Dry Matter Production and Rate of Change of Harvest Index at High Temperature in Peanut

P. Q. Craufurd,* P. V. Vara Prasad, and R. J. Summerfield

ABSTRACT

The concept of a linear increase in harvest index, dHI/dt, has proven very useful for crop simulation modeling. The effect of high temperature on the response of dHI/dt of pods and seeds of peanut (Arachis hypogaea L.) has not been described. The objectives of this work were to determine (i) whether dHI/dt was linear at high temperature, (ii) whether high temperature affected dHI/dt and/or the timing of the linear phase of increase in HI, and (iii) whether there was genotypic variation in the response of dHI/dt to high temperature. Four peanut genotypes varying in heat tolerance were grown in pots at either 28/22 or 38/22°C from 21 to 90 d after planting (DAP). Plants were harvested on 10 occasions starting 27 DAP and total dry matter accumulation and partitioning measured. High temperature reduced total dry weight by 20 to 35%, seed HI by 0 to 65%, and seed dry weight by 23 to 78%. At 28/22°C, dHI/dt for pods and seeds was linear and varied from 0.0058 to 0.0109 d⁻¹. At 38/22°C, dHI/dt of pods and seeds was also linear and varied from 0.0028 to 0.0089 d⁻¹. There were genotypic differences in response to temperature. High temperature had no effect on dHI/dt in moderately tolerant genotypes 796 and 47-16. In susceptible genotypes ICGV 86016 and ICGV 87282, the start of pod and seed filling was delayed by 5 to 9 d and dHI/dt reduced by 20 to 65% at 38/22°C. Reductions in pod and seed dry weight at 38/22°C were therefore due to reductions in total dry matter and dHI/dt, depending on the heat tolerance of the genotype. Crop models need to account for genotypic differences in the response of timing and rate of dHI/dt to high temperature to successfully simulate yields in warmer environments.

A linear increase in harvest index (HI) over time is a common feature of seed production in a wide range of crop species, including soybean [Glycine max (L.) Merr.] (Spaeth and Sinclair, 1985), peanut (Hammer et al., 1995), sorghum [Sorghum bicolor (L.) Moench] (Muchow, 1988), maize (Zea mays L.) (Muchow, 1990), sunflower (Helianthus annuus L.) (Bange et al., 1998), and wheat (Triticum aestivum L.) (Moot et al., 1996). This concept has proven particularly useful for crop simulation modeling, because only total dry matter production and a constant rate of change of HI (dHI/dt) is needed to model reproductive yield (e.g., Hammer et al., 1995). In an analysis of 22 case studies, however, Bindi et al. (1999) concluded that although dHI/dt remains stable over a range of growth conditions, including fertility and irrigation treatments, there was some evidence of instability across sowing dates. Long days reduce partitioning to fruits and seeds in peanut (Flohr et al., 1990; Nigam et al., 1994). In addition seasonal variation in temperature, and genotypic responses to temperature, may also cause instability in dHI/dt (Hammer et al., 1995).

The effect of temperature on dHI/dt in peanut genotype ‘Early Bunch’ has been quantified by Hammer et al. (1995). In Early Bunch, dHI/dt was constant at 0.0084 d⁻¹ between 20 and 28°C. However, at mean temperatures >28°C dHI/dt falls rapidly, reaching zero at about 31°C. Bell et al. (1993a) have also shown that dHI/dt is constant at mean temperatures of 18 to 23°C during pod filling. The value of dHI/dt also varies among peanut genotypes (Bell et al., 1993a; Bennett et al., 1993; Nigam et al., 1994). For example, Bell et al. (1993a) found that dHI/dt varied from 0.0050 to 0.0140 HI d⁻¹ among four genotypes grown under identical conditions.

Peanuts in semiarid environments frequently experience mean daily temperatures greater than 27°C during pod filling, particularly in environments prone to terminal drought, and such temperatures may affect development and partitioning. Heat tolerant genotypes have been identified in Niger on the basis of partitioning to pods at high (mean 32 to 34°C) temperatures (Greenberg et al., 1992; ICRISAT, 1994). The objectives of this work were to determine (i) whether dHI/dt is linear at high temperature, (ii) whether high temperature affects dHI/dt and the timing of the linear phase of increase in HI, and (iii) whether there is genotypic variation in dHI/dt and its response to high temperature in peanut.

