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NITROGEN ACCUMULATION AND PARTITIONING BY WINGED BEAN IN RESPONSE TO SUPPORT SYSTEMS

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SUMMARY

An experiment was carried out to determine the partitioning and accumulation of nitrogen in plant components, nitrogenase activity and their relationships with seed yield of a local cultivar of winged bean (*Psophocarpus tetragonolobus* (L.) DC.) grown on three support systems of 0, 1, and 2 m height under field conditions. Total nitrogen accumulation and nitrogen partitioning were determined throughout the growing season by measuring nitrogen content and concentration in above-ground plant tissues (leaves, stems, petioles and pods). Support heights of 1 and 2 m significantly increased total nitrogen accumulation in component parts of the plant, nitrogenase activity, nodulation, total dry matter accumulation and seed yield compared with the control. Plants grown on supports accumulated significantly higher leaf nitrogen at the vegetative stages and the contribution of seed nitrogen was also significantly higher compared with unsupported plants. Nitrogenase activity increased with onset of flowering but declined during the pod formation stage in plants grown on a support system. Unsupported plants showed higher nitrogenase activity prior to flowering possibly due to lack of photosynthate and, consequently, early senescence of leaves.

INTRODUCTION

Winged bean (*Psophocarpus tetragonolobus* (L.) DC.) is one of the most potentially important, under-utilized crops and an exceptionally productive food crop in the humid tropical regions of the world (Lynd *et al*., 1983). It is an indeterminate, climbing, annual or perennial herb (Eagleton *et al*., 1985) which requires some kind of support to achieve high yields (Thompson and Haryono, 1980).

Information on the patterns of nitrogen (N) accumulation over time and the partitioning of N among plant parts in winged bean is important in cropping systems for the tropics (Weil and Belmont, 1991). Studies on winged bean yields have concentrated mainly on pod, seed and tuber production (Herath and Fernandez, 1978; Ruegg, 1981; Lynd *et al*., 1983) whilst studies on plant growth have concentrated mainly on the effects of photoperiod on time to flowering, tuberization, vegetative growth (Wong, 1983) and pod set (Data and Pratt, 1980), relative growth rates (Stephenson, 1978), dry matter (DM) and N accumulation (Shamsuddin and Aini, 1978). Weil and Belmont (1991)

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investigated DM and N accumulation with single-staked supports but no comparison was made between plants grown on support systems and unsupported. The importance of N for maximizing photosynthesis, DM and seed yields has been demonstrated for several legume crops (Cure *et al.*, 1985; Muchow and Sinclair, 1986).

Quantitative information on N accumulation, its partitioning to leaf N and the partitioning of N to grain yield is required for the development of crop growth models to allow the assessment of production risk (Muchow *et al.*, 1993). In grain legumes, N accumulation is closely linked to biomass accumulation as crop radiation use efficiency is determined by the amount of leaf N per unit leaf area (Sinclair and Horie, 1989). There have been a number of studies on N accumulation and distribution in individual grain legumes, for example, soyabean, mungbean, cowpea (Muchow *et al.*, 1993) and pigeonpea (Dalal, 1980). There is, however, little published information on similar studies for grain legumes under tropical field conditions. Some information on the effect of support systems on seed yields are available but there is little experimental evidence on N partitioning and its significance to increased seed yield of winged bean. This experiment was designed to investigate the partitioning of N in relation to seed yield in winged bean grown on support and without support systems.

MATERIALS AND METHODS

Cultural practices and management

The experiment was conducted between August 1994 and January 1995 at the Universiti Putra Malaysia Farm, Malaysia. At each planting point three to four seeds were sown and seedlings were thinned to one plant per point at two weeks after seedling emergence. Between-row and between-plant spacings in the row were 60 cm and 30 cm respectively, and the spacing between one double row and another was 90 cm, corresponding to 44×10^3 plants ha^{-1}. The insecticides Ambush (permethrin) and Logor 40 (dimethoate) and the fungicides Benlate (benomyl) and Anvil 5SC (hexaconazole) were applied periodically for the control of pests and diseases.

Experimental treatments and design

The experiment consisted of three treatments: i) plants grown on the ground surface, that is, unsupported, ii) plants grown on a wire trellis support 1 m in height and iii) plants grown on a support 2 m in height. The experiment was laid out in a randomized complete block design with eight replications.

