

Expl Agric. (1998), volume 34, pp. 99–112

Printed in Great Britain

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GROUNDNUT GROWTH AND DEVELOPMENT IN CONTRASTING ENVIRONMENTS 1. GROWTH AND PLANT DENSITY RESPONSES

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(Accepted 24 July 1997)

SUMMARY

Data from studies of growth and development, and response to plant density in common groundnut (*Arachis hypogaea*) cultivars were examined from published studies. Data were available from the humid tropics of Indonesia, the semi-arid tropics of north-west Australia and the humid coastal and inland elevated areas of north-east Australia. Temperature and irradiance played a major role in determining crop duration, individual plant size and partitioning of dry matter to pods across environments, and these plant characteristics provided the major determinants of pod yield and response to plant density. Crop duration was shortest in humid tropical and subtropical environments, with both high and low temperatures apparently delaying crop maturity. A relatively small individual plant size in humid tropical environments was due to a combination of low incident irradiance and short duration, with very high plant densities needed to maximize dry matter production. The progressive decline in harvest indices in more tropical environments was due to a decline in pod numbers per plant. Although increased plant density resulted in greater numbers of pod initials in the humid tropics, a high proportion of these pods did not contain developed seeds and pod yield at high densities remained relatively low at $\leq 2.5 \text{ t ha}^{-1}$.

INTRODUCTION

Despite being grown over a wide range of environmental conditions (lat 40°S–lat 40°N), the role of environmental factors (temperature, photoperiod and irradiance) in determining variations in the growth and development of groundnut (*Arachis hypogaea* L.) crops in contrasting environments remains poorly defined. Whilst the effects of temperature on photosynthesis and dry matter (DM) accumulation are reasonably well understood (Ketrings *et al.*, 1982; Marshall *et al.*, 1992; Bell *et al.*, 1992; 1994a; b), the role of temperature in determining phenological development remains less clear. For example, while temperature has been shown to play a dominant role in the rate of progression to flowering (Bunting and Elston, 1980; Leong and Ong, 1983; Bell *et al.*, 1991c), the temperature dependence of post-flowering rates of development has been studied less extensively. Despite attempts to relate accumulation of thermal time to groundnut maturity (Mills, 1964; Ketrings and Wheless, 1989), the prediction of crop duration in contrasting environments still requires an empirical approach (for example, Hammer *et al.*, 1996).

Photoperiod has been shown to influence post-flowering reproductive development, mainly via its effects on the numbers of established pods and the subsequent partitioning of DM to those pods (Witzenberger *et al.*, 1985; Bagnall and King, 1991). However the effects of long photoperiods in subtropical environments has been shown to be moderated by the effect of cool night temperatures, which appear to reduce the photoperiod sensitivity of groundnuts (Bell *et al.*, 1991a). The actual impact of long photoperiods experienced in more subtropical groundnut-producing regions is therefore unclear.

The effects of intensity of incident irradiance and the daily amount of photosynthetically active incident radiation on crop growth and development are not well understood, particularly in terms of the effect on the season-long balance between vegetative and reproductive growth. Reducing incident irradiance by shading has been shown to reduce the size of the reproductive sink in terms of fewer flowers, pegs and pods (Hang *et al.*, 1984; Bagnall and King, 1991), but most reports only investigate the effects of reduced irradiance during restricted periods of crop growth. Examples from emergence to flowering (Williams, 1979), 21-day periods (Hang *et al.*, 1984) and from the beginning of pod-fill to maturity (Stirling *et al.*, 1990). There is evidence (Williams *et al.*, 1975; Prabowo *et al.*, 1990; McDonagh *et al.*, 1993) that groundnuts grown under conditions of low irradiance and high temperatures, such as in the wet tropics of Asia or lowland areas in Zimbabwe, have relatively low harvest indices although the reasons for this have not been investigated.

It is evident from the published literature that environmental factors can have a profound effect on the growth and development of groundnuts grown in contrasting environments. In this paper we use published data from a series of experiments involving common Virginia and Spanish cultivars of groundnuts, grown from the humid tropics to the elevated subtropics, to examine the effects of wide variations in environmental conditions on crop growth and response to plant density. The second paper in this series (Bell and Wright, 1998) uses these data sets to derive a model of heat unit accumulation to predict groundnut maturity, and to examine photo-thermal interactions and their effect on potential harvest index.

