Expl Agric. (1989), volume 25, pp. 77–86
Printed in Great Britain

POPULATION, GROWTH AND WATER USE OF GROUNDNUT MAINTAINED ON STORED WATER. III. DRY MATTER, WATER USE AND LIGHT INTERCEPTION

By S. N. AZAM-ALI†, L. P. SIMMONDS†‡, R. C. NAGESWARA RAO§ *and* J. H. WILLIAMS§

†*Department of Physiology and Environmental Science, University of Nottingham School of Agriculture, Sutton Bonington, Loughborough, Leics. LE12 5RD, England and* §*International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru PO, Andhra Pradesh 502 324, India*

(*Accepted 1 May 1988*)

SUMMARY

At a field site in central India, four populations of groundnut (*Arachis hypogaea* L.) were grown on stored water to investigate how the production of shoot and root dry matter is related to transpired water and intercepted radiation. Throughout the season, total dry matter was closely related to transpiration (slope = 3.0 mg dry matter g^{-1} water) and the amount of radiation intercepted by foliage (slope = 0.74 g dry matter MJ^{-1} radiation intercepted). Accumulated transpiration increased linearly with intercepted radiation at 0.37 kg water MJ^{-1} in the sparser stands. In the densest spacing, the initial slope of the relation at 0.28 kg MJ^{-1} decreased later in the season because water deficits curtailed growth without a concomitant reduction in the interception of radiation.

S. N. Azam-Ali, L. P. Simmonds, R. C. Nageswara Rao y J. H. Williams: *Población, crecimiento y aprovechamiento de agua del cacahuete mantenido a base de agua almacenada. III. Materia seca, aprovechamiento del agua e intercepción de la luz.*

RESUMEN

En una localidad en la India central se cultivaron cuatro poblaciones de cacahuete (*Arachis hypogaea* L.) a base de agua almacenada, para investigar la relación entre la producción de materia seca de retoños y de raíces, y el agua transpirada y radiación interceptada. A lo largo de la estación, la materia seca total estaba estrechamente relacionada con la transpiración (pendiente = 3,0 mg de materia seca g^{-1} de agua) y la cantidad de radiación interceptada por las hojas (pendiente = 0,74 g de materia seca MJ^{-1} de radiación interceptada). La transpiración acumulada aumentó de forma lineal con la radiación interceptada a 0,37 kg de agua MJ^{-1} en las poblaciones menos densas. En el espaciamiento más denso, la pendiente inicial de la relación a 0,28 kg MJ^{-1} disminuyó más tarde en la estación porque la falta de agua redujo el crecimiento sin que haya una reducción concurrente de la intercepción de radiación.

INTRODUCTION

The availability of water to plant roots and the interception of solar energy by leaves are two major constraints on the growth of crops. There is much evidence, particularly early in the season, that crops accumulate dry matter at a

Submitted as Journal Article No. 537 by the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT).

‡ Present address: Department of Soil Science, University of Reading, London Road, Reading, RG1 5AQ, England.

rate which is proportional to the amount of radiation that their foliage intercepts (Loomis and Gerakhis, 1975; Biscoe and Gallagher, 1978). Similarly, many studies have demonstrated that crops accumulate dry matter at a rate which is approximately proportional to the water lost in transpiration over the same period (Stewart *et al.*, 1975; Fischer and Turner, 1978; Doyle and Fischer, 1979; Ong *et al.*, 1987). The correlation between dry matter production and radiation interception becomes less close when water is limiting, or when leaves senesce, but the link between dry matter and transpiration remains over a wide range of climates (De Wit, 1958; Azam-Ali *et al.*, 1984). When water is scarce, one possible method of using it to maximum effect is to alter the density of the plant stand (Bond *et al.*, 1964; Muchow *et al.*, 1982). In practice, this is one of the few options open to many farmers in dry regions. However, little is known about the complex interaction between plant population, water use and light interception.