Support system

Support systems were constructed six weeks after seed germination. The support system consisted of wooden sticks (6.3 cm in width), plastic-coated steel wire and raffia string. Wooden sticks were buried to a depth of 45–60 cm at the end of each row. Steel wires were drawn across, one at the lower part

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(approximately 0.3 m above the ground surface) then another at the top of the stick. Raffia string was then strung between the two steel wires to support the climbing plants.

Leaf senescence and absorbance of photosynthetically active radiation (PAR)

After seedling emergence preselected random areas of 4 m^2 of a unit plot in each treatment were sampled at three-week intervals from week 9 and until week 20 for the determination of leaf senescence. Absorption of PAR by plants was measured by LI-189 Quantum at 2-week intervals from week 8 to week 20.

Separation of plant parts and determination of nitrogen concentration

After seedling emergence 16 plants from each treatment were harvested at weekly intervals from 6 to 10 weeks, and thereafter at fortnightly intervals until 20 weeks of growth for the determination of total DM. The same plant samples were used for the determination of N. Sampled plants were separated into stems, leaves, petioles and pods (when available) and all plant parts were rinsed with water, dried, ground and analysed for total N.

Approximately 250 mg of ground plant material was subjected to Kjeldahl digestion in a 100 ml digestion flask containing 5 ml concentrated H_2SO_4 and heated for about six to seven minutes at 450 °C, after which 10 ml H_2O_2 was added. The clear digest was then cooled and diluted to the mark with distilled water. Approximately 10–50 ml of the digest solution was kept in a tightly-capped plastic bottle, and later analysed for total N on a Chem Lab auto-analyser. Details of the micro-Kjeldhal and the use of an auto-analyser were as described by Bremner and Mulvaney (1982).

Estimation of nitrogen fixation

Nitrogen fixation was estimated by the acetylene reduction assay (ARA) method. The accuracy of ARA, which is a closed system (Oti-Boateng and Silsbury (1993), has received serious criticisms (Minchin *et al.*, 1994), since acetylene itself can induce a decline in nitrogenase activity during a 1-h incubation period of the assay (Minchin *et al.*, 1983). However, this method is an acceptable tool for observing large relative differences in nitrogen fixation (Vessey, 1994) and its use is justified in this study to show trends over the plant growth period. In this experiment extreme care was taken to remove the entire root system with minimum loss of plant material. The volume of excavation of the root systems was about 0.4 cm^3 and $>95\%$ nodule was collected. At each harvest (between about 0900 and 1000 hours on each occasion) the soil was shaken gently off the nodulated root systems which were placed immediately in 0.5-l Fowler jars. Each jar was fitted with an air tight lid incorporating a suba seal as an injection port. About 10% of the air in the Fowler jar was withdrawn by using a syringe and needle, and this volume of air was replaced with instrument-grade acetylene. The root systems were incubated in duplicate and samples taken at 30 and 60 min in each replication. Duplicate 10 ml gas samples were then collected

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from each jar, using double-ended needles and evacuated venoject tubes, and later assayed for ethylene, the product of acetylene reduction. Using a micro-syringe, 1.0 ml of each gas sample was withdrawn from the tube and injected immediately into a Hewlett Packard gas chromatograph (Model 5830 A) which had been calibrated with an ethylene standard. The gas chromatograph was fitted with a stainless steel column, 2 m in length and 2 mm in diameter, packed with a Porapak N (80–100 mesh) and with a flame ionization detector (FID). Nitrogen, used as the carrier gas, had a flow rate of 42 ml min^{-1} and the column injection and FID temperatures were maintained at 100 °C, 110 °C and 120 °C respectively.

Statistical analysis

The data were analysed using a Statistical Analysis System (SAS, 1987). Following the analysis of variance procedures, differences among treatment means were determined using the least significant differences (LSD) comparison method. Correlation analysis was performed to estimate the relationship between different traits.

