

**GROUNDNUT GROWTH AND DEVELOPMENT IN
CONTRASTING ENVIRONMENTS
2. HEAT UNIT ACCUMULATION AND PHOTO-THERMAL
EFFECTS ON HARVEST INDEX**

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(Accepted 24 July 1997)

SUMMARY

When the same cultivars of groundnuts (*Arachis hypogaea*) were grown under a wide range of environmental conditions, temperature and irradiance played a major role in determining crop duration and partitioning of dry matter to pods, the latter assessed by harvest index. Utilizing published data for the Virginia groundnut cultivar Early Bunch under non-limiting conditions, we show that accumulation of thermal time using three cardinal temperatures ($T_b = 9^\circ\text{C}$, $T_o = 29^\circ\text{C}$ and $T_m = 39^\circ\text{C}$) has considerable potential for predicting crop maturity. In sixteen sowings ranging from the wet tropics in Indonesia to the elevated subtropics in Australia, harvest date for Early Bunch corresponded to the accumulation of 1808 (± 23) degree-days after sowing. In all sowings except one in the semi-arid tropics, this value of thermal time was within eight calendar days of actual harvest maturity. Harvest index varied greatly with both location and sowing date, ranging from 0.31 (Indonesia) to 0.58 (subtropical Australia). Using total short-wave solar radiation incident during the growing season and calculated values of thermal time, the growing season for each sowing in each location was described in terms of a photo-thermal quotient (PTQ, $\text{MJ m}^{-2} \text{ degree-day}^{-1}$). Values for PTQ ranged from 0.99 (Indonesia) to 2.11 (subtropical Australia). Variation in harvest index could be explained largely by a curvilinear function of PTQ ($R^2 = 0.98$), provided data were not confounded by the effects of photoperiod. In the semi-arid tropical environment, decreases in photoperiod associated with delayed sowing were the dominant factor controlling harvest index.

INTRODUCTION

Environmental factors play a major role in determining groundnut growth and development, but the understanding of the responses by groundnuts to factors such as temperature, photoperiod and irradiance is poor. The first paper in this series (Bell and Wright, 1998) has shown the extent to which contrasting environmental conditions affect a common set of groundnut cultivars grown under non-limiting conditions. Individual plant size, crop duration and partitioning of dry matter (DM) between vegetative and reproductive growth differed markedly between environments.

The primary factor determining the rate of phenological development (and hence crop duration) in groundnuts is temperature (Fortanier, 1957; Ong, 1986), although moisture stress (Ketrings, 1986; Ketrings and Wheless, 1989) and

photoperiod (Flohr *et al.*, 1990) can modify the underlying response. The concept of thermal time is used to describe the phenological response to temperature in many crops, with particular success in terms of describing rates of progression towards key events like flowering (Angus *et al.*, 1981; Roberts and Summerfield, 1987; Mohamed *et al.*, 1988). Thermal time calculations usually involve three cardinal temperatures (i) a base temperature (T_b) below which no development occurs, (ii) an optimum temperature (T_o) at which development proceeds at a maximum rate and (iii) a maximum temperature (T_m) above which no development occurs.

There is general agreement that for groundnuts, values of T_b and T_o lie within the range 9–13 °C and 27–32 °C respectively (Williams and Boote, 1995), although genotypic variation is significant (Bell *et al.*, 1991b) and precise optima have been defined for only a few processes. Information about T_m in groundnuts is limited to the process of germination (Mohamed *et al.*, 1988), with values ranging from 41 to 47 °C among genotypes. Currently, groundnut simulation models use either an arbitrary value of T_m based on other physiological processes like denaturation of plant membranes (PNUTGRO model, $T_m = 55$ °C; Boote *et al.*, 1989), or have not allowed for a T_m in the calculation of thermal time (Hammer *et al.*, 1996). The latter situation in particular has caused problems when considering phenological development in environments with widely contrasting temperature regimes.