The previous two papers in this series (Rao *et al.*, 1989; Simmonds and Williams, 1989) described the growth of roots and shoots and the evaporation from four populations of groundnut grown at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), near Hyderabad, India. This paper describes the seasonal accumulation of dry matter above and below ground in the same four groundnut populations in relation to the uptake of water and the interception of radiation by foliage.

MATERIALS AND METHODS

A full account of the management of the groundnut stands is given by Rao *et al.* (1989). Briefly, the groundnuts (cv. TMV-2) were grown at four spacings: 35 × 10, 70 × 10, 120 × 10 and 120 × 120 cm, referred to as spacings A, B, C and D, respectively. Irrigation was applied four times until 44 days after sowing (DAS), but less than 5 mm was applied thereafter. Measurements of shoot dry matter (five harvests) and root growth (three harvests) were made on a number of occasions between 47 and 97 DAS: details are given by Rao *et al.* (1989). Evaporation over 5-day intervals between 50 and 95 DAS was estimated from measurements of soil water content made using a neutron moisture meter. Simmonds and Williams (1989) describe the measurements of water use, and the techniques used to partition total evaporation between transpiration and direct evaporation from the soil surface.

Measurement of radiation interception

In the A, B and C spacings, the amount of radiation intercepted by foliage was measured using tube solarimeters mounted above and below the canopies. Two tubes were installed below the canopy in each of the replicate plots such that a total of 14, 7 and 4 rows were spanned in the A, B and C spacings, respectively. The combined output of each pair of solarimeters was scanned at 15 minute intervals on a data logger (Campbell Instruments) and the fractional interception, f, of each stand was calculated by comparing measurements made below the canopy with contemporary measurements made using a solarimeter mounted 1.5 m above ground level in the field. Daily totals of radiation intercepted (S_i) by each spacing were calculated by multiplying the fractional interception by the irradiance recorded on the above-canopy instrument. Interception in the D spacing could not be measured using tube solarimeters because the plants were so widely spaced.

Estimates of fractional ground cover in all spacings were derived from measurements of irradiance at the soil surface made using quantum sensors (Lamda Instruments) at 76, 84, 85 and 88 DAS. The technique was similar to that described by Sivakumar and Virmani (1984). Sensors were positioned on wooden tracks placed perpendicular to the direction of the rows, and each track spanned a single row width. Integrated counts over three minutes were obtained at 5 cm intervals along the track using integrators (Delta-T Devices). The fraction of incident radiation intercepted by foliage at each position across the inter-row space was determined by comparing these counts with the irradiance measured simultaneously by a similar instrument positioned above the canopy. Readings were made between 1000 and 1400 local time when the sun was near its zenith. The analysis of the quantum sensor records is discussed later, in the light of the experimental results.

RESULTS

Crop water use

The average transpiration rate between successive harvests, and the cumulative transpiration between 47 and 97 DAS, is presented in Table 1. In the D spacing, only 16 mm of water was transpired during the experimental period, and the resolution of the measurements of changes in profile water content was inadequate to determine transpiration over shorter periods. In the densest spacing (A) the transpiration rate reached 3 mm d^{-1} soon after the irrigation at 44 DAS, but declined sharply after about 60 DAS. The maximum rate of transpiration achieved at each spacing was approximately proportional to the

Table 1. *Average daily transpiration rate and cumulative transpiration estimated using a neutron probe, taking account of direct evaporation from the soil surface*

Days after sowing	A spacing	B spacing	C spacing	D spacing
	Average transpiration rate (mm d^{-1})			
47-60	2.66	2.00	1.31	–
61-75	2.41	1.97	1.12	–
76-90	2.14	1.84	1.15	–
91-97	1.31	1.80	1.28	–
	Cumulative transpiration (mm)			
47-97	113	96	60	

numbers of plants per unit land area. However, as plant density decreased, the stands were able to maintain rates of transpiration close to their maximum for progressively longer periods.

Radiation interception

Daily intercepted radiation (S_i, Fig. 1) increased from the beginning of the measurement period until about 60 DAS, after which the fractions of incident radiation intercepted by foliage remained fairly constant. The amount of radiation intercepted between sequential harvests was calculated by integrating the appropriate areas under the curves in Fig. 1. Similarly seasonal intercepted radiation was obtained by integrating the total area under each curve.