MATERIALS AND METHODS

The experiment was conducted during the summer months of 1996 in the controlled environment facilities at the Plant Environment Laboratory of the Department of Agriculture, The University of Reading, UK (51°27′N lat. and 005°6′W long.).

Genotypes and Plant Husbandry

Two Spanish genotypes, ‘ICGV 86015’ and ‘796’, and two Virginia genotypes, ‘ICGV 87282’ and ‘47-16’, were used, seeds of which were obtained from the ICRISAT Asia Centre located at Hyderabad in India. Genotypes 796 and 47-16 are tolerant and ICGV 86015 and ICGV 87282 are susceptible to high temperature (Greenberg et al., 1992; ICRISAT, 1994).

Uniform seeds of each genotype were selected and treated with Apron Combi 453 FS [(methyl-(2-methoxyacetyle)-n-(2,6-xyllyl)-DL-(alanite)]=2-(thiazol-4-yl) benzimidazole:2-(1,3-thiazol-4-yl benz-imidazole)] + [tetramethylthiuram disul-fide: bis (dimethylthiocarbamoyldisulfide)] (Ciba Agriculture, Cambridge, UK) as a precautionary measure against seedborne diseases. Seeds were pre-germinated on moist filter paper in Petri dishes kept in the dark for two days at 25°C, until radicles became visible. The germinated seeds were planted on 6 June 1996 (0 DAP, days after planting), one per 15-L pot (30 cm wide by 25 cm high) at a depth of 2.5 cm. The pots were

Abbreviations: DAP, days after planting; HI, harvest index; dHI/dt, rate of change of harvest index.
covered with aluminum foil on the sides to reduce radiative soil heating. The rooting medium comprised sand, gravel, vermiculite, and loamless peat compost mixed in proportions of 4:2:1 by volume, respectively. A commercial controlled-release, 90-d duration fertilizer (0.15 kg kg\(^{-1}\) N, 0.10 kg kg\(^{-1}\) P, 0.12 kg kg\(^{-1}\) K, 0.02 kg kg\(^{-1}\) MgO plus trace elements; Osmocote Plus, Scotts UK Ltd., Ipswich, UK) was incorporated into the mixture at the manufacturer’s recommended rate of 5 g L\(^{-1}\). Seeds were not inoculated with *Rhizobium* and therefore plants were wholly dependent on inorganic nitrogen. All pots were soaked with tap water and allowed to drain for 24 h before planting; thereafter they were irrigated to maintain field capacity through an automatic drip irrigation system.

Release of predators (*Phytoseiulus persimilis* A.-Henriot) and foliar sprays of Torque (a.i. fenbutatin oxide, bis[tris(2-methyl-2-phenylpropyl]tin] oxide) controlled a mild incidence of red spider mite (*Tetranychus urticae* Koch). Thrips (*Thrips tabaci* Lindeman) were controlled by release of the predator *Amblyseius cucumeris* Oudemans. Plants were also sprayed with Repulse (a.i. chlorothalonil; 2.45, 6-tetrachloro-1, 3-benzenedicarbonitrile) to prevent leaf spot (*Cercospora* sp.).

### Observations and Data Analysis

Duration from planting to the appearance of first fully opened flowers (R1; Boote, 1982), pegs (R2), pods (R3), and seeds (R5) were noted on all plants. A set of five plants were harvested every 7 d between 27 and 90 DAP, giving 10 harvests in total for growth analysis.

At each harvest, plants were carefully removed from each pot without damaging the root systems and separated into roots, leaves, stems, pegs, pods, and seeds. The numbers of pegs and pods per plant were recorded and roots were washed carefully with water to remove the potting medium. Weights of roots, leaves, stems, pegs, pods, and seeds, per plant were recorded after oven-drying these components to a constant weight for 3 d at 80°C. Total dry weight, pod harvest index (the ratio of pod to total dry weight, inclusive of roots), seed to pod ratio, and seed harvest index (the ratio of seed to total dry weight), were calculated from the weights of individual components. Values of seed dry weight were adjusted by a factor of 2.33 to allow for the high-energy cost of synthesis of kernels with high oil and protein contents (Sinclair and de Wit, 1975). The oil and protein composition was assumed to be the same in all genotypes. Oil and protein contents were also assumed to increase in equal proportion during kernel growth (Bell et al., 1993a,b) and the correction factor was not varied over time.