Assimilate distribution between vegetative and reproductive plant parts in groundnuts is not well understood. However, there are presumed to be strong links between phenology and assimilate distribution, as both the numbers and the potential duration of growth of a given organ are determined by phenology (Williams and Boote, 1995). Similarly, source capacity (determined by the incident irradiance, interception of that irradiance and radiation use efficiency) can have a major impact on numbers of pods that are both initiated and that contain developed seeds (Bell and Wright, 1998). It is not surprising therefore that environments with differing rates of phenological development due to contrasting temperatures, and which experience differing levels of daily incident radiation, should develop differing patterns of assimilate distribution resulting in differing harvest indices (McDonagh *et al.*, 1993; Bell *et al.*, 1994b).

Harvest index (HI) has been used extensively to estimate pod or seed yields from total biomass in crop models that focus on resource capture (Sinclair, 1986; Hammer *et al.*, 1996). Although Hammer *et al.* (1996) were able to use a temperature function to account for variation in the rate of HI increase in groundnuts grown in contrasting environments, they were unable to account successfully for differences in final HI. To overcome such limitations a means of estimating potential HI in a given environment is required, preferably in combination with an estimator of maturity based on thermal time. In this paper we use published data for the Virginia groundnut cv. Early Bunch to derive estimates of thermal time to maturity, and to evaluate the effects of temperature and incident irradiance on HI.

MATERIALS AND METHODS

The analyses in this paper 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 the south-eastern United States – all with the semi-erect, medium maturity Virginia cv. Early Bunch. Details of previously unpublished data and references to published studies are listed in Bell and Wright (1998).

Maturity was determined using internal pericarp colour (Sanders *et al.*, 1982) in all experiments, with frequent destructive sampling during the final weeks of crop growth to determine optimum harvest time for each sowing. HI values used in this paper refer to the ratio of pod dry weight:total dry weight (excluding roots), with pod weights determined on commercially acceptable pods (that is, pods that contain sound mature seed). All experiments were well irrigated and pests and foliage diseases were strictly controlled to maximize retention of vegetative dry weight until maturity, and so to provide unbiased estimates of the potential HI for each sowing.

Thermal time (degree-days) was calculated from daily maximum and minimum temperatures, with curve fitting to estimate hourly temperature during a 24-h period. Cumulative thermal time from sowing to maturity was calculated using the existing methods employed in the PNUTGRO (Boote *et al.*, 1989) and QNUT (Hammer *et al.*, 1996) crop models. In addition, thermal time was calculated using a revised version of the QNUT model (QPHEN) derived from the Early Bunch data set.

PNUTGRO used a linear model with three cardinal temperatures ($T_b = 11\text{ }^\circ\text{C}$, $T_o = 28\text{--}32\text{ }^\circ\text{C}$ and $T_m = 55\text{ }^\circ\text{C}$) to calculate thermal time, while QNUT used only $T_b = 9\text{ }^\circ\text{C}$ and $T_o = 29\text{ }^\circ\text{C}$, with no decline in thermal time accumulation at temperatures $> T_o$. In the derivation of QPHEN we used an iterative process, in combination with the values of T_b and T_o used in QNUT, to estimate a value of T_m that best predicted thermal time to maturity across all environments. Mean values of accumulated thermal time at maturity were calculated using each phenology model for the 16 sowings in the data set. These estimates of thermal time to maturity were used to predict crop duration (days to maturity) in each sowing, with predicted crop duration plotted against observed crop duration for each phenology model.

A photo-thermal quotient (PTQ, $\text{MJ m}^{-2} \text{ degree-day}^{-1}$) was derived for each sowing at each location by dividing average daily short-wave radiation from sowing to maturity ($\text{MJ m}^{-2} \text{ d}^{-1}$) by the average daily accumulated thermal time (degree-days d^{-1}) derived using the QPHEN model. Crop HI was plotted as a curvilinear function of PTQ for all data sets except those from the semi-arid tropical environment in north-west Australia. In the latter environment, the relationship between photoperiod (-3° elevation) and HI in sowing dates

ranging from December to March was investigated using standard linear regression techniques.