RESULTS

Nitrogen accumulation in plant parts

Nitrogen accumulation up to the pre-flowering stage was rather slow, but began to accelerate with the onset of flowering (10–11 weeks) in supported plants. Sharp increases in total plant N occurred during flowering and early pod formation stages in supported plants but in the case of unsupported plants N accumulation was very slow (Fig. 1). Prior to or during the flowering stage the leaves and stems were the major sites of N accumulation. However, the pods gained substantial amounts of N during the reproductive stage. At this stage leaves gained approximately 44% of total N accumulation averaged over the support system. The amount of N in leaves, stems, petioles and pods varied according to the support system. The highest and lowest accumulations of total N after 20 weeks were 6.30 and 2.10 g $plant^{-1}$ respectively and these values occurred with a support system height of 2 m and in unsupported plants respectively. Plants grown with a support height of 1 m obtained moderate N accumulation (4.06 g $plant^{-1}$) which was significantly higher than that of unsupported control plants, but lower than that of plants with a support system height of 2 m (Fig. 1).

Nitrogen accumulation in leaves, petioles and pods was significantly affected by the treatment variables. Plants grown with a support system height of 2 m gained significantly and produced the highest N content of leaves at all stages (Table 1). Plants grown with a support system height of 1 m and unsupported plants recorded intermediate and significantly the lowest leaf nitrogen contents respectively. During the initial 14 weeks of sampling, there was an increase in leaf N in all treatments followed by a decline from 14 to 18 weeks. The N content of petioles also reached a peak between 12 and 14 weeks, the initial pod filling period (Table 1).

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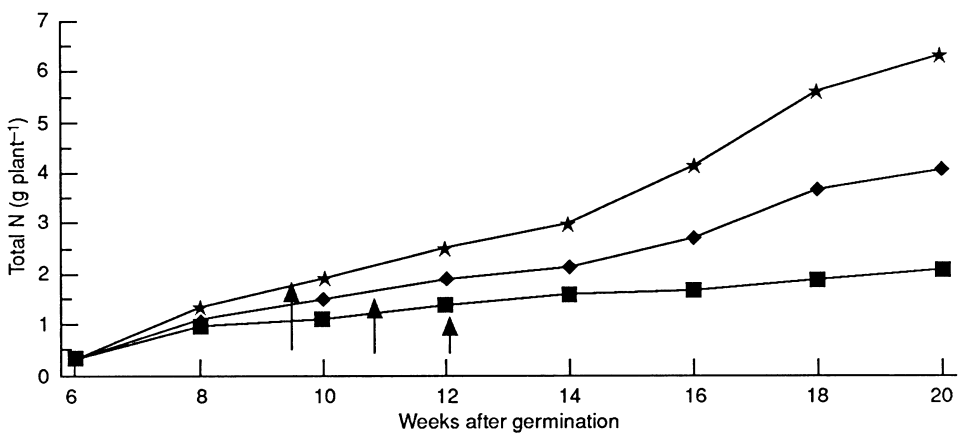


Fig. 1. Total nitrogen (N) accumulation of winged bean grown on support systems of varying heights (—■— unsupported control; —◆— support system height of 1 m; —*— support system height of 2 m). Arrows indicate time of flowering; s.e. at 6 weeks after germination (WAG) = 0.01; s.e. at 8 WAG = 0.11; s.e. at 10 WAG = 0.05; s.e. at 12 WAG = 0.09; s.e. at 14 WAG = 0.14; s.e. at 16 WAG = 0.07; s.e. at 18 WAG = 0.34; s.e. at 20 WAG = 0.20.

The N accumulation in pods increased rapidly with plant age in all treatments, plants growing on support systems 2 m in height producing the highest pod N. Plants grown on support systems 1 m in height and unsupported plants produced moderate and lowest pod N contents per plant (Table 1). The N content of stems was unaffected by the height of the support system (Table 1).