Typical records of the proportion of quanta intercepted by foliage at various positions across the space between adjacent rows are shown in Fig. 2 for each spacing. In each case there was a sharp change in interception corresponding to the lateral extension of foliage. Hence the plants in the D spacing could reasonably be regarded as flat discs which completely shaded the soil below; the lateral extension (r) of the disc was taken arbitrarily to be the distance from the stem at which 50% of incident radiation was intercepted. In the A, B and C spacings, the foliage of adjacent plants overlapped along the axis of each row, but not between rows: these canopies effectively comprised bands of dense foliage within which the interception of radiation by leaves was virtually complete. The lateral extension (i.e. the half-width) of the band was estimated as the distance from the row at which radiation interception was 50%. Estimates of the lateral extension (in cm) of the disc (D spacing) or bands (A, B and C spacings) of foliage are indicated by the arrows on the horizontal axes in Fig. 2. During the period of measurements, solar angle varied between 24° and 29°

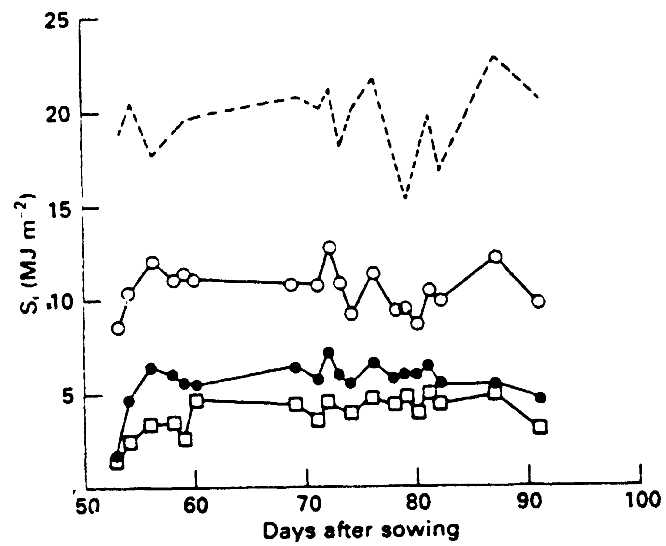

Fig. 1. Daily radiation interception (S_i) by the foliage of the A (○), B (●) and C (□) spacings between 53 and 91 DAS. The incident radiation on each day (MJ m^{-2}) is shown by the dashed line.

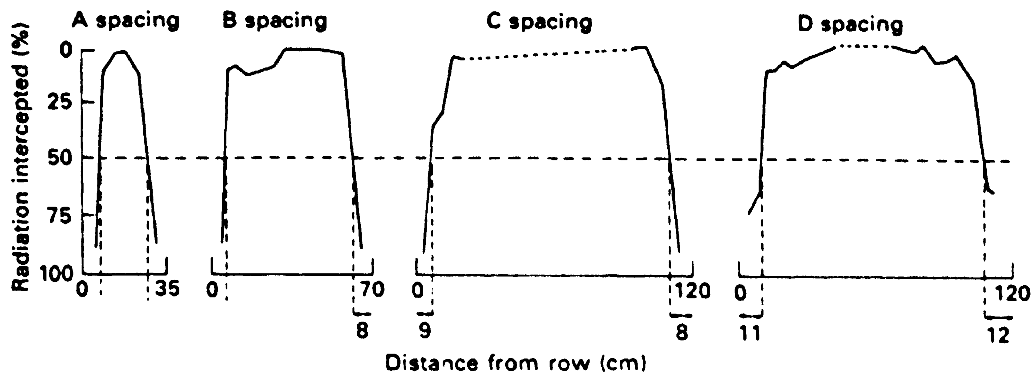

Fig. 2. Examples of the variation across the space between adjacent rows in the percentage of incident radiation intercepted by foliage. The horizontal axes represent distance (cm) from the row. The arrows indicate the distance (in cm) from the nearest row at which 50% of incident radiation penetrated to the soil surface: these distances were used as a measure of the lateral extension of plants in order to calculate fractional ground cover.

from the vertical. Consequently, the distance (r) from the row at which radiation interception was 50% differed slightly for the south and north sides of the rows. The average lateral extension was therefore calculated as the mean of the two corresponding values of r. Fractional ground cover (f′) in each of the spacings was calculated as the ratio of the band or disc areas to the total ground area.