MATERIALS AND METHODS

The analyses in these papers use data from a number of published experiments conducted in the humid tropics of Indonesia, the semi-arid tropics of north-west Australia, the subtropics of north-east Australia (in both coastal lowland and inland elevated locations) and the humid subtropics of south-eastern USA. The duration of the growing season, average maximum and minimum temperatures and daily incident short-wave radiation are shown in Table 1 for each experiment from which data are cited, along with a reference to the detailed experiments where available. Details of procedures from already published individual experiments are not provided here, except to say that all experiments were grown under optimal agronomic conditions (non-limiting conditions with respect to nutrients, pests and diseases) with full irrigation. The previously unreported experiments

Table 1. Growing season (sowing to harvest dates), average daily maximum and minimum temperatures and incident short-wave solar radiation for studies in Australia, Indonesia and the United States. Where applicable, references to detailed publications are shown

Location and sowing number	Growing season	Average daily temperatures		Average incident radiation (MJ m ⁻² d ⁻¹)	Reference
		Maximum (°C)	Minimum (°C)		
<i>Australia</i>					
Kingaroy (lat 26°33'S long 151°50'E)					
S1	1/11/84–11/3/85	29.4	16.0	27.3	Bell <i>et al.</i> , 1993
S2	5/12/84–10/4/85	28.8	15.8	24.0	Bell <i>et al.</i> , 1993
S3	21/11/85–9/4/86	29.6	16.0	26.4	Bell <i>et al.</i> , 1993
S4	9/11/87–7/4/88	29.4	15.8	25.3	M. J. Bell (unpublished data)
S5	24/11/89–10/4/90	29.1	16.7	24.6	Bell <i>et al.</i> , 1992, 1994c
Bundaberg (lat 24°50'S long 152°26'E)					
S1	12/12/89–6/4/90	29.4	20.1	23.1	Bell <i>et al.</i> , 1992, 1994c
Kununurra (lat 15°45'S long 128°45'E)					
S1	1/12/82–11/4/83	36.5	24.1	22.8	Bell, 1986
S2	29/12/82–9/5/83	35.1	23.1	21.9	Bell, 1986
S3	18/1/83–9/6/83	34.0	21.8	21.3	Bell, 1986
S4	8/2/83–23/6/83	32.9	20.9	20.5	Bell, 1986
S5	1/3/83–13/7/83	31.8	19.4	20.0	Bell, 1986
S6	5/12/82–18/4/83	36.5	24.2	22.8	M. J. Bell (unpublished data)
<i>Indonesia</i>					
Jambegede (lat 8°5'S long 112°28'E)					
S1	24/2/86–9/6/86	31.5	20.0	16.0	Shorter <i>et al.</i> , 1992
S2	14/5/86–26/9/86	31.2	18.9	17.9	Shorter <i>et al.</i> , 1992
S3	27/8/86–9/12/86	31.0	20.5	19.3	Shorter <i>et al.</i> , 1992
S4	7/1/87–21/4/87	31.4	20.8	15.5	Shorter <i>et al.</i> , 1992
S5	5/5/87–19/8/87	32.2	18.8	17.7	Adisarwanto <i>et al.</i> , 1992
S6	28/2/88–11/6/88	32.9	22.7	16.2	Adisarwanto <i>et al.</i> , 1992
Muneng (lat 7°46'S long 113°6'E)					
S1	16/7/88–29/10/88	33.2	22.2	17.4	Adisarwanto <i>et al.</i> , 1992
Maros (lat 5°0'S long 119°30'E)					
S1	11/6/87–18/9/87	32.8	22.0	21.3	Prabowo., 1992
<i>United States of America</i>					
Gainesville (lat 29°40'N long 82°40'W)					
S1	15/5/90–17/9/90	34.4	21.1	21.1	Bennett <i>et al.</i> , 1993

referred to in Table 1 as Kununurra S6 and Kingaroy S4 are briefly described below.

