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

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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.

R. C. Nageswara Rao, L. P. Simmonds, S. N. Azam-Ali y J. H. Williams: *Población, crecimiento y aprovechamiento de agua del cacahuete mantenido a base de agua almacenada. I. Crecimiento de raíces y retoños.*

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.

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INTRODUCTION

For crops experiencing no shortage of water and nutrients the responses of growth and yield to population density are well known, and can usually be interpreted in terms of competition between plants for light (Shinozaki and Kira, 1956). However, the relation between crop productivity and planting geometry is more complex when growth is restricted by the supply of water. Increasing the plant population may increase the availability of water by encouraging a more extensive root system (Azam-Ali *et al.*, 1984) and by reducing wasteful evaporation from the soil surface. Within-row advection may also be reduced (Hanks *et al.*, 1971) thereby reducing the saturation deficit of the air with respect to leaf temperature and consequently increasing the amount of dry matter produced per unit of water transpired (Sinclair *et al.*, 1984; Ong *et al.*, 1987). On the other hand a dense stand will deplete soil water more rapidly, conserving little for use during reproductive growth, which may adversely affect grain yield (Passioura, 1972; Alessi and Power, 1982). The complexity of the system is evident from the variety of relations between yield and plant spacing reported for rain-fed crops grown in Botswana (Jones, 1986).

The objective of the experiment described in this series of papers was to examine the influence of plant population on the productivity of groundnut stands grown on stored water. The experiment was conducted during the post-rainy season at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Hyderabad, India on a profile containing about 125 mm of plant-extractable water. Potential evaporation for the period of growth on stored water was over 300 mm.

This paper describes the growth of roots and shoots and discusses the distribution of roots and the partitioning of dry matter above and below ground. The limited information available suggests that the relation between planting density and root:shoot ratio is complex. Work in Botswana by the Dryland Farming Research Scheme (DLFRS, 1981) showed that widening the row spacing from 37 to 150 cm reduced radiation interception by a factor of three, but had relatively little impact on the distribution of roots. Conversely, Kirby and Rackham (1971) reported that the root:shoot ratio of droughted barley increased with population.

Subsequent papers in this series describe evaporation from plant and soil surfaces (Simmonds and Williams, 1989) and examine dry matter production in relation to light interception and water use (Azam-Ali *et al.*, 1989). A final paper discusses the implications of differences in the allocation of dry matter between roots and shoots for the water relations of the stands (Simmonds and Azam-Ali, 1989).

MATERIALS AND METHODS

Site, crops and season

Stands of groundnut were sown on 3 December 1981, and measurements were made between 16 January and the final harvest on 10 March 1982 (44 to

97 days after sowing, DAS). The cultivar used, TMV2, is an erect bunch type of medium duration commonly grown by Indian farmers. The soil was an alfisol with a texture ranging from loamy sand near the surface to clay lower in the profile. There was a gravel layer from about 1.8 m deep at the northern end of the site to about 1 m at the southern end. Before sowing, di-ammonium phosphate fertilizer (18% N, 46% P_2O_5) was applied at a rate equivalent to 100 kg ha^{-1}.

Seed was sown by hand in four arrangements. There were three row spacings (35, 70 and 120 cm) with seeds placed 10 cm apart within the rows, and one square arrangement with seeds sown at 120 X 120 cm. These arrangements are hereafter referred to as A, B, C and D, respectively. In all spacings the established population was close to 80% of the seeds sown. The field was divided into three replicate blocks of 30 X 10 m. Plots containing the four spacings were randomized within each block, and the dimensions of individual plots depended on plant spacing.

Irrigation was applied through perforated pipes at 2, 11, 27 and 44 DAS to ensure uniform crop establishment. After 44 DAS plants grew on water stored in the profile, except for a 5 mm irrigation at 72 DAS to encourage penetration of pegs through the soil surface. No measurable rain fell during the experiment.