The distribution of N accumulation is shown in Fig. 2. During the vegetative phase N contents in leaf, stem and petiole accounted for 54–72, 21–36 and 7–10% respectively of total N accumulation per plant. At the reproductive phase, N contents in leaves, stems and petioles declined by 8–28, 1–6 and 3–5% respectively. The pods gained 13–37% of the total N accumulated by the whole plant. In

Table 1. Nitrogen accumulation (g plant^{-1}) in leaves, stems, petioles and pods of winged bean as influenced by plant age and the height of the support system

	Support system height (m)															
Weeks after germination	0	1	2	s.e.	0	1	2	s.e.	0	1	2	s.e.	0	1	2	s.e.
	Leaf N				Stem N				Petiole N				Pod N			
6	0.35	0.36	0.38	0.02	0.05	0.05	0.05	0.001	0.03	0.03	0.03	0.001	—	—	—	—
8	0.71	0.81	1.03	0.10	0.17	0.17	0.18	0.01	0.10	0.09	0.09	0.005	—	—	—	—
10	0.62	0.95	1.35	0.03	0.36	0.39	0.39	0.03	0.11	0.14	0.13	0.01	—	—	—	—
12	0.75	1.15	1.59	0.08	0.46	0.47	0.45	0.03	0.12	0.15	0.17	0.01	0.06	0.12	0.30	0.01
14	0.80	1.24	1.80	0.13	0.59	0.55	0.52	0.04	0.11	0.15	0.17	0.01	0.08	0.21	0.47	0.02
16	0.77	1.25	1.70	0.09	0.59	0.62	0.57	0.06	0.10	0.14	0.15	0.01	0.16	0.58	1.47	0.08
18	0.68	1.14	1.65	0.10	0.57	0.60	0.56	0.08	0.09	0.13	0.14	0.02	0.46	1.53	2.97	0.33
20	0.65	1.12	1.63	0.05	0.55	0.56	0.55	0.03	0.09	0.13	0.13	0.01	0.81	2.26	3.95	0.16

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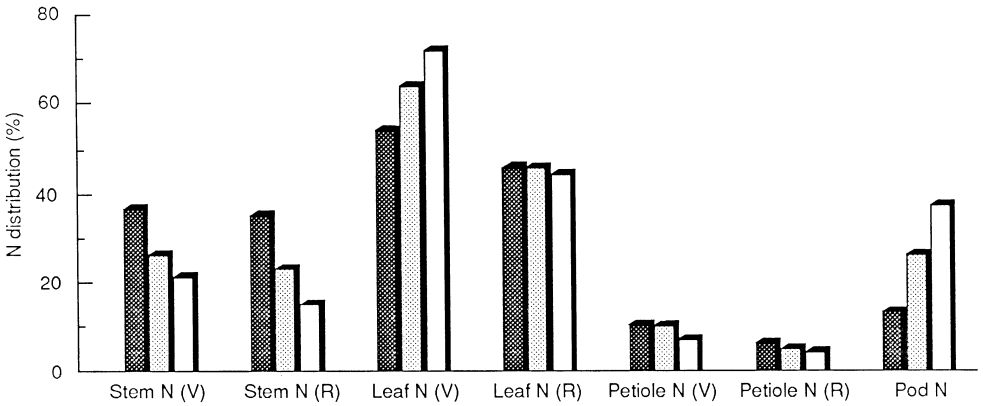


Fig. 2. Nitrogen (N) distribution at vegetative (V) and reproductive (R) growth stages of winged bean grown on support systems of varying heights (—■— unsupported control; ▨ support system height of 1 m; □ support system height of 2 m). S.e. stem N(V) = 0.88; s.e. stem N(R) = 0.78; s.e. leaf N(V) = 0.75; s.e. leaf N(R) = 0.78; s.e. petiole N(V) = 0.49; s.e. petiole N(R) = 0.29; s.e. pod N = 0.45.

this experiment, plants grown with a support system height of 2 m produced significantly higher leaf N during the vegetative phase, and pod N during the reproductive phase compared with unsupported plants. During the reproductive phase, there was a greater decline in leaf N , an intermediate decline in stem N and a lower decline in petiole N in plants with a support system height of 2 m. It appeared that remobilization of leaf N contributed more towards grain formation in plants with a support system height of 2 m. Plants grown with a support system height of 1 m, contributed a smaller portion of leaf, petiole and stem N towards grain formation compared with plants grown with a support system height of 2 m. The contributions of leaf, stem and petiole N towards grain N were intermediate in plants grown with a support system height of 1 m and lowest in unsupported plants.

Nodule dry weight and nitrogenase activity

Nodule DM per plant was significantly affected by the treatment variables. At 12 weeks after germination, nodulation increased rapidly for each treatment to a maximum of 1.48 g for unsupported plants and 2.08 and 2.67 g for support system heights of 1 and 2 m, respectively (Fig. 3). Plants grown with support systems produced maximum nodulation at the beginning of the pod formation stage while unsupported plants produced maximum nodulation at flowering time, then began to decline at full flower or at the initial pod formation stage.