The Kununurra (S6) study compared the effects of plant density (88 273 and 394 000 plants ha⁻¹) and plant rectangularity (ratios of intra:inter row spacing of 1:1, 1:2.15 and 1:7.19) on growth and yield of the early-maturing Spanish cv. White Spanish, the semi-erect, medium maturing Virginia cv. Early Bunch and the prostrate, late maturing Virginia cv. Florunner. The trial was conducted under solid set, overhead sprinkler irrigation on a sandy soil in the Ord River irrigation area of north-west Australia. Experimental techniques were similar to those reported in Bell *et al.* (1987) for a larger initial study using only cv. Florunner. Crop nutrition was optimal, and pests and diseases were controlled to avoid any significant limitation to growth.

The Kingaroy S4 study was undertaken to complement sowing date studies in East Java, Indonesia comparing growth and development of the Spanish and Virginia cultivars of differing origins under irrigated conditions in differing environments. The experiment was undertaken on a deep, red clay-loam (Oxisol) soil with nutrients and water in optimal supply and pests and diseases controlled as necessary to avoid growth limitations. Experimental techniques were similar to those reported in Bell *et al.* (1993a).

The Virginia cv. Early Bunch was sown on 17 occasions in the experiments listed in Table 1, although one data set from Jambegede, Indonesia was not complete due to the effects of bacterial wilt (*Pseudomonas solanacearum*) on plant survival late in the season. These sowings took place in all three Australian environments, in Jambegede, Indonesia and in Gainesville, USA. The Spanish cv. McCubbin and its near-identical parent cv. White Spanish (R. Shorter, Queensland Department of Primary Industries unpublished data, 1985) were sown on nine occasions in similar environments to those for cv. Early Bunch, except for the environment at Bundaberg, Australia. The Indonesian cultivars, Tapir and Gajah, were sown on six and eight occasions respectively including all Indonesian locations, and Kingaroy and Bundaberg in Australia.

Growth and crop duration were compared in sowings with similar plant populations (90 000 to 120 000 plants ha⁻¹) across environments, whilst responses to plant population in contrasting environments in Indonesia and Australia were analysed for the Spanish cultivars, McCubbin and Gajah. The method derived by Gardner and Gardner (1983), and subsequently employed by Bell *et al.* (1991b), was used to quantify population responses in the contrasting environments. This method describes the plant population response under well watered conditions using parameters derived from the relationships between individual plant size and plant density, and between individual plant dry weight and pod dry weight.

RESULTS

Environmental conditions and crop duration

The environments in which groundnut crops were grown differed markedly in

both temperature and daily incident radiation (Table 1). Crop durations (sowing to harvest) ranged from 100 d in Bundaberg to 134 d in Kingaroy for Spanish cultivars, and from 112 d at Jambegede to 142 d in a mid-January sowing at Kununurra for the Virginia cv. Early Bunch. Average maximum temperatures ranged from 36.5 °C at Kununurra to 28.8 °C at Kingaroy, with these same environments also providing the extremes in minimum temperatures (24.3–15.8 °C). The range in daily incident short-wave radiation among environments also varied widely, ranging from 27.3 MJ m⁻² d⁻¹ in an early sowing at Kingaroy to 15.5 MJ m⁻² d⁻¹ in a wet-season sowing at Jambegede. When crop duration was taken into account, short-wave radiation incident during the crop growing season ranged from 1630 MJ m⁻² for a Spanish cultivar in Jambegede to 3670 MJ m⁻² for a Virginia cultivar at Kingaroy.

Plant size, dry matter production and harvest index

Data shown in Table 2 summarize the growth characteristics of two groups of Spanish cultivars (McCubbin/White Spanish, and the slightly earlier-maturing Gajah/Tapir) and the Virginian cv. Early Bunch grown at similar plant densities across the test environments. Variation in DM production between cultivars was minimal under Indonesian conditions but quite marked at Kingaroy and Bundaberg. In these subtropical locations variation in DM production was consistent with differences in both crop duration (Early Bunch ≥ McCubbin/

Table 2. Total biomass excluding roots (g m⁻²), pod yields (g m⁻²), average plant size (g), crop duration (sowing–maturity, d) and harvest indices at maturity for Spanish and Virginia groundnut cultivars grown in Australian and Indonesian environments under non-limiting conditions and plant populations (90 000–120 000 plants ha⁻¹). Data are averages over a number of trials and sowing dates, with the number of data points contributing to each mean indicated