RESULTS

Estimation of T_m for QPHEN

Choice of T_m had a major impact on accumulated heat units from sowing to maturity in hotter environments, but had only minimal effects in cooler subtropical locations. With $T_b = 9^\circ\text{C}$ and $T_o = 29^\circ\text{C}$, raising T_m from 35 to 50°C caused average degree-days from sowing to maturity to increase in all environments. Increases were greatest in Kununurra and Gainesville (30%), followed by Indonesia (7.5%), Kingaroy (5%) and Bundaberg (3%). The most appropriate value of T_m , determined as the temperature that minimized the variation in accumulated degree-days from sowing to maturity across the 16 data sets (Fig. 1), was 39°C .

The mean degree-days accumulated from sowing to maturity across all data sets ranged from 1731 ± 49 for PNUTGRO to 2066 ± 64 for QNUT, with the new temperature combination of $9/29/39^\circ\text{C}$ (QPHEN) producing an intermediate mean with lower variation (1809 ± 22). The ability of each phenology model to account for both high- and low-temperature environments was examined by expressing the thermal time to maturity for each sowing date as a percentage of the mean thermal time to maturity for each phenology model, and plotting this value as a function of the mean daily temperature for each sowing. This analysis

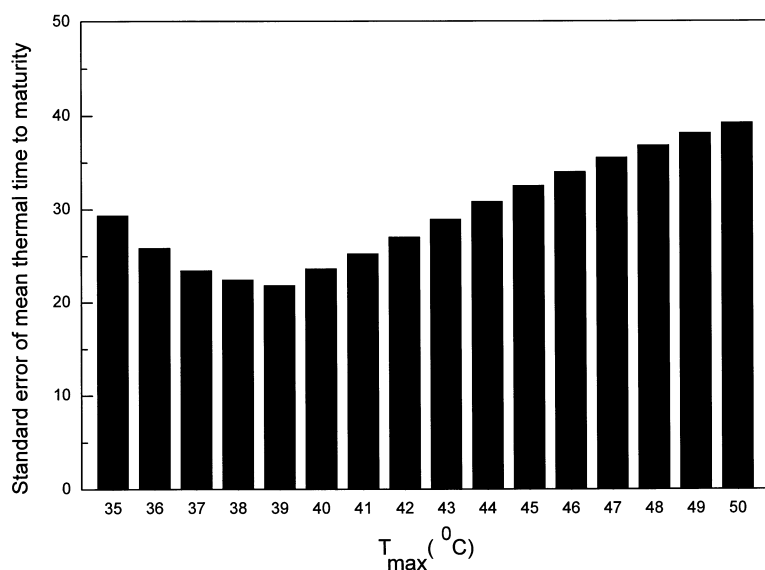


Fig. 1. Effects of the temperature chosen to represent T_m on the unexplained variation in accumulated thermal time from sowing to maturity, calculated for 16 sowings of groundnuts cv. Early Bunch in contrasting environments. Thermal time was calculated using $T_b = 9^\circ\text{C}$ and $T_o = 28^\circ\text{C}$ in a linear model with three cardinal temperatures.