Nitrogenase activity was significantly affected by the treatment variables. Nitrogenase activity increased gradually over time, reached a peak at week 10 and thereafter declined sharply in all the treatments (Fig. 4). The highest (70.05 μmol ethylene plant^{-1} h^{-1}) and lowest (35.64 μmol ethylene plant^{-1} h^{-1}) nitrogenase activity were obtained in plants grown on a support system with

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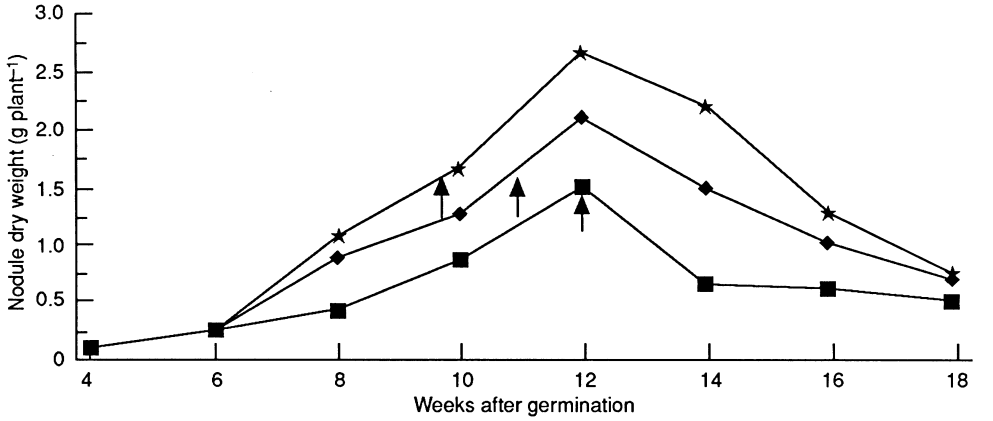


Fig. 3. Nodule mass accumulation of winged bean grown on support systems of varying heights (—■— unsupported; —◆— support system height of 1 m; —*— support system height of 2 m). Arrows indicate time of flowering; s.e. at 4 weeks after germination (WAG) = 0.002; s.e. at 6 WAG = 0.002; s.e. at 8 WAG = 0.005; s.e. at 10 WAG = 0.012; s.e. at 12 WAG = 0.007; s.e. at 14 WAG = 0.007; s.e. at 16 WAG = 0.009; s.e. at 18 WAG = 0.004.

a height of 2 m and in unsupported plants, respectively, whilst that of plants on a support system 1 m in height had moderate activity (59.50 μmol ethylene plant^{-1} h^{-1}). Nitrogenase activity increased with the onset of flowering, but declined during the pod formation stage in plants grown with a support system height of 2 m. However, unsupported plants showed peak nitrogenase activity prior to the flowering stage which might have been due to an earlier leaf senescence which started at 8 weeks.