Shoot growth

Development and growth of shoots were measured on five occasions between 47 and 97 DAS. At each harvest, samples of two adjacent 1 m rows were removed at random from each plot, except in the D spacing where three plants were harvested at random. Plants were pulled up after soil around the pods had been loosened, and the pods removed. The numbers of pods were recorded. Dry weights of shoots and pods were measured after oven-drying for 48 h at 80°C.

The growth and distribution of roots

Roots were sampled in the A, B and C spacings only at 60, 76 and 90 DAS. A trench 1 m deep was dug in each replicate of the three row spacings: the trenches were perpendicular to the rows, and spanned the distance between adjacent rows. A cubic coring tool (10 X 10 X 10 cm) was inserted horizontally into the face of the trench, and the roots washed from the soil in the sample using a 2 mm sieve. Samples were taken every 10 cm to a depth of 1 m, and at either 10 cm intervals (A and B) or 15 cm intervals (C spacing) across the inter-row space. The trench face was advanced at least 50 cm along the row before each sampling to avoid edge effects. Unfortunately, the remains of old building foundations were discovered at 76 DAS in the pit beneath one replicate of the A spacing which was then abandoned.

The weight of root was determined after drying cleaned samples in an oven for 24 h at 70°C. The lengths of about 150 randomly selected samples were measured before drying using the automated line intersection method of Rowse and Phillips (1974). The lengths of root in the remaining samples were estimated using the relation obtained between length and weight per unit soil volume.

RESULTS

The distribution of roots

The mean weight of root per unit soil volume ($\bar{W}_v$) for each sampling depth, averaging results obtained at all positions across the inter-row space, is shown in Fig. 1. At all dates and in all spacings W_v declined with depth. The A spacing produced more root than the C spacing throughout the profile, the B spacing generally being intermediate. The spacings also differed in the proportion of the total root weight that was produced at depth. For example, by 76 DAS more than 14% of the root weight in the A spacing was below 50 cm depth, whereas the corresponding figure for the C spacing never exceeded 6%. In all spacings the root system continued to grow throughout the season: between 60 and 90 DAS $\bar{W}_v$ almost doubled throughout the profile in each spacing.

The relation between the length and weight of root per unit soil volume is shown in Fig. 2. A third order polynomial relating the length of root per unit soil volume (l_v) to the weight per unit volume (W_v) was fitted by regression. Using untransformed data, there was a tendency for the residuals in the regression model to increase with W_v. Visual examination of plots of residuals against fitted values suggested that this tendency was reduced substantially by taking the square-root transformation of the data before executing the regression. The regression equation and the fitted line are shown in Fig. 2. The specific root length decreased from a maximum of approximately 110 m g^{-1} when W_v was small to less than 40 m g^{-1} when W_v exceeded 400 g m^{-3}. The larger rooting densities occurred near the soil surface where segments of relatively thick tap

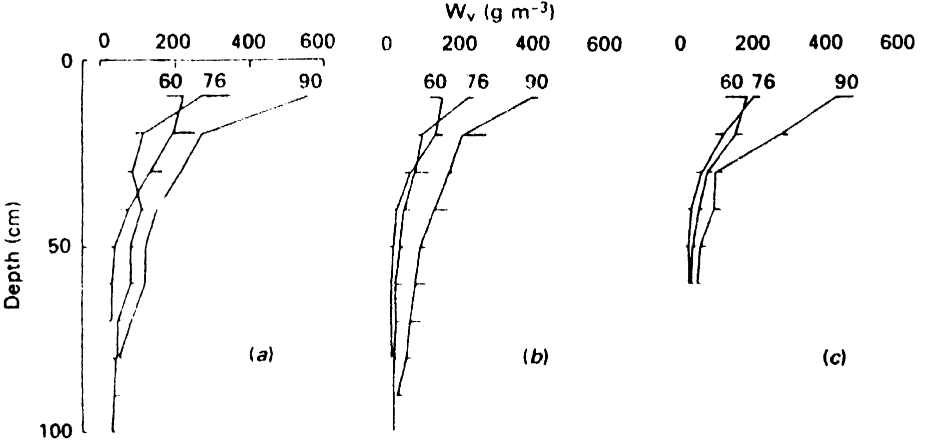

Fig. 1. Mean weight of root per unit soil volume ($\bar{W}_v$) at each depth in the A, B and C spacings (Figs a, b and c, respectively). The numbers on the curves denote days after sowing. Bars indicate the standard errors of the mean values for the replicate plots.