Lateral extension in the D spacing was slightly greater than in the three row spacings. This was due in part to a greater number of branches per plant in the D spacing, as well as increased leaf expansion (Table 2). The area of ground covered per plant (A_p) was calculated for the row spacings as twice the lateral extension of the band of foliage multiplied by the intra-row spacing (10 cm). In the D spacing, the area of the disc provided an estimate of A_p. In the row spacings, A_p increased only slightly with increasing row width. By contrast, plants in the D spacing were able to cover 2.4 times as much ground as plants in the C spacing, because they were able to expand along both the intra- and inter-row axes without the leaves of adjacent plants overlapping.

There was close agreement between ground cover (f′) and the average daily fraction (f) of incident radiation intercepted by foliage in the three row spacings (Table 2). The solarimeter measurements showed little change in f between 55

Table 2. *Fractional interception of radiation measured using solarimeters (f), ground cover estimated using quantum sensors (f′), ground area covered per plant (A_p) and the mean number of branches per plant (all values are averages between 76 and 88 DAS)*

Spacing	f	f′	Ap (cm²)	No. branches plant⁻¹
A	0.48	0.50	150	5
B	0.25	0.26	160	5
C	0.18	0.14	170	5
D	–	0.04	415	9

and 90 DAS, indicating there was little further lateral extension of plants over this period.

Dry matter production and water use

Because plant growth is closely related to transpiration, the productivity of a crop can be expressed in terms of a dry matter:water ratio, q, (the ratio of dry matter produced to water transpired). The relation between shoot dry weight and transpiration during the experimental period is shown in Fig. 3a. The D spacing was excluded because of the difficulty in measuring transpiration over short periods. The average value of q based on the values for cumulative transpiration and shoot dry weight at final harvest was 1.57 mg g^{-1}. For most of the season the A spacing produced consistently more *shoot* dry matter per unit of water transpired than the other spacings. But when roots were included in the dry matter component (Fig. 3b), the relation was linear throughout the season, and there were no apparent differences in slope between spacings. The bulked value of q calculated on the basis of the total weight of roots and shoots in the A, B and C spacings was 3.00 mg g^{-1}; the D spacing was excluded because roots were not measured.

Dry matter production and radiation interception

The relation between the accumulated dry weight of shoots between 47 and 90 DAS and the amount of radiation intercepted over the same period is shown in Fig. 4a. The slope of the line is the dry matter:light quotient, e, which in this case was 0.39 g MJ^{-1}. The relation between *total* dry matter and accumula-