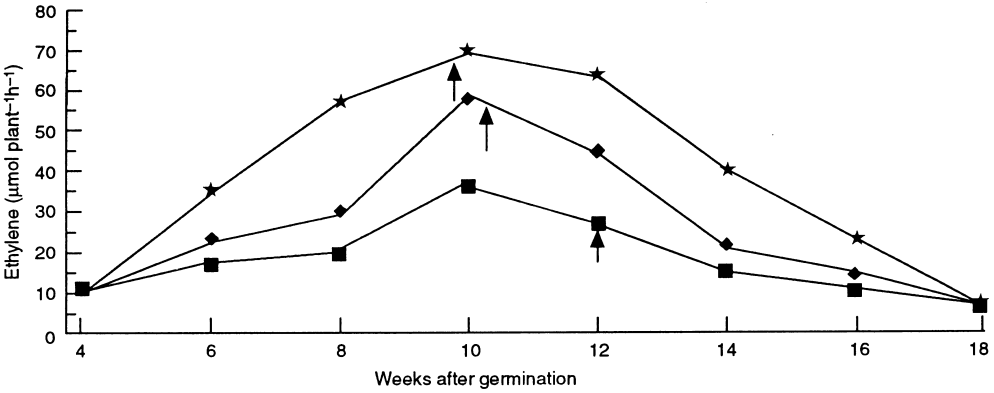


Fig. 4. Nitrogenase activity of nodulated root systems of winged bean grown on support systems of varying heights (—■— unsupported; —◆— support system height of 1 m; —*— support system height of 2 m). Arrows indicate time of flowering; s.e. at 4 weeks after germination (WAG) = 0.93; s.e. at 6 WAG = 1.30; s.e. at 8 WAG = 1.66; s.e. at 10 WAG = 2.59; s.e. at 12 WAG = 1.02; s.e. at 14 WAG = 0.41; s.e. at 16 WAG = 0.31; s.e at 18 WAG = 0.34.

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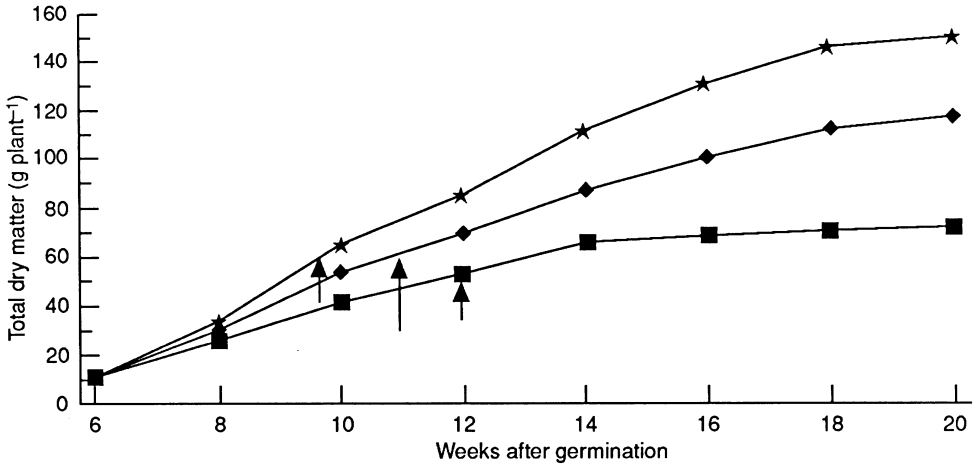


Fig. 5. Total dry matter accumulation of winged bean grown on support systems of varying heights (—■— unsupported; —◆— support system height of 1 m; —*— support system height of 2 m). Arrows indicate time of flowering; s.e. at 6 weeks after germination (WAG) = 0.04; s.e. at 8 WAG = 0.47; s.e. at 10 WAG = 0.66; s.e. at 12 WAG = 0.93; s.e. at 14 WAG = 1.96; s.e. at 16 WAG = 1.34; s.e. at 18 WAG = 1.31; s.e. at 20 WAG = 1.39.

Total dry matter accumulation and flowering

The DM accumulation showed significant variation among the different support systems. During early plant growth (6–8 weeks) the DM accumulation was unaffected by the type of support system. Beyond 8 weeks, support systems clearly had an additive effect on DM accumulation at all sampling dates up to maturity. DM accumulation increased rapidly up to 18 weeks in plants grown on support systems and was rapid up to 14 weeks in unsupported plants (Fig. 5). Plants grown on a 2-m support accumulated the largest DM followed by those on a 1-m support and thereafter the unsupported control plants. Flowering commenced between 10 and 12 weeks after emergence. Plants grown with support system heights of 1 and 2 m flowered about one to two weeks earlier than unsupported plants (Fig. 5).

Leaf senescence and light penetration

The most and least leaf senescence were observed in unsupported plants and those grown with a support system height of 2 m. Intermediate senescence was recorded with a support system height of 1 m (Table 2). Leaf senescence started much earlier (week 9) in unsupported plants but, in supported plants, leaf senescence was delayed until week 12–15 and the increased trend marked with ageing of plants in all treatments. Absorption of PAR was also affected significantly by the treatment variables being much greater for plants grown with a support system height of 2 m than for unsupported plants (Table 3).