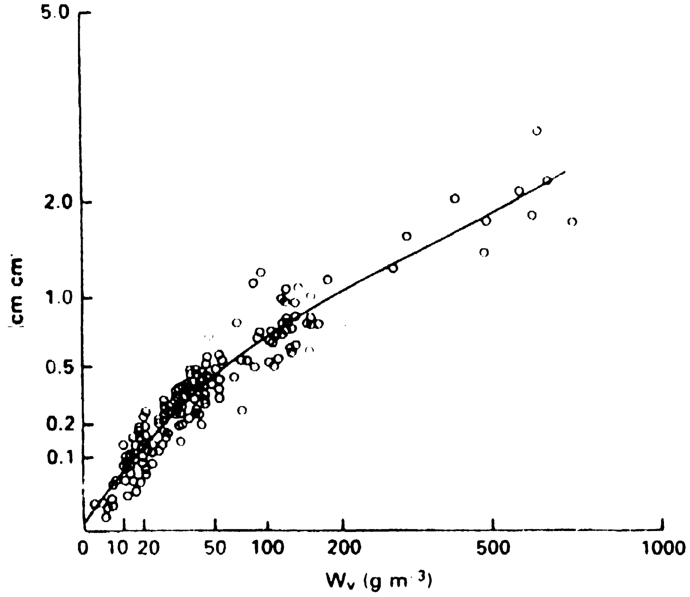

Fig. 2. **Relation** between the length (l_v) and weight (W_v) of root per unit soil volume. The equation of the fitted line is:

$$l_v^{0.5} = 0.0305 + 0.111\ W_v^{0.5} - 0.00386\ W_v + 0.0000683\ W_v^{1.5} \quad (r^2 = 0.91)$$

root or primary lateral roots were responsible for the small specific root lengths.

For each spacing at each sampling date, the variation of root length density (l_v) with both depth (z) and lateral distance from the row (d) was examined by fitting a series of polynomial regression models, the most complex of which included terms to the third order in z, the second order in d, and the first and second order interactions of z and d. The stepwise regression technique implemented in GENSTAT via the MINIMIZE statement was used to select the 'best' model on the basis of minimizing the residual mean square. The dependent variable in the model was the square root of l_v: the square-root transformation apparently reduced the tendency for the residuals in the fitted model to increase with fitted values of the dependent variable. The values of l_v used were pooled from all three replicate plots. The estimates of the parameters in the 'best' models for each combination of spacing and sampling date are shown in Appendix 1. All of the parameters were significant at $P<0.05$. As an illustration, Fig. 3 (which was derived from the regression model) shows the spatial arrangement of root length density for the C spacing at 76 DAS.

In the A spacing at all dates, and in the B spacing until 76 DAS, there was no significant change in root length density across the inter-row space (Appendix 1). In the C spacing there was a significant decrease in l_v with increasing distance from the row. In the wide row spacings there was also a significant depth/distance from row interaction which had the effect of reducing the lateral variation in l_v with increasing depth.