Location	Cultivar	Total biomass	Pod yields	Average plant size	Duration	Harvest index†
<i>Spanish cultivars</i>						
Kingaroy	McCubbin/White Spanish (n = 5)	1005	497	104.7	128	0.49
	Gajah/Tapir (n = 3)	816	383	84.7	118	0.47
Bundaberg	McCubbin (n = 1)	1012	445	115.0	100	0.44
	Tapir (n = 1)	887	393	63.3	100	0.44
Kununurra	White Spanish (n = 1)	977	385	118.0	111	0.39
Jambegede	McCubbin (n = 2)	728	214	58.2	112	0.29
	Gajah/Tapir (n = 6)	692	218	57.6	105	0.31
Muneng	Gajah (n = 1)	604	149	50.3	105	0.25
<i>Virginia cultivars</i>						
Kingaroy	Early Bunch (n = 5)	1155	627	126.0	136	0.54
Bundaberg	Early Bunch (n = 1)	1105	554	125.6	115	0.50
Kununurra	Early Bunch (n = 6)	995	456	108.5	133	0.47
Jambegede	Early Bunch (n = 2)	676	216	52.5	113	0.32

†Harvest index = proportion of available dry matter partitioned to reproductive components.

White Spanish > Gajah/Tapir) and in individual plant size (through the ability of each cultivar to expand to produce a full crop canopy at that plant population).

Growth of the same cultivar in different environments resulted in marked changes in individual plant size (and hence total DM production), and in the partitioning of available DM to reproductive components assessed by harvest index (HI). Average plant size in the Indonesian environments ranged from approximately 40% (Early Bunch) to 65% (Gajah/Tapir) of that in the Kingaroy sowings and, whilst a small component of this difference was due to slight variation in plant density between experiments, the effect on DM production was similarly large.

Partitioning of DM into pods declined progressively in all cultivars as production environments moved closer to the tropics, with HIs under Indonesian conditions only 55–65% of that measured at Kingaroy. These lower HIs, combined with the lower biomass production, resulted in pod yields under Indonesian conditions which were between 35% (Early Bunch) and 55% (Gajah/Tapir) of those achieved in the Kingaroy environment. Lower HIs of cultivars grown under Indonesian (wet tropical) conditions were associated with substantially lower numbers of pods. For instance, comparisons between the Kingaroy and Jambegede or Muneng experiments (referenced in Table 2), show pod numbers m^{-2} at Kingaroy were more than twice those recorded at the same plant density in Indonesia for cv. McCubbin (750 *v.* 300 pods m^{-2}), and 80% higher for cultivars Gajah/Tapir (450 *v.* 250 pods m^{-2}).

Environmental influence on plant density response

Having shown that all cultivars, when grown at similar plant densities, could produce larger individual plants with more pods in subtropical environments (such as Kingaroy and Bundaberg), it was hypothesized that yield and DM responses to plant density should be quite different between the tropics and subtropics. This was confirmed by examining the contrasting responses to plant density shown by the Spanish types cv. McCubbin at Kingaroy and cv. Gajah at Muneng (Fig. 1). Similar plant density responses to those of the Muneng study have also been obtained for cv. Gajah at Jambegede (Adisarwanto *et al.*, 1992), while those for cv. McCubbin at Kingaroy were consistent across three sowing dates and two seasons (Bell *et al.*, 1991b).

McCubbin at Kingaroy showed only a slight increase in DM in response to plant densities greater than 100 000 plants ha^{-1} , whilst pod yield was even less responsive. In contrast, the Muneng study showed much greater DM responses to increasing plant density up to at least 500 000 plants ha^{-1} (the limit evaluated in the study). Pod yield was much less responsive, with an apparent reduction in HI at high densities. We fitted the Gardner and Gardner (1983) model to these data sets in order to derive coefficients that quantify the contrasting density responses (Table 3). Differences among these coefficients highlight the differences in crop growth between environments which were described above (see Table 2).