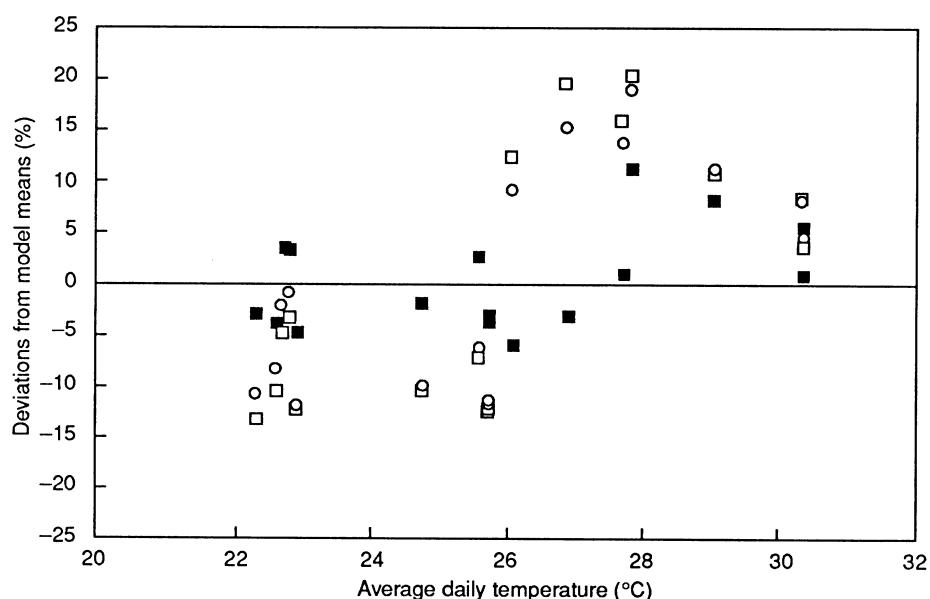


Fig. 2. Effects of average growing season temperature on the variation about the mean degree-days from sowing to maturity for groundnuts cv. Early Bunch using QPHEN (■), QNUT (□) and PNUTGRO (○) methods of calculation of thermal time.

(Fig. 2) suggests that both QNUT and PNUTGRO were not able to adequately predict degree-day accumulation across average temperatures which ranged from 22.5 to 30.5 °C. In particular, degree-day accumulation in low temperature environments was well below the overall mean and in hotter environments was well above the overall mean. The QPHEN predictions were much less temperature dependent and showed lower variability.

The inability of QNUT and PNUTGRO to predict adequately the thermal time accumulation across the range of groundnut growing environments meant that these models were unable to predict accurately the occurrence of key crop growth stages and ultimately, maturity (Fig. 3). Using the mean accumulated heat units to maturity for each model to represent the 'predicted' crop duration, PNUTGRO maturity estimates ranged from up to 26 d too early in the hot Kununurra environment, to as much as 31 d too late in the cooler Kingaroy environment. The range for QNUT was similar (that is 28 d too early to 29 d too late in Kununurra and Kingaroy respectively).

The QPHEN predictions were much more accurate (Fig. 3), with no systematic deviations in predicted maturity in particular environments. With the exception of one sowing date in Kununurra, where QPHEN predicted maturity 14 d earlier than the actual harvest date, all harvest dates were predicted with an accuracy of ± 8 d. Given the qualitative nature of the internal pericarp method for maturity determination, this represents an acceptable degree of variation.

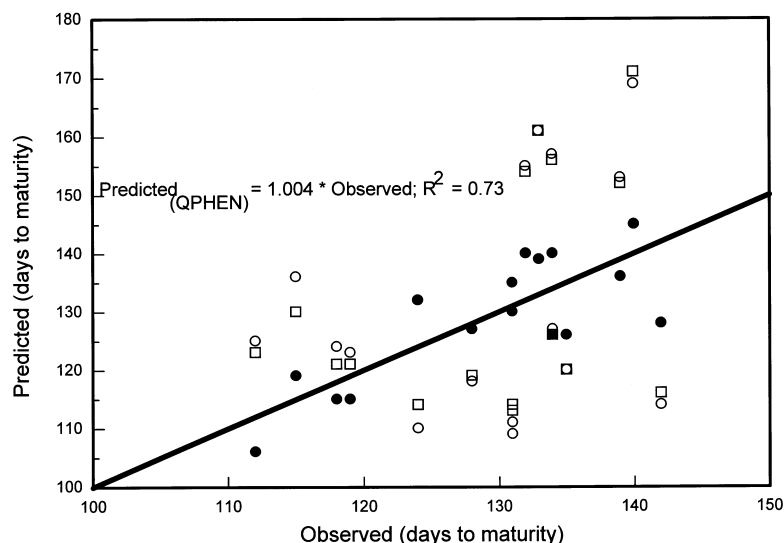


Fig. 3. Predicted *v.* observed days from sowing to maturity for groundnuts cv. Early Bunch using output from the QPHEN (●), QNUT (○) and PNUTGRO (□) phenology models. The solid line is the 1:1 line, while the equation is the regression for the QPHEN output ($n=16$)