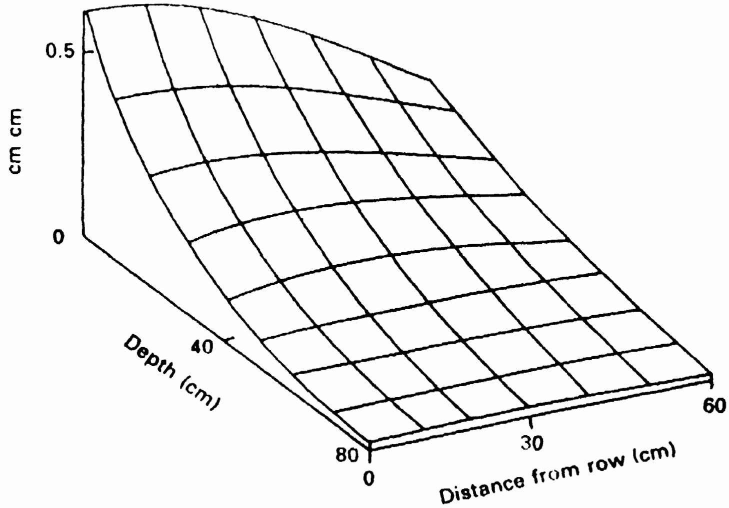

Fig. 3. Spatial distribution of the root length per unit soil volume (l_V) in the C spacing at 76 days after sowing. This plot was derived from the multiple regression of l_V on terms involving depth and distance from the row (Appendix 1).

Root, shoot and pod growth

The overall size of the root system in each spacing at each sampling date is shown in Table 1, expressed in terms of both the total weight (W_a) and length (l_a) of roots beneath unit land area. At all dates W_a and l_a in the densest stand were between about 30 and 45% larger than in the C spacing, the B spacing generally being intermediate.

The weight of shoots (including pods) per unit land area was more strongly influenced by plant spacing than the weight of roots (Table 1). Before 60 DAS the shoot weights per plant in the A, B and C spacings were similar, so the weights per unit land area were approximately proportional to population. As the season progressed, the shoot weights per plant in the denser stands were less than in the wider spacings, so the differences between treatments in the weights per unit land area became proportionally smaller. In the D spacing the shoot weights per plant were between 2.5 and 6 times larger than in the row crops; however, the weights per unit land area were small because plants were so widely spaced. The greater sensitivity of shoot weight per unit land area to plant spacing compared with that of W_a caused the ratio of root to total weight to increase from a seasonal average of 0.30 in the A spacing to 0.46 in the C spacing (Table 1).

The influence of population on total dry matter production and yield is summarized in Fig. 4, which is based on the values obtained at the latest date when roots were measured (90 DAS). Although roots were not sampled in the D spacing, the root:total weight ratio was assumed to be the same as in the C spacing. The total dry matter produced per unit land area increased with planting density. The relation was curvilinear since the amount of dry matter

Table 1. *The mean weights of shoots (including pods) and the total weight and length of the root systems per unit land area*

Spacing	Days after sowing	Shoot plus pod weight (g m^{-2})	Root weight W_a (g m^{-2})	Root length l_a (km m^{-2})	Root:total weight ratio
A	47	49	–	–	–
A	60	134	58	3.8	0.30
A	76	206	68	4.7	0.24
A	90	267	143	6.6	0.36
A	97	230	–	–	–
B	47	30	–	–	–
B	60	68	41	2.7	0.38
B	76	113	58	3.7	0.33
B	90	155	120	5.6	0.43
B	97	147	–	–	–
C	47	16	–	–	–
C	60	44	44	2.8	0.49
C	76	71	49	3.2	0.41
C	90	105	101	4.6	0.49
C	97	100	–	–	–
D	47	2	–	–	–
D	60	10	–	–	–
D	76	18	–	–	–
D	90	38	–	–	–
D	97	37	–	–	–
SE of difference of means		8.2	16.7	0.72	0.047
Analysis of variance†					
Main effects					
Spacing		***	**	**	***
Date		***	***	***	**
Interactions					
Spacing X date		***	ns	ns	ns

†*** and ** denote significance at the 1 and 2% levels, respectively, whereas 'ns' denotes lack of significance at the 5% level.

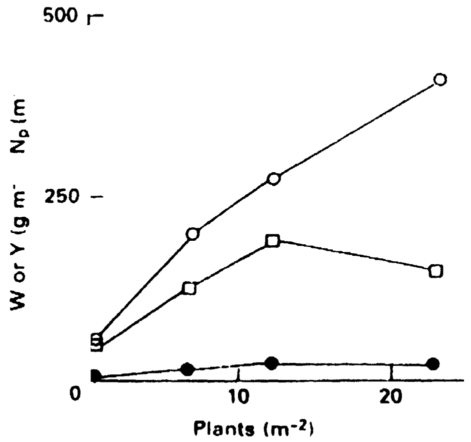

Fig. 4. The influence of population on total dry matter (W, o), pod yield (Y, •) and pod number (N_p, o) per unit land area at 90 days after sowing.