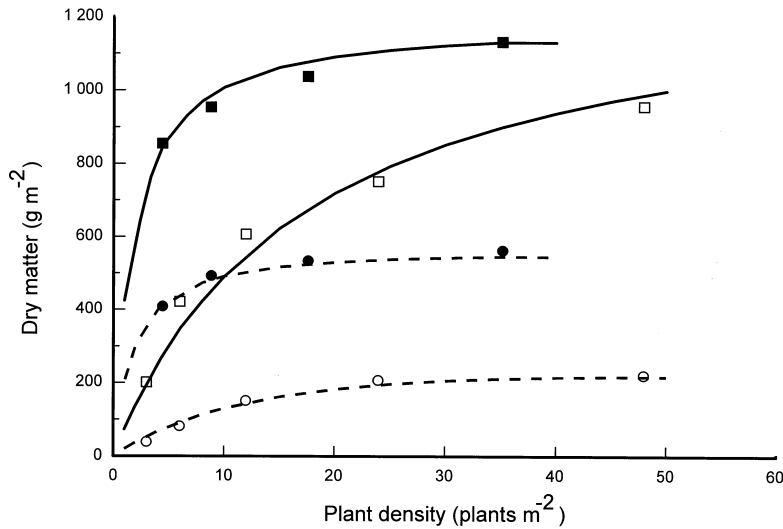


Fig. 1. Effects of plant density on production of total above-ground biomass (TDM) and pod yield (pod DM) for the Spanish groundnut cultivars McCubbin (TDM —■—; pod DM —●—) grown at Kingaroy Australia and Gajah (TDM —□—; pod DM —○—) grown at Muneng, Indonesia.

The analysis suggests that the effects of smaller plant size on total DM production per unit area at 90 000–120 000 plants ha⁻¹ in the Indonesian environments (Table 2) could be overcome effectively by sowing at much higher plant densities to produce similar maximum total DM (TDM_{max}). However these increases in plant density had to be quite substantial, with the $P_{0.5}$ coefficient (density needed to produce half the maximum DM) at Muneng approximately ten times that at Kingaroy. The reasons for such large differences can be explained by the apparent inability of plants in the Indonesian environments to grow sufficiently large at low density. The ‘maximum plant size’ (D_m) coefficient which describes this trait (namely, the extrapolated maximum plant size assuming no interplant competition) ranged from 77 g plant⁻¹ at Muneng to 660 g plant⁻¹ at Kingaroy.

The differences in partitioning DM were again illustrated, with the model ‘reproductive index’ (RI , the rate of increase in pod weight relative to the increase

Table 3. Model coefficients for maximum total dry matter (TDM_{max} , kg ha⁻¹), maximum plant size (D_m , kg), plant density at 50% maximum dry matter ($P_{0.5}$), plants ha⁻¹), reproductive index (RI) and minimum plant size for pod yield (d_0 , kg) to describe the plant population response of irrigated Spanish groundnut cultivars Gajah, grown in a humid tropical environment at Muneng, Indonesia and McCubbin grown in a subtropical environment at Kingaroy, Australia

Location	Cultivar	TDM_{max}	D_m	$P_{0.5}$	RI	d_0
Muneng (Indonesia)	Gajah	12 000	0.077	175 000	0.30	0.0055
Kingaroy (Australia)	McCubbin	11 300	0.660	18 000	0.49	0.0005

in total DM) at Kingaroy approximately 50% greater than at Muneng. In addition, there were clear trends for a greater reduction in pod yield per plant at high densities in the Indonesian environment (indicated by the smaller 'minimum plant size for pod yield' coefficient, d_0 , at Kingaroy), which resulted in the smaller response of pod yield to high density compared with that of DM.

The observed differences between environments in *RI*, and in pod yield per plant at high density, were examined in terms of total pod numbers (that is, all pods initiated on the end of a peg, regardless of the stage of development) and the proportion of those pods which contributed to final pod yield (Fig. 2 and Fig. 3 respectively). Large differences in total pod numbers were evident between environments, particularly at low plant densities. At Jambegede, pod numbers continued to increase with increasing density up to 500 000 plants ha^{-1} (the highest density tested), but even then pod numbers were less than 60% of the maximum achieved in the Kingaroy crop. At the highest density evaluated at Kingaroy (376 000 plants ha^{-1}), pod numbers per plant had only fallen to values that were similar to those at the lowest density tested (62 500 plants ha^{-1}) at Jambegede (24–25 pods plant^{-1}).