Within each temperature regime the treatments were laid out as a randomized complete block design with five replicates. Harvest indices and ratios expressed as percentages were angular transformed before analysis of variance was carried out. Analysis of variance for all measured and derived variables was performed by Genstat 5 (Genstat 5 Committee, 1987) as a split-plot design with temperature regimes as unreplicated main plots and genotypes and replicates as subplots. The coefficient of variation ranged from 3.6 to 11%.

The relations between pod and seed HI and time after planting (t) were examined for each treatment and genotype combination. Effects of temperature and genotype on the slope (dHI/dt) and intercept of these relations were tested by comparison of linear regressions (Mead et al., 1993). Start of the linear increase in pod and seed HI (i.e., x-intercept) was estimated from these linear relations.

### Environmental Conditions

The experiment was conducted in two adjacent polyethylene covered tunnels (polytunnels; 25 m long by 8 m wide by 3 m high at apex) aligned east-west, one maintained at an optimum day/night temperature of 28/22°C (mean 25°C) and the other at a warm day/ optimum night temperature of 38/22°C (mean 30°C). Photo- and thermo-periods in the polytunnels were both 12 h d\(^{-1}\). Photoperiod was controlled by a manually operated blackout facility. Day and night temperatures were controlled in the poly-tunnels by heating and venting. Each tunnel had an 88 kW h capacity heater which blows air down both sides of each tunnel through 30-cm-diam. plastic ducts with holes approximately every 20 cm. Air was constantly circulated within the polytunnel. In the roof of the tunnels, were three polyethylene ducts connected to three fans for venting. The venting fans were switched on in two stages (to avoid a drop in the temperature too rapidly) and created a partial vacuum in the polythene ducts, causing air to be sucked into the ducts at the opposite end of the tunnel. An aspirated and shielded thermocouple mounted at 1.5-m height in the center of each tunnel and connected to a solid-state controller (Nobel Engineering, Bognor Regis) was used to control temperature by adding or losing (by venting) heat.

Air temperatures were monitored continuously at canopy height in the center and at both ends of the tunnels using aspirated and shielded thermocouples connected to a data-logger (Delta-T Devices, Cambridge, UK). The difference in mean temperature within the tunnel was <0.5°C. Carbon dioxide was not controlled but tunnels were vented and were not gas-tight; CO\(_2\) concentration was assumed to be similar in both tunnels. Relative humidity was maintained at 70(±5)% during the day using automatic sprinklers to wet the floor. The poly-tunnels were naturally lit and transmitted about 75% of the incoming photosynthetically active radiation (PAR). The oil and protein composition was assumed to be the same in all genotypes. Oil and protein contents were also assumed to increase in equal proportion during kernel growth (Bell et al., 1993a,b) and the correction factor was not varied over time.
and hence had higher pod and seed dry weights at 90 DAP (Table 1). Pod and seed HI (untransformed) averaged 49 and 41% in Spanish and 27 and 22% in Virginia genotypes, respectively. Root-to-shoot ratios were also greater in Spanish than Virginia genotypes.

High temperature significantly reduced total dry matter production (P < 0.001). The reduction was about 23% in genotypes ICGV 86015, 796 and 47-16, and 35% in ICGV 87282 (Table 1). Root-to-shoot ratio was reduced by high temperature (P < 0.01) by between 20 and 35%. Pod and seed dry weights were also significantly (P < 0.001) reduced by high temperature, particularly in ICGV 87282 where seed dry weight was reduced by nearly 80% (Table 1). Seed to pod ratio (shelling percentage), which varied among genotypes from 58 to 82% (untransformed) at 28/22°C, was only significantly reduced by high temperature in ICGV 86015 (Table 1).

### Rate of Change of Harvest Index

Relations between pod (data not shown) and seed HI (Fig. 2) and time after planting were linear at both 28/22°C and 38/22°C in all four genotypes. There were significant effects of temperature, genotype, and their interaction (Table 2) on the intercept and slope of the linear relation between pod and seed HI and time (Table 3). The start of the linear increase in HI, and dHI/dt, therefore varied among genotypes at 28/22°C and 38/22°C. Further comparisons of the slopes and intercepts were made to compare the four genotypes at 28/22°C, and to compare the effects of temperature on individual genotypes. Pod and seed growth, however, had not ended in any genotype before the final harvest at 90 DAP and therefore the effect of temperature and genotype on the duration of the phase of linear increase in HI could not be determined.