Photo-thermal quotients (PTQ) and relationship with HI

Derived values of photo-thermal quotient (PTQ) were used as a quantitative index of the temperature and radiation regimes for each sowing date or location. Environmental variation in PTQ was large, with values ranging from 0.99 to 2.10 MJ m⁻² degree-day⁻¹ as production moved from the wet tropics to the cooler subtropics. Using the QPHEN thermal time estimate for maturity (that is, 1809 degree-days), the variation in seasonal incident radiation between environments was very large (1800–3800 MJ m⁻²). This statistic illustrates the potentially large advantage offered by subtropical environments for DM production and yield, assuming other agronomic and environmental limitations can be overcome.

Values of PTQ were plotted against HI for all available data sets (Fig. 4), with a significant non-linear relationship obtained (equation not shown; $R^2=0.55$, $n=16$). However, within the full data set there were clear indications of a subset of environments (representing the six sowings undertaken at various times of the year in Kununurra) in which HI actually declined with increasing PTQ. These data were not used in determining the relationship shown in Fig. 4 ($R^2=0.98$, $n=10$), even though the mean value for the six Kununurra data sets falls almost exactly on the fitted curve (PTQ = 1.57, HI = 0.47).

The Kununurra data were examined more closely in order to determine the reason for the apparent sowing date dependence of the departure from the generally positive PTQ–HI relationship. In the light of existing evidence of the effects of photoperiod on assimilate partitioning, the variation in HI in the Kununurra data sets was examined in relation to the average photoperiod (-3° elevation) during the period from sowing to maturity (Fig. 5). This analysis

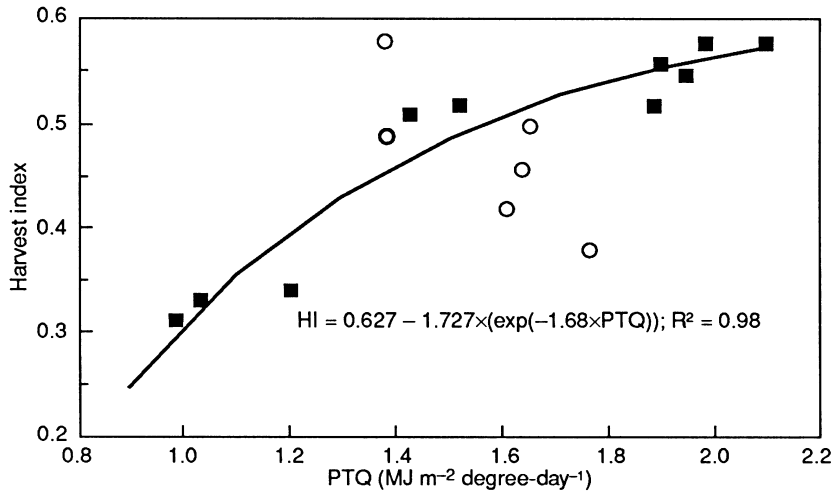


Fig. 4. Relationship between photo-thermal quotient (PTQ) and harvest index (HI) of groundnuts cv. Early Bunch. The equation refers to the solid line ($n = 10$), derived from all sowings (■) except those at Kununurra (○).

showed a highly significant negative linear relationship between HI and photoperiod ($R^2 = 0.90$). The strength of this relationship suggests that within the relatively narrow range of PTQ represented by the Kununurra sowings (1.4 to 1.7 $\text{MJ m}^{-2} \text{ degree-day}^{-1}$), variation in HI could be explained almost entirely by an effect of photoperiod.