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Table 2. Leaf senescence (g m^{-2}) of winged bean grown on support systems of varying heights

Support system height (m)	Weeks after germination					Total
	9	9–12	12–15	15–18	18–20	
0	16.00	70.88	115.00	136.50	147.33	485.76
1	2.75	18.13	43.25	64.13	112.63	240.89
2	0.75	5.00	16.00	28.25	100.75	150.75
s.e.	0.38	0.41	1.35	1.22	1.58	3.08

Table 3. Absorption of photosynthetically active radiation (μmol s^{-1} m^{-2}) by winged bean plants grown on support systems of varying heights

Support system height (m)	Weeks after germination						
	8	10	12	14	16	18	20
0	794	1033	1085	1075	925	895	825
1	805	1049	1095	1150	1045	970	965
2	818	1070	1150	1205	1075	1025	995
s.e.	2.17	1.48	2.51	3.73	2.37	3.60	3.09

Seed yield

Plants grown with a support system height of 2 m and unsupported plants produced the highest and the lowest seed yields respectively while those grown on a 1-m support system had moderately high seed production (Fig. 6). Greater seed yields were achieved as a result of more pods per plant, increased seed size and a

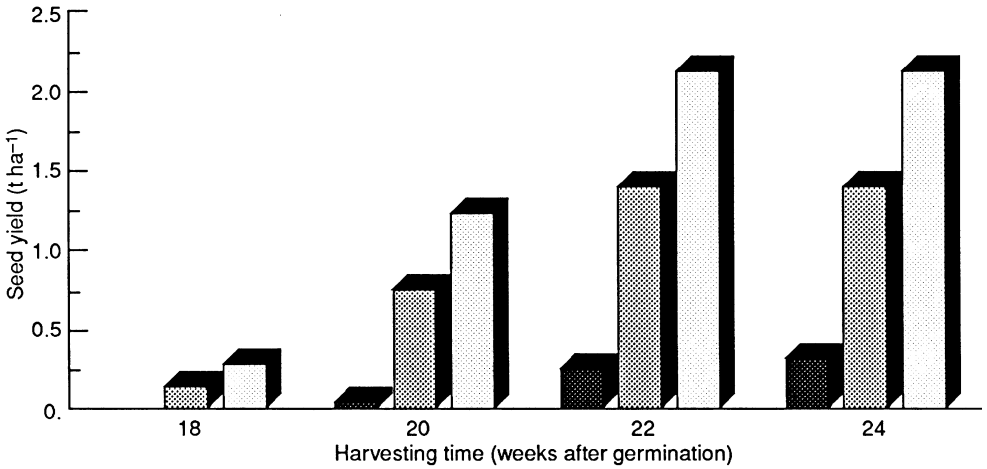


Fig. 6. Seed yield (cumulative) of winged bean grown on support systems of varying heights (■ unsupported; ▨ support system height of 1 m; ⁘ support system height of 2 m); s.e. at 18 weeks after germination (WAG) = 0.004; s.e. at 20 WAG = 0.03; s.e. at 22 WAG = 0.01; s.e. at 24 WAG = 0.05.

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Table 4. Yield and yield attributes of winged bean at 20 weeks after germination grown on support systems of varying heights

Support system height (m)	Number of pods per plant	Pod length (cm)	Number of seeds per pod	100-seed weight (g)
0	4.25	20.86	10.00	29.53
1.0	9.00	23.52	10.96	36.38
2.0	13.00	24.50	11.44	37.01
s.e.	0.46	1.44	0.06	0.31

Table 5. Regression analysis and correlation coefficient of different parameters

Regression equation	Correlation coefficient (r)
$Y_1 = -7.056 + 8.66\,x_1$	0.89**
$Y_2 = -5.503 + 29.25\,x_2$	0.83**
$Y_3 = -32.07 + 0.56\,x_3$	0.99**
$Y_4 = -1.833 + 0.053\,x_4$	0.92**

Y_1, Y_2 and Y_3 = seed yield; Y_4 = total N; x_1 = total N; x_2 = leaf N; x_3 and x_4 = total dry matter; ** significant at 0.01 level of probability.

larger number of seeds per pod (Table 4). There was a highly significant positive linear relationship between seed yield and total N content of the plant (Table 5). The slopes indicated that for every 1.0 g N content, 8.66 g seed yield was gained. Similarly, leaf N content per plant showed a significant and strong positive correlation with seed yield and total DM also showed a strong and positive correlation with total N accumulated per plant (Table 5).