Temperature had a similar effect on dHI/dt for pods and seeds in all genotypes and dHI/dt values for pod and seed were comparable (Table 3). At 28/22°C the linear phase of seed HI began between 40 and 57 DAP, 2 to 9 d after pod-filling started. Values of seed dHI/ dt at 28/22°C were significantly (P < 0.05) greater in genotype ICGV 86015 (0.0096 HI d⁻¹) than in genotypes 796 and ICGV 87282 (common slope of 0.0079 HI d⁻¹) and 47-16 (0.0062 HI d⁻¹). Lower seed dry weights at 90 DAP in genotypes ICGV 87282 and 47-16 were therefore due to smaller values of dHI/dt and shorter durations of seed filling.

### Table 1. Total dry matter, root to shoot ratio (angular transformed), pod dry weight, pod harvest index (HI, angular transformed), seed to pod ratio (angular transformed), seed dry weight, and seed HI (angular transformed) of four peanut genotypes (ICGV 86015, 796, ICGV 87282 and 47-16) grown at air temperatures of 28/22°C (mean = 25°C) or 38/22°C (mean = 30°C) from 21 to 90 DAP. Data are the means of five replicates, sampled at 90 DAP.

<table>
<thead>
<tr>
<th>Variable</th>
<th>ICGV 86015</th>
<th>796</th>
<th>ICGV 87282</th>
<th>47-16</th>
<th>SED (3, 28 df)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total dry matter (g plant⁻¹)</td>
<td>148.9</td>
<td>114.3</td>
<td>158.6</td>
<td>129.7</td>
<td>179.6</td>
</tr>
<tr>
<td>Root to shoot ratio (%)</td>
<td>29.9</td>
<td>23.9</td>
<td>26.2</td>
<td>22.4</td>
<td>22.7</td>
</tr>
<tr>
<td>Pod HI (%)</td>
<td>46.4</td>
<td>39.0</td>
<td>42.7</td>
<td>40.0</td>
<td>35.1</td>
</tr>
<tr>
<td>Pod dry weight (g plant⁻¹)</td>
<td>78.0</td>
<td>45.4</td>
<td>73.5</td>
<td>53.6</td>
<td>59.4</td>
</tr>
<tr>
<td>Seed to pod ratio (%)</td>
<td>54.6</td>
<td>37.9</td>
<td>57.2</td>
<td>52.5</td>
<td>49.4</td>
</tr>
<tr>
<td>Seed dry weight (g plant⁻¹)</td>
<td>63.8</td>
<td>26.6</td>
<td>61.7</td>
<td>42.8</td>
<td>45.0</td>
</tr>
<tr>
<td>Seed HI (%)</td>
<td>40.9</td>
<td>28.8</td>
<td>38.5</td>
<td>35.1</td>
<td>30.1</td>
</tr>
</tbody>
</table>

** Indicates significance at P = 0.01.
*** Indicates significance at P = 0.001.

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**Table 1.** Total dry matter, root to shoot ratio (angular transformed), pod dry weight, pod harvest index (HI, angular transformed), seed to pod ratio (angular transformed), seed dry weight, and seed HI (angular transformed) of four peanut genotypes (ICGV 86015, 796, ICGV 87282 and 47-16) grown at air temperatures of 28/22°C (mean = 25°C) or 38/22°C (mean = 30°C) from 21 to 90 DAP. Data are the means of five replicates, sampled at 90 DAP.

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**Table 2.** Mean squares for comparison of regressions of pod and seed HI and time (Table 3) on the intercept and slope of the linear relation between pod and seed HI and time (Table 3). The start of the linear increase in HI, and dHI/dt, therefore varied among genotypes at 28/22°C and 38/22°C. Further comparisons of the slopes and intercepts were made to compare the four genotypes at 28/22°C, and to compare the effects of temperature on individual genotypes. Pod and seed growth, however, had not ended in any genotype before the final harvest at 90 DAP and therefore the effect of temperature and genotype on the duration of the phase of linear increase in HI could not be determined.