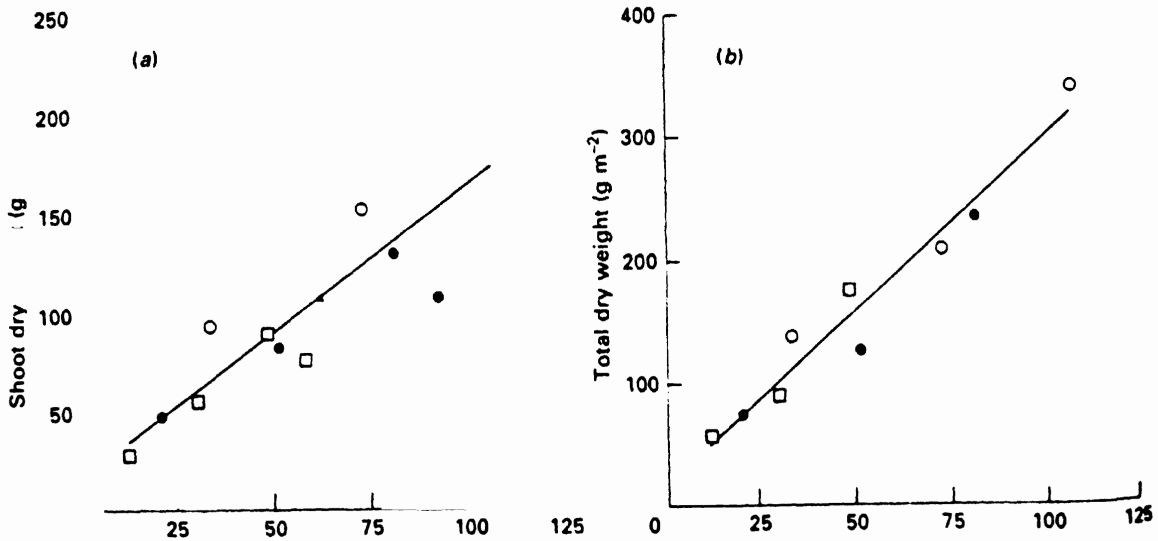

Fig. 3. (a) The relation between shoot dry weight and transpiration; slope = 1.57 (±0.21) mg g^{-1} (r^2 = 0.83). (b) The relation between total dry weight and transpiration; slope = 3.00 (±0.27) mg g^{-1} (r^2 = 0.94). (o, A spacing; •, B spacing; □, C spacing.)

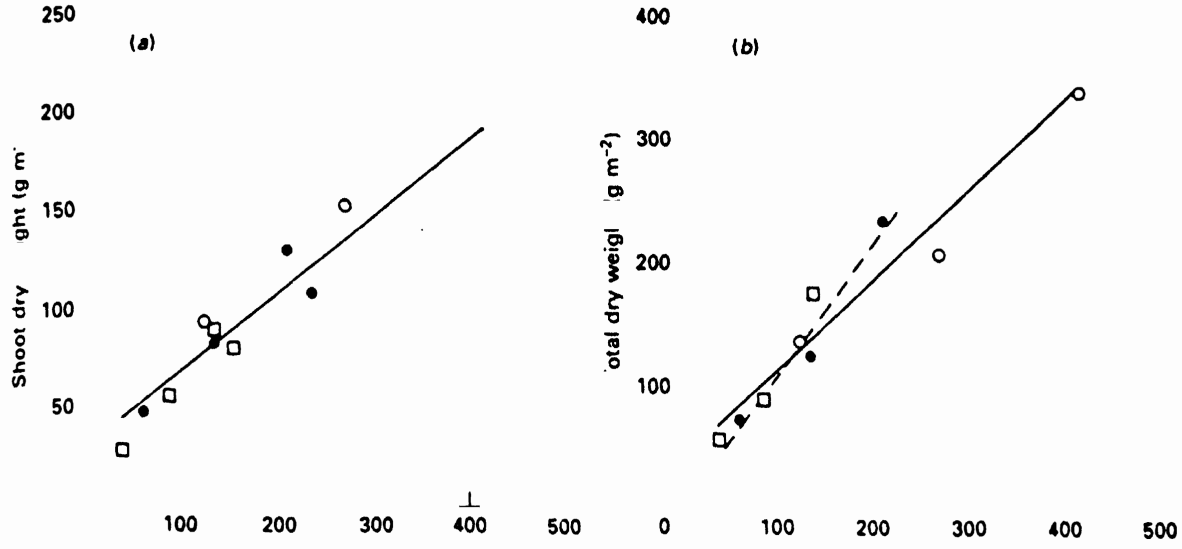

Fig. 4. (a) The relation between shoot dry weight and cumulative intercepted radiation; slope = 0.39 (±0.05) g MJ^{-1} (r^2 = 0.87). (b) The relation between total dry weight and cumulative intercepted radiation; slope for all points (solid line) = 0.74 (±0.07) g MJ^{-1} (r^2 = 0.87); slope for B and C spacings (dashed line) = 1.09 (±0.14) g MJ^{-1} (r^2 = 0.92). (o, A spacing; •, B spacing; □, C spacing.)