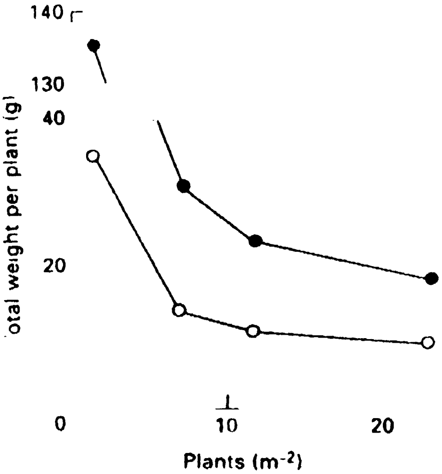

Fig. 5. The relation between total weight per plant and population at 60 (o) and 90 (•) days after sowing. It was assumed that the root:total weight ratio in the D spacing was the same as in the C spacing.

produced per plant decreased as plants were more closely spaced, but there was no indication that dry matter production had reached a maximum in the densest stand. The influence of population on the dry matter produced per plant became more marked as the season progressed (Fig. 5), suggesting that competition between plants for limiting resources (presumably water) became more intense.

Pod weights were small because the crops were harvested about 30 days before maturity. Even so, there was evidence that yield in the densest stand was no greater than when plants were more widely spaced (Fig. 4). The number of pods per unit land area (which may be an index of potential pod yield) was less in the A spacing than in the B spacing (Fig. 4).

DISCUSSION

The curvilinear response of crop dry matter production to population density is consistent with the hypothesis that there is an upper limit to productivity determined by the resources available, and that this limit is approached when crops achieve complete ground cover (e.g. Shinozaki and Kira, 1956). Important features of the three row crops were that the within-row spacing was the same (10 cm) and the foliage of adjacent rows never intermingled, even in the narrowest row spacing. Because the degree of inter-plant competition for light was similar in the A, B and C spacings, similar amounts of dry matter were produced per plant early in the season when water was plentiful. By contrast, plants in the D spacing did not compete for light and produced substantially more dry matter per plant throughout the season. As the soil profile dried, the amount of dry matter produced per plant in the A and B spacings fell below that in the C spacing, presumably as a result of shortage of water in the denser stands. Further discussion and supporting evidence appear in subsequent papers which describe water use (Simmonds and Williams, 1989) and the interception of radiation by foliage (Azam-Ali *et al.*, 1989).

Although the information on pod growth was limited because of the premature final harvest, the results are consistent with other studies of crops grown on limited water (ICRISAT, 1982; Azam-Ali *et al.*, 1984; Jones, 1986) which demonstrated that the best yields are achieved at intermediate populations in which plants have access to more water during reproductive growth. Pod growth in relation to the timing of water use is discussed by Simmonds and Williams (1989).

When water is in short supply, the response of crop dry matter production to planting density depends partly on the influence of plant spacing on the distribution of roots, and hence its influence on the access plants have to water. In all spacings, rooting was sparse below 30 cm depth, as l_v never exceeded 0.15 cm cm^{-3} even in the densest stand. A number of studies (e.g. Cooper *et al.*, 1986) have suggested that for droughted annual crops a root density of at least 1 cm cm^{-3} is required to remove the 'potentially extractable' water by crop maturity; a similar conclusion was reached in the theoretical analysis of van Noordwijk (1983). Hence the greater root proliferation at depth in the denser stands increased the water available to the crop during the growing season (see Simmonds and Williams, 1989). This may partly explain why dry matter production did not reach a maximum as population increased. A similar stimulation of root production at depth as planting density increased has been found in other studies (Kirby and Rackham, 1971; Azam-Ali *et al.*, 1984).