Temperature had a similar effect on dHI/dt for pods and seeds in all genotypes and dHI/dt values for pod and seed were comparable (Table 3). At 28/22°C the linear phase of seed HI began between 40 and 57 DAP, 2 to 9 d after pod-filling started. Values of seed dHI/ dt at 28/22°C were significantly (P < 0.05) greater in genotype ICGV 86015 (0.0096 HI d⁻¹) than in genotypes 796 and ICGV 87282 (common slope of 0.0079 HI d⁻¹) and 47-16 (0.0062 HI d⁻¹). Lower seed dry weights at 90 DAP in genotypes ICGV 87282 and 47-16 were therefore due to smaller values of dHI/dt and shorter durations of seed filling.

**Table 2.** Mean squares for comparison of regressions of pod and seed harvest index (HI) of four peanut genotypes grown at a mean day/night temperature of 28/22°C and 38/22°C from 21 to 90 DAP.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Df</th>
<th>Pod HI</th>
<th>Seed HI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sample date</td>
<td>1</td>
<td>7457***</td>
<td>2768***</td>
</tr>
<tr>
<td>Temperature</td>
<td>1</td>
<td>749***</td>
<td>493***</td>
</tr>
<tr>
<td>Genotype</td>
<td>3</td>
<td>837***</td>
<td>406***</td>
</tr>
<tr>
<td>Genotype × Temperature</td>
<td>3</td>
<td>102***</td>
<td>82***</td>
</tr>
<tr>
<td>Time × Genotype</td>
<td>3</td>
<td>170***</td>
<td>11*</td>
</tr>
<tr>
<td>Time × Temperature</td>
<td>1</td>
<td>140***</td>
<td>70***</td>
</tr>
<tr>
<td>Time × Genotype × Temperature</td>
<td>3</td>
<td>29***</td>
<td>12*</td>
</tr>
<tr>
<td>Residual</td>
<td>34</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>Total</td>
<td>49</td>
<td>202</td>
<td>62</td>
</tr>
</tbody>
</table>

* Indicates significance at P = 0.05
*** Indicates significance at P = 0.001.
High temperature significantly affected the onset of the linear phase of pod and seed HI and the value of dHI/dt, and the effect varied among genotypes (Table 3). In genotype 47-16, neither the start of the linear phase nor the value of dHI/dt for pod or seed filling were affected by high temperature ($P > 0.30$), and common regressions could be fitted to describe the response to time (Table 3, Fig. 2). In genotype 796, high temperature had no effect on dHI/dt of pods and seeds, but did significantly ($P < 0.01$) delay the start of pod and seed filling by 5 d. In genotypes ICGV 86015 and ICGV 87282, however, high temperature delayed the start of pod and seed filling and reduced the value of dHI/dt ($P < 0.001$) (Table 3). The value of dHI/dt in genotype ICGV 87282 was particularly sensitive to high temperature, and was reduced from 0.0076 at 28/22°C to 0.0028 HI d$^{-1}$ at 38/22°C. Genotype ICGV 86015 was the only genotype where high temperature had a greater effect on seed than pod filling, delaying the start of the linear phase of HI by 6 d for pods and 9 d for seeds, and reducing dHI/dt by 20% for pods and 30% for seeds. This differential effect of high temperature on pod and seed dHI/dt was reflected in the seed to pod ratio (Table 1).

**DISCUSSION**

This study has confirmed that the increase in pod and seed HI in peanut is linear in both Spanish and Virginia genotypes at near optimum (25°C) and high (30°C) mean temperatures. The values of dHI/dt for pods among the four genotypes, which at 28/22°C ranged from 0.0058 to 0.0109 HI d$^{-1}$, were similar to reported values for other genotypes of 0.0057 to 0.0082 d$^{-1}$ (Stirling and Black, 1991), 0.0072 d$^{-1}$ (Bennett et al., 1993) and 0.0080 d$^{-1}$ (Hammer et al., 1995). Values of dHI/dt for seeds were similar to those for pods, between 0.0062 and 0.0096 HI d$^{-1}$, and the value of 0.0063 HI d$^{-1}$ reported by Wheeler et al. (1997). There is, therefore, significant variation in dHI/dt among peanut genotypes.