ted intercepted radiation is shown in Fig. 4b. The slope of the solid line (the regression line based on all the points) was 0.74 g MJ^{-1}. However, the relation for the A spacing appeared to be somewhat different from that for the B and C spacings. The dashed line shows the regression for the B and C spacings only: the slope of this line was 1.09 g MJ^{-1}, and the intercept did not differ significantly from zero. The final two harvests of the A spacing (75 and 90 DAS) fell below the dashed line. This departure from linearity after 60 DAS suggests that the increment in dry matter per unit of radiation intercepted was less than that observed earlier in the season or in the sparser stands.

The anomalous behaviour of the A spacing as the season progressed probably occurred because transpiration (and therefore growth) became restricted by the shortage of water, whereas there was no concomitant reduction in f. A comparison of cumulative transpiration with accumulated radiation interception is shown in Fig. 5, and illustrates the seasonal influence of drought in the A spacing. For the B and C spacings, transpiration increased linearly with intercepted radiation at 0.37 kg MJ^{-1}; transpiration (and therefore the production of dry matter) was able to keep pace with radiation interception, suggesting that the supply of water did not become a severe limitation. The response in the A spacing was different. First, the initial gradient of the relation was only 0.28 kg MJ^{-1}; even early in the season the uptake of water by roots appeared to be less able to sustain the evaporative demand on the foliage. Second, the slope of the relation decreased as the season progressed, suggesting that transpiration became increasingly restricted by the supply of water as the profile dried.

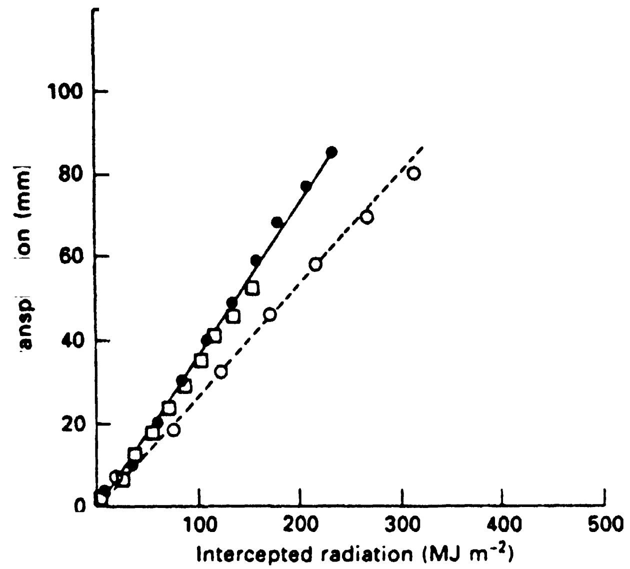

Fig. 5. The relation between cumulative transpiration and cumulative radiation interception; slope for B and C spacings = 0.37 (±0.01) kg MJ^{-1} (r^2 = 0.98); initial slope for A spacing (fitted through first five points) = 0.28 (±0.01) kg MJ^{-1} (r^2 = 0.98). (○, A spacing; ●, B spacing; □, C spacing.)

DISCUSSION

This study provides further experimental evidence that the production of dry matter is a predictable function of transpired water and, when water is not limiting, of radiation interception by foliage. The analysis is unusual for two reasons. First, it includes the contribution of roots to the total dry weight; their omission may account for the poor correlations observed by some workers (e.g. Teare *et al.*, 1973, for sorghum). Second, total evaporation was partitioned into plant and soil components. When roots were included, dry matter and transpiration were well correlated over a range of plant populations, despite there being large differences between the spacings in the proportion of dry matter allocated to roots (Rao *et al.*, 1989).