Although the total length and weight of the root system decreased with wider row spacings, roots in the C spacing still ramified the whole of the inter-row space to at least 80 cm depth. Like DLFRS (1982) and Teare *et al.* (1973), we found little change in rooting density across the space between wide rows. The ability of roots to exploit the space between wide rows was in marked contrast to that of the leaves, which had little capacity to compensate for a small population because of the bunch habit of the cultivar. The remarkable capacity of widely spaced plants to explore the soil between rows was costly in terms of the investment of dry matter required. The root:total weight ratios of 0.3 to 0.5 approach the maximum reported for annual crops (excluding root crops). Values in this range have been observed during the early stem-elongation stage for cereals grown in hot, dry climates (Myers, 1980, for sorghum; Gregory *et al.*, 1984, for barley; Azam-Ali *et al.*, 1984, for millet). In our crops, a large proportion of the root weight was associated with thick lateral roots, so the average specific root length was only about 60 m g^{-1}, compared with typical values of around 200 m g^{-1} for cereals grown in a cool temperate region (McGowan *et al.*, 1984) and 90 m g^{-1} for barley grown in the hotter and drier environment of northern Syria (Gregory *et al.*, 1984). Compared with these cereals, groundnut has to invest considerably more dry matter to produce a given length of root, which is perhaps consistent with the large root:total weight ratios observed.

The total lengths of the root systems in our crops (4.6 to 6.6 km m^{-2} at 90 DAS) are within the range reported elsewhere for groundnut. The value of l_a for unirrigated crops grown on deep sandy soil in Florida can exceed 9 km m^{-2} (Robertson *et al.*, 1980), whereas a corresponding value for a rainy season crop grown at the same site as our experiment was only about 3 km m^{-2} (Gregory and Reddy, 1982). There are conflicting reports about the seasonal pattern of root growth in groundnut. In the rainy season crop studied by Gregory and Reddy, l_a did not increase after 55 DAS (i.e. during pod filling), whereas the root system of the droughted crop described by Robertson *et al.*, like ours, approximately doubled in length between 65 and 95 DAS. It appears that groundnut is capable of a large investment in root growth throughout the season, although substantial root growth during pod filling seems to be maintained only when water is in short supply.

The large influence of row spacing on the relative sizes of 'water-capturing' and 'water-utilizing' structures had important implications for the water relations of the stands. The impact of differing root:shoot ratios on the responses of stomata and transpiration to soil drying is discussed by Simmonds and Azam-Ali (1989).

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Appendix 1. *Regression coefficients describing the relation between the square root of root length per unit soil volume ($l_v^{0.5}$) and depth (z) and distance from the row (d)*†

Spacing	A	A	B	B	B	C	C	C
Days after sowing	60	76	60	76	90	60	76	90
Variance accounted for (%)	95	87	85	92	88	96	98	97
Parameters								
Constant	35.81	32.22	32.28	42.23	47.04	41.37	37.61	53.35
z ($\times 10^{-1}$)	−3.999	−2.336	−4.482	−3.540	−3.539	−10.05	−5.161	−11.15
z^2 ($\times 10^{-3}$)				9.267		14.35		17.71
z^3 ($\times 10^{-5}$)			1.497	−2.960		−8.983	1.852	−12.94
d ($\times 10^{-1}$)				−5.622	−6.005	−1.695		−5.479
d^2 ($\times 10^{-3}$)					5.963		−3.874	8.327
zd ($\times 10^{-2}$)				1.995				
zd^2 ($\times 10^{-5}$)					11.77	6.544	11.60	−10.21
z^2d ($\times 10^{-5}$)				−16.44				7.231
z^2d^2 ($\times 10^{-7}$)						−6.595	−8.282	

† Units: l_v (cm cm^{-3}); z and d (cm).
All coefficients were significant at the $P < 0.05$ level.
Only one replicate of the A spacing was sampled at 90 days after sowing, and was excluded from this analysis.