The lack of pod yield response to plant densities of $>250\,000$ plants ha^{-1} in Indonesian studies, despite continued increases in the total pod number, can be explained by an examination of the proportion of total pod weight that was commercially acceptable (contained partially or fully developed seed) at final harvest (Fig. 3). Data show that at densities of $>180\,000$ plants ha^{-1} the proportion of total pod weight that was represented in the harvestable yield fell quite rapidly to near 50% by 500 000 plants ha^{-1} . In other words, increases in plant density beyond a critical level resulted in an increased proportion of pod numbers that did not contribute to harvestable yield.

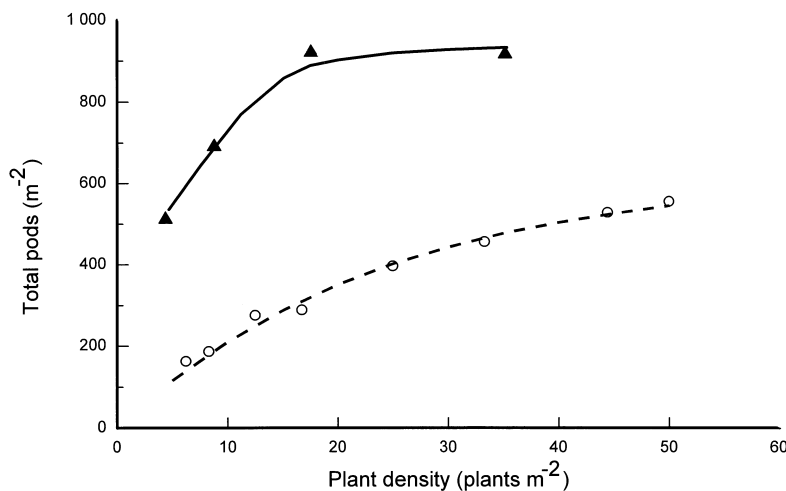


Fig. 2. Effects of plant density on total pods m^{-2} for groundnuts cv. McCubbin (—▲—) grown at Kingaroy, Australia and groundnuts cv. Gajah (---○---) grown at Jambegede, Indonesia.

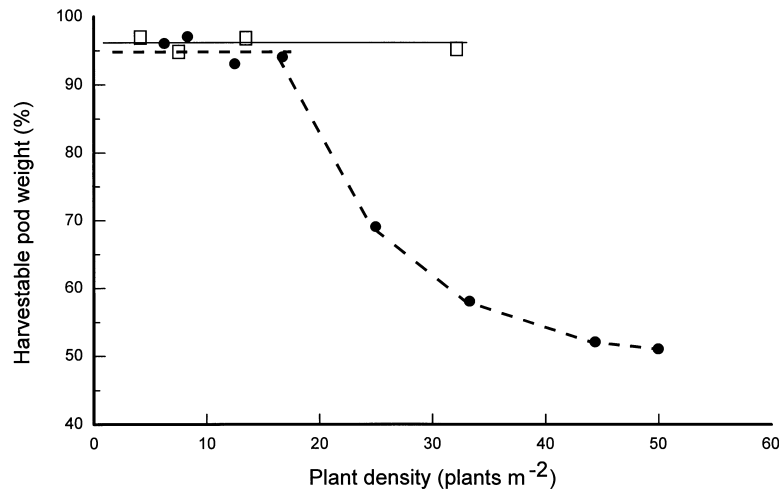


Fig. 3. Effects of plant density on the proportion of total pod number that contributes to pod yield for groundnuts cv. Gajah at Jambegede, Indonesia (—●—) and groundnuts cv. McCubbin at Kingaroy, Australia (—□—).

DISCUSSION

There is a lack of published data sets in which common cultivars of groundnuts, or other crops, have been grown across a wide range of environments using similar agronomic practices. Collation and subsequent analysis of data sets for the same groundnut cultivars has provided a unique opportunity to examine closely the effects of environmental factors on crop growth. The change in conditions from the cool subtropics at Kingaroy to the humid tropics in Indonesia has influenced groundnut growth in two ways – first, by reducing individual plant size (particularly at low density) and secondly, by reducing harvest index in environments with higher temperatures and lower incident irradiance. These phenomena are discussed in relation to their impact on crop agronomy and yield potential, and in terms of possible causal factors.