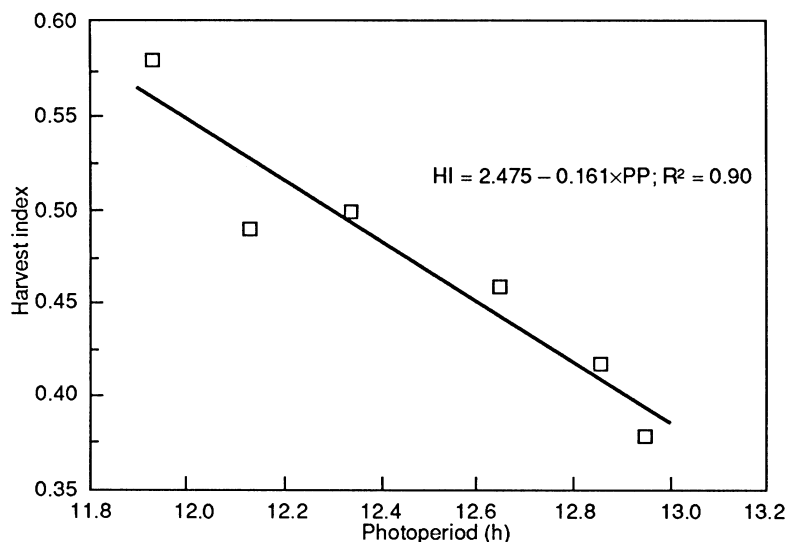


Fig. 5. The relationship between harvest index (HI) at maturity and average photoperiod (-3° altitude) for groundnuts cv. Early Bunch sown between 5 December and 1 March (□) over the 1982–83 growing season at Kununurra. The equation refers to the fitted line ($n = 6$).

DISCUSSION

Currently, two of the least understood phenomena in groundnut growth and development are the determination of time to maturity and the partitioning of assimilate between vegetative and reproductive growth. The analyses conducted on this unique, multi-environment data set provide significant advances in the understanding of both these factors.

The potential for using accumulated thermal time as a predictor of crop maturity in diverse production environments has been recognized in the development of current crop models (for example in wheat, Ritchie, 1991; and in maize, Kiniry, 1991). Indeed, both recently developed groundnut models, PNUTGRO V1.02 (Boote *et al.*, 1989) and QNUT (Hammer *et al.*, 1996) use thermal time accumulation to predict the onset of various growth stages and maturity. However, this paper has shown (Fig. 3) that both models have considerable difficulty in predicting maturity across environments with contrasting temperature regimes.

The limitations in the QNUT model were due to the lack of allowance for a reduction in the rate of development at high temperatures. Hammer *et al.* (1996) overcame these limitations by using different threshold values of thermal time for key events (for example, the onset of linear HI) in environments with widely differing temperature regimes. However the authors noted that the resulting empirical nature of such an approach was unsatisfactory, and that there was a need to quantify the effects of high temperatures on rates of phenological development. The inclusion of an appropriate value for T_m (identified from our analyses as being 39 °C in Fig. 1) has overcome these limitations.

Boote *et al.* (1992) recognized that problems also existed in the PNUTGRO phenology predictions (using $T_b = 11$ °C, $T_o = 28-32$ °C and $T_m = 55$ °C for all growth stages) when comparing data sets from India and the United States. Predicted rates of development were too high under high temperatures and too slow under moderate to cool temperatures during pod filling. It was suggested that differing developmental responses to temperature by vegetative and reproductive plant parts may be responsible, as this was consistent with the observations of Wood (1968) and Williams *et al.* (1975). However, a more appropriate value of T_m , in combination with a lower T_b (as suggested by Leong and Ong (1983) and Mohamed *et al.* (1988) and used by Hammer *et al.* (1996) in QNUT), would overcome most of these difficulties.

The current unreliability of remote prediction of crop maturity has led to the continued reliance on labour-intensive field or locality-specific 'hull scrape' (Williams and Drexler, 1989) or internal pericarp colour (Sanders *et al.*, 1982) indicators of crop maturity. These indicators, whilst useful for confirming optimum harvest time in a given field, have limited predictive ability and are of little value in predicting crop duration in new production environments. Meinke and Hammer (1996) have illustrated the potential for crop models in identifying potential new areas for industry expansion. However, such an analysis requires a

detailed understanding of the influence of environmental factors on crop phenological development. The predictive capacity shown by the QPHEN model (Fig. 3) represents a significant advance in this regard.