DISCUSSION

Nitrogen content differed among plant components due to variable DM accumulation among the treatments. Plants grown with support system heights of 2 and 1 m had higher N accumulation rates than unsupported plants. At the vegetative stage 56–72% of total plant N was partitioned to the leaf, which confirms the results of Muchow *et al.* (1993), and the assumption in the soyabean model of Sinclair (1986). Concentrations of N in above-ground plant parts decreased consistently from the onset of flowering with a rapid decrease from the start of pod filling until maturity. Leaf N concentration decreased more than stem and petiole N concentrations. The decline in leaf N concentration presumably reflected the mobilization of N to developing pods, and the results suggested that leaf N played a significant role in grain development. Therefore, leaf N was the dominant source of mobilized N in winged bean. Peoples *et al.* (1983) found similar results in several grain legumes. Bushby and Lawn (1992) also reported

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similar results for mungbean genotypes, and showed that leaf N concentration decreased consistently from the start of pod fill until maturity. The net accumulation of N was in direct proportion to net biomass accumulation, and there were differences among support systems.

The proportion of grain N derived from mobilization varied between 13 and 37%. The mobilization was related to the amount of N available for redistribution rather than the ability of plants to continue N_2 fixation during pod filling. In the present study, the decline in leaf N in supported plants was associated with grain development and also with the senescence of leaves due to ageing. The main cause of the decline in leaf N in unsupported plants was the early senescence of leaves due to mutual shading.

Rates of N fixation in unsupported plants were less than those in supported plants. Unsupported plants showed a slow rate of accumulation of nodule mass compared with supported plants. Unsupported plants were less effective at nodulation due to low PAR absorption and the consequent limited supply of available photosynthate. Supported plants had well oriented leaves, which absorbed more PAR resulting in more assimilate production and N fixation. These results suggested that nodulation was directly related to N fixation. Earlier work showed that N fixation was largely regulated by the supply of recently manufactured assimilates to nodules, leaves being the major source of photosynthates (Wan Mohamad *et al.*, 1986). Kumarasinghe and Kumarasinghe (1981) also stated that nitrogenase activity was governed by nodule efficiency and rate of photosynthesis, increasing with onset of flowering, but declining with pod formation.

Total DM accumulation of the unsupported control plants was reduced because these plants were not able to utilize the vertical space, and plant competition was severe due to the limited horizontal space available. These plants suffered a greater shading effect. As a consequence early leaf senescence was higher limiting the source of photosynthates and resulting in insufficient photosynthate translocation. On the contrary, plants supported at heights of 1 and 2 m utilized more vertical space and enjoyed more light interception by the well oriented leaves. Thus, accumulation and remobilization of photosynthates were much higher during the grain formation period with satisfactory total DM accumulation. Consequently, plants supported at heights of 1 and 2 m had higher rates of nodule activity at the pre-flowering stage and maintained higher rates of N fixation during the initial pod filling.

High seed yield was a result of more pods per plant, increased seed size and a larger number of seeds per pod. Grain yield per unit area was a function of the yield of individual plants times plant density. Yield per plant was governed by the number of pods per plant, number of seeds per pod and seed size. In grain legumes, both yield and yield attributes are generally influenced significantly by plant density. Although the same plant density was maintained per unit area for the different support systems, unsupported plants did not utilize the same vertical space as supported plants. Winged bean is a broad leaved species which bears pods

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beneath the foliage. In an over-crowded plant canopy of unsupported plants it was unable to maximize pod production, and the lower yield was due to mutual shading.

Yield improvement in winged bean must be achieved through increases in total biomass and N accumulation. Indeterminate climbing winged bean grown on a support system can accumulate more biomass and N compared with unsupported plants. It is concluded that in addition to N fixation and accumulation, partitioning and remobilization of N plays an important role in the vegetative growth and seed yield of winged bean. Additional studies to examine N accumulation, partitioning and remobilization in winged bean grown with support systems could lead to a better understanding of the role of biological N fixation in increasing seed production of winged bean. The physiological constraints to enhanced performance of unsupported plants need to be evaluated further.

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