The small individual plant size (Tables 2 and 3) in more tropical environments, particularly in the Indonesian experiments, is due primarily to short crop duration and a low cumulative incident radiation during the season (Table 1). Rapid rates of progression towards flowering at mean daily temperatures of 26–27 °C (Leong and Ong, 1983; Bell *et al.*, 1991c) would have meant that plants experienced only a limited number of days at relatively low levels of irradiance before flowering occurred. These conditions would result in plants with only a small vegetative framework upon which subsequent development of flowers and pods could occur. The resultant small plant size at flowering, combined with considerably reduced rates of vegetative growth during reproductive development (Ketring *et al.*, 1982), would result in individual plant size remaining small relative to that achieved in cooler, higher radiation climates. It is therefore not surprising that total DM production in Indonesian environments was much more

responsive to increased plant density (Fig. 1). The fact that population model estimates of TDM_{max} at high densities in Indonesian environments were similar to those at Kingaroy (Table 3), despite lower incident irradiance, can be explained by the limitations to radiation use efficiency posed by low night temperatures in the Kingaroy environment (Bell *et al.*, 1992).

It is also interesting to note that crop durations in the sowings at Kununurra were either no shorter than those of comparable cultivars in Indonesian or Bundaberg sowings (White Spanish) or were considerably longer (Early Bunch, Table 2). This was despite mean daily temperatures at Kununurra which were significantly higher than in other environments (by as much as 4–5 °C in some sowings). This response suggests that temperatures above an as yet undefined optimum may actually have delayed crop maturation, as observed in other species (Hammer *et al.*, 1989). Studies on groundnuts have indicated that there is a high temperature effect which slows the rate of germination (Mohamed *et al.*, 1988). A re-analysis of data from Fortanier (1957) by Ong (1986) suggested that high temperature can retard crop development, although insufficient data exists to define accurately the temperature (T_{max}) at which crop development ceases (Hammer *et al.*, 1996). A subsequent paper in this series (Bell and Wright, 1998) uses data for Early Bunch from the environments in this study to derive such an estimate of T_{max} .

Low pod yields and resultant low harvest indices are characteristic of groundnuts grown in the wet tropics (Dart *et al.*, 1983; McDonagh *et al.*, 1993) and the data from these studies confirm this observation for both Virginia and Spanish cultivars. The analysis of plant growth at common densities, and the plant density experiments at Kingaroy, Muneng and Jambegede strongly suggest that this difference was due to an inability of crops in wet tropical environments to establish a large pod load (Fig. 2).

We propose that these effects were due to the balance between crop duration and the amount of incident irradiance available for growth in each environment. Results of shading experiments suggest that pod number is determined by the source capacity at the time of pod loading (Hang *et al.*, 1984; Stirling *et al.*, 1990), with source capacity determined by both the daily incident irradiance and the proportion of that irradiance intercepted by the crop canopy. The higher daily irradiance in the Kingaroy environment, therefore, should result in higher pod numbers for a similar level of canopy development at the time of pod loading. This hypothesis is consistent with the observed data.

Similarly, the contrasting responses of pod number to plant density (Fig. 2) will be a function of the source capacity at the time of pod addition (that is, the degree of canopy cover). The short duration of crops grown in Indonesia, combined with the small plant size, means that more plants per m² will be required to achieve full canopy cover (and hence maximum source capacity) than at Kingaroy. The rapid rise in pod numbers with increasing plant densities at Jambegede may therefore reflect greater source capacity with increasing density at the time of pod addition. At Kingaroy, in contrast, maximum source capacity at the time of pod addition

was reached with much lower densities due to larger individual plant size achieved during the longer pre-podding period.

As plant density increased, the observed decline in the proportion of total pod weight represented by 'full pods' in the Indonesian environments (Fig. 3) was indicative of a system in which the assimilatory requirements of the sinks (that is, the developing pods) exceeded the capacity of the crop canopy (source) to supply those requirements, either by current assimilation or by remobilization of stored reserves (Bell *et al.*, 1993b). Such a situation could then cause a cessation of the continued development of a proportion of the total pod load so that a balance between source capacity and sink requirements was restored.