The marked differences in yields and in partitioning of assimilate between vegetative and reproductive plant parts in environments with differing radiation and temperature regimes (Bell and Wright, 1998) suggested the need to develop a method of describing production environments quantitatively in terms of these variables. The development of QPHEN has allowed accurate calculation of thermal time accumulation under contrasting temperatures, and by combining this information with daily incident radiation and deriving values of PTQ, production environments can be compared directly in terms of the potential for biomass production. Such an analysis highlights the potentially large productivity in subtropical environments like Kingaroy, provided that plant populations are managed to maximize radiation interception (Bell *et al.*, 1993) and cultivars in which cool night temperatures have minimal effect on radiation use efficiency are chosen (Bell *et al.*, 1994a). Conversely, yield potential in wet tropical environments with small PTQ (about $1.0 \text{ MJ m}^{-2} \text{ degree-day}^{-1}$) will always remain relatively low unless very high plant populations can be combined with long duration cultivars to maximize intercepted radiation. Even in this case, the data of Bell and Wright (1998) suggest that pod yields may be less responsive than biomass production to such practices.

We have shown that in the absence of other environmental stresses (for example, adverse photoperiods, Fig. 5), variation in PTQ can account for most of the variation in HI in Early Bunch between environments (Fig. 4). Crop growth models that use biomass accumulation and increases in HI to predict pod yields (Sinclair, 1986; Hammer *et al.*, 1996) currently have difficulty in accounting for the variation in HI under contrasting environmental conditions, so derivation of PTQ values from long-term weather data may provide a way of setting potential HI in different environments.

The physiological basis for the association between PTQ and HI ($R^2 = 0.98$), and indeed the precise form of this relationship in the absence of the confounding influences of differences in photoperiod between and within (Fig. 4) production environments, is difficult to determine from the available data. Ong and Squire (1984) have shown a close relationship between spikelet or grain number in millet (*Pennisetum typhoides* S. & H.) and 'thermal interception rate' (radiation intercepted per unit of thermal time – a similar environmental index to PTQ). This is a similar finding to our results for groundnuts in that the large differences in HI between subtropical Australia and the wet tropics of Indonesia were a direct result of low pod yields resulting from low numbers of pods initiated, and subsequently filled, in the Indonesian sowings. However, as similar daily assimilatory fluxes were required to support a pod in each environment (Bell and Wright, 1998), differences in pod number could be related directly to differing crop growth rates. It was therefore likely that the daily incident radiation component of PTQ was the dominant factor in the HI–PTQ relationship, and this was confirmed using step-

wise multiple linear regression. Daily incident radiation as a single factor in the model could account for a large proportion of the variation in HI ($R^2 = 0.84$, data not shown). Similar observations have been made in shading studies at Kingaroy with both Early Bunch and the Spanish cv. McCubbin (M. J. Bell, Queensland Department of Primary Industries unpublished data, 1996).

Finally, HI data from the Kununurra sowings (Fig. 5) clearly indicate the potential impact of photoperiod on assimilate distribution patterns in sensitive groundnut cultivars. Bagnall and King (1991) have shown that Early Bunch can respond to photoperiod in controlled environment studies. The photoperiod range at Kununurra over which significant photoperiod responses were recorded (about 12–13 h at -3° elevation) corresponded to the lower limits of those investigated by Flohr *et al.* (1990). These photoperiods were considerably shorter than those experienced by plants grown in subtropical environments, for example, the sowings at Bundaberg, 13.3 h for a mid-December sowing (Bell *et al.*, 1992) or Gainesville, Florida, 13.9 h for a mid-May sowing (Bennett *et al.*, 1993). Warm night temperatures during those studies (20.1°C for Bundaberg, 21.1°C for Gainesville) would ensure that plants in those sowings were also capable of responding to photoperiod (Bell *et al.*, 1991a), with assimilate distribution and HI at maturity a result of the interaction between PTQ and photoperiod. There is therefore some doubt as to the exact nature of the HI–PTQ relationship (Fig. 4) at intermediate values of PTQ. Further research in this area, possibly employing shading treatments to vary PTQ in environments where the effects of photoperiod are minimal, is required before such a relationship can be employed with confidence in crop models.

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

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