Evidence was presented to show that the simple linear relation between dry matter production and radiation interception breaks down when water is in short supply. The value of e for the B and C spacings remained constant during the season, and was close to the value of 1.25 g MJ^{-1} calculated on the basis of shoot weight by Marshall and Willey (1983) for groundnut grown at the same site in the rainy season. In the A spacing, values of e were smaller, and e decreased as the season progressed. Simmonds and Williams (1989) showed that much larger soil water deficits were incurred in the A spacing than in the sparser stands, suggesting that stomatal closure in response to water deficit may have been responsible for the small values of e recorded in the dense stand. The

influence of plant population on the response of canopy conductance to soil drying is discussed by Simmonds and Azam-Ali (1989).

For the range of planting densities described in this account, groundnut was unable to compensate significantly for small populations by the increased productivity of individual plants. This is in contrast with observations on pearl millet (Azam-Ali *et al.*, 1984) in which the smallest population was able to achieve the highest yield at final harvest largely through the contribution of viable tillers. In the case of groundnuts, Table 2 shows that in the D spacing individual plants produced, on average, nine branches compared with five in all other populations. However, although widely spaced plants were able to intercept more than twice as much light per plant, this degree of compensation did not substantially increase productivity assessed per unit area of ground. The groundnut cultivar used in this study had an erect bunch habit: a runner type, in which stems spread laterally along the ground, might have been better suited to produce compensatory growth at low planting density.

Acknowledgements. This work was funded by the Overseas Development Administration of the UK and by ICRISAT. We are grateful to staff of the Groundnut Physiology Section at ICRISAT for their considerable help and to J. L. Monteith for comments and suggestions.

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JA 539

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Expl Agric. (1989), volume 25, pp. 51–61
Printed in Great Britain

POPULATION, GROWTH AND WATER USE OF GROUNDNUT MAINTAINED ON STORED WATER. I. ROOT AND SHOOT GROWTH

By R. C. NAGESWARA RAO†, L. P. SIMMONDS‡ §, S. N. AZAM-ALI‡ *and* J. H. WILLIAMS†

†*International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru PO, Andhra Pradesh 502 324, India and*
‡*Department of Physiology and Environmental Science, University of Nottingham School of Agriculture, Sutton Bonington, Loughborough, Leics. LE12 5RD, England*

(Accepted 1 May 1988)

SUMMARY

The growth of roots and shoots was measured in stands of groundnut grown at a number of populations on stored water in central India. Total weight and length of roots per unit land area increased with population density, but the proportional increases were much less than for shoot weight. Consequently the root:total weight ratio increased from 0.3 in the densest stand to almost 0.5 in the widely spaced crop. The denser stands produced a greater proportion of their roots at depth. In wide rows there was little change in rooting density across the inter-row space.

Total dry matter per unit land area increased with population, although the weight per plant was less in denser stands. Although the crops were harvested prematurely, pod yield per unit land area, unlike total dry matter, was no greater in dense stands than in more widely spaced crops. The greatest number of pods per unit land area was recorded at an intermediate population density.

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RESUMEN

Se midió el crecimiento de raíces y retoños en masas de cacahuete cultivadas en la India central bajo distintos régimenes de población, a base de agua almacenada. El peso total y el largo de las raíces por unidad de superficie aumentaron al incrementar la densidad de población, pero los aumentos proporcionales fueron mucho menores que para el peso de los retoños. Como resultado, la relación raíz:peso total aumentó de 0,3 en la masa más densa hasta casi 0,5 en el cultivo de hileras bien separadas. Las masas de mayor densidad rindieron una mayor proporción de raíces profundas. En las hileras bien separadas, hubo poco cambio en la densidad de las raíces que cruzaban el espacio entre las hileras.

La materia seca total por unidad de superficie aumentó al incrementar la población, aunque el peso por planta fue menor en masas de mayor densidad. Aunque los cultivos se cosecharon temprano, el rendimiento de vainas por unidad de superficie, a diferencia de la materia seca, no presentó variaciones mayores en las masas densas que en los cultivos de mayor espaciamiento. La mayor cantidad de vainas por unidad de superficie se registró a una densidad de población intermedia.

Submitted as Journal Article No. 538 by the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT).

§ Present address: Department of Soil Science, University of Reading, London Road, Reading RG1 5AQ, England.