There was no evidence of a change in source capacity during pod fill in the Indonesian studies by factors such as reduced canopy cover, lower incident irradiance or a reduction in radiation use efficiency (Bell *et al.*, 1993b). Foliage diseases were controlled in all experiments in Indonesia such that canopy cover was maintained throughout the season (Adisarwanto *et al.*, 1992), and there were no consistent reductions in incident irradiance during pod filling in the studies which were mostly conducted during the dry season. Similarly, the analyses undertaken in Hammer *et al.* (1996) indicated that there was no reduction in radiation use efficiency during pod filling. We suggest therefore that competition between active sinks (developing pods, and possibly the large number of vegetative apices represented by the high plant densities) during pod-fill resulted in the abortion of a percentage of developing seeds and the subsequent limitation to pod yields at high planting density.

There is considerable evidence of the ability of groundnut plants to regulate the size of the developing reproductive sink and the pattern of assimilate distribution in response to prevailing environmental stresses (Ketring *et al.*, 1982; Ashley, 1984; Bell *et al.*, 1993b). In any given genotype, the proportion of flowers that produces pegs, the proportion of pegs that produces pods and the proportion of pods that produces viable seed can vary in response to cultural and environmental factors (Bunting and Elston, 1980). There has been no work reported on the critical assimilatory requirements to initiate, and subsequently maintain, the development of each phase of reproductive development at a given node in groundnuts. However, Beech *et al.* (1989) undertook such an analysis in another indeterminate crop species – guar (*Cyamopsis tetragonoloba*). In that study, the authors derived an estimate of the daily assimilate flux required per generative growing point (pod) from the linear relationship between crop growth rate and the numbers of pods supported by those crops. A similar analysis using this approach for groundnuts may account for the variation in pod number between Indonesian and subtropical Australian environments. For example, during periods of full canopy cover, crop growth rates for cv. McCubbin sown at 88 000 or 176 000 plants ha⁻¹ at Kingaroy ranged from 124 to 164 kg ha⁻¹ d⁻¹ over four sowing dates in two seasons ($n = 7$; Bell *et al.*, 1993a). At Jambegede, crop growth rates of cv. Gajah sown at densities of 250 000, 333 000, 444 000 and 500 000 plants ha⁻¹ ranged from 73 to 102 kg ha⁻¹ d⁻¹ ($n = 4$) (Adisarwanto *et al.*, 1992). The corresponding values of total

pod numbers ranged from 620 to 905 pods m^{-2} at Kingaroy and from 410 to 560 pods m^{-2} at Jambegede. Calculations of daily assimilate flux per reproductive growing point ($\text{mg pod}^{-1} \text{d}^{-1}$) using this data provide values of 18.8 ± 0.60 for Kingaroy and 18.0 ± 0.46 for Jambegede. These fluxes are approximately double the values of 9.9–11.3 $\text{mg pod}^{-1} \text{d}^{-1}$ obtained for guar by Beech *et al.* (1989), with good agreement between the markedly contrasting environments.

Data for commercial pod number (pods containing sound mature seeds at harvest) were not available for the Indonesian study. At Kingaroy these numbers ranged from 435 to 585 pods m^{-2} , with calculated assimilate fluxes per filled pod of $27.9 \pm 1.0 \text{ mg pod}^{-1} \text{d}^{-1}$ – a substantial increase relative to that required to simply initiate the pod. This phenomenon of differential assimilate requirements for different stages of reproductive development may explain the lack of pod yield response to increasing plant density in Indonesia (Fig. 3). We hypothesize that increases in plant density resulted in an increased source capacity, achieved by more complete radiation interception, sufficient to supply enough extra assimilate for the initiation of new pods but insufficient to sustain subsequent filling or seed development.

The analysis of yield variation between environments using the assimilate flux approach seems worthy of further research. The considerable agreement in assimilate thresholds for pod initiation across contrasting environments suggests that this parameter may be relatively conservative, and hence of particular interest to crop modellers. The development of relationships between crop growth rates and reproductive sink size may overcome current difficulties of predicting the potential size of the reproductive sink in contrasting production environments as exemplified by Hammer *et al.* (1996).

Acknowledgements. The experimental work in Indonesia and Kingaroy was funded partially by the Australian Centre for International Agricultural Research (ACIAR) during projects PN8419 and PN8834.

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