also, when percentage distribution of total nodule weight was examined, neither growth stage nor cultivar was found to affect nodulation of basal and lateral roots. Breeders selecting for extensive root systems in cowpea in an effort to maximize sites for nodulation and to increase nutrient uptake efficiency (Adepetu and Akapa, 1977) should consider the importance of these root types in cowpea nodulation.

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