<table>
<thead>
<tr>
<th>Genotype</th>
<th>Temperature (°C)</th>
<th>Pod X-Intercept (d ± SE)</th>
<th>Pod Slope (10$^{-2}$ ± SE)</th>
<th>Seed X-Intercept (d ± SE)</th>
<th>Seed Slope (10$^{-2}$ ± SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>ICGV 86015</td>
<td>28/22</td>
<td>42.5 (0.89)</td>
<td>1.09 (0.035)</td>
<td>47.8 (1.37)</td>
<td>0.96 (0.052)</td>
</tr>
<tr>
<td></td>
<td>38/22</td>
<td>48.8 (1.65)</td>
<td>0.89 (0.060)</td>
<td>56.7 (1.01)</td>
<td>0.69 (0.035)</td>
</tr>
<tr>
<td>796</td>
<td>28/22</td>
<td>38.0 (1.79)</td>
<td>0.90 (0.030)</td>
<td>40.0 (1.42)</td>
<td>0.78 (0.033)</td>
</tr>
<tr>
<td></td>
<td>38/22</td>
<td>42.7 (1.30)</td>
<td>0.65 (0.017)</td>
<td>45.1 (2.40)</td>
<td>0.76 (0.086)</td>
</tr>
<tr>
<td>ICGV 87282</td>
<td>28/22</td>
<td>44.3 (1.93)</td>
<td>0.76 (0.055)</td>
<td>53.0 (2.58)</td>
<td>0.76 (0.029)</td>
</tr>
<tr>
<td></td>
<td>38/22</td>
<td>49.1 (1.44)</td>
<td>0.29 (0.017)</td>
<td>56.6 (2.53)</td>
<td>0.28 (0.029)</td>
</tr>
<tr>
<td>47-16</td>
<td>28/22</td>
<td>51.0 (1.61)</td>
<td>0.58 (0.038)</td>
<td>55.3 (1.64)</td>
<td>0.62 (0.046)</td>
</tr>
<tr>
<td></td>
<td>38/22</td>
<td>51.0 (1.61)</td>
<td>0.58 (0.038)</td>
<td>55.3 (1.64)</td>
<td>0.62 (0.046)</td>
</tr>
</tbody>
</table>
High temperature had a significant effect on pod and seed HI in some genotypes, and this was associated both with effects on dHI/dt and the timing of the onset of the linear phase of pod and seed filling. Hammer et al. (1995) showed in genotype Early Bunch that dHI/dt for pods was 0.0084 d⁻¹ at mean temperature of 25°C, declining to 0.0045 d⁻¹ at 30°C, a reduction of about 50%. Among the genotypes studied here a negative response to high temperature (mean 30°C) for pod and seed dHI/dt was observed in ICGV 86015 (20 to 30% reduction) and ICGV 87282 (60 to 65% reduction), whereas in genotypes 796 and 47-16 no reduction in dHI/dt was observed. Similarly, Wheeler et al. (1997) reported no effect of 6 d exposure at pegging to mean temperatures of 30 to 45°C on seed dHI/dt in genotype ICGV 86021. Therefore, the response of genotype Early Bunch to temperature quantified by Hammer et al. (1995) may not be appropriate for all genotypes. One factor that may have confounded the response to temperature of genotype Early Bunch is photoperiod; long days with mean photoperiods >12 h d⁻¹ reduce partitioning to fruits and seeds (Flohr et al., 1990). Many of the studies with Early Bunch were conducted at latitudes of 24 to 30°N and hence under potentially long days. Results presented here, and those of Wheeler et al. (1997), are, however, all from a 12 h d⁻¹ photoperiod to remove any potentially confounding effects of photoperiod.

In some of the genotypes examined here, high temperature delayed the start of pod and seed-filling by as much as 10 d—a substantial effect in short-duration genotypes with a pod-filling period of 60 d or less. Stress, whether water, heat, or nutrient, has been reported to slow the rate of plant development (Craufurd et al., 1993), including the rate of pod addition in peanut (Williams and Boote, 1995). These effects have important consequences for the durations of developmental and growth phases. For example, Wheeler et al. (1997) found that the start of seed filling was progressively delayed by as much as 7 d by exposure to temperature treatments between 30 and 45°C for 6 d. Stirling and Black (1991) and Ketting and Wheless (1989) also observed delays in reproductive development following high temperature (maximum temperature >35°C) events. This delay in development may be as significant as the reduction in dHI/dt for final pod and seed yield, particularly if the pod or seed filling duration is also shortened.

Genotypes clearly differed in their responses to high temperature and hence in heat tolerance/susceptibility. Seed dry weight was reduced by 20 to 30% in genotypes 796 and 47-16, 58% in ICGV 86015 and 78% in ICGV 87282. In genotypes 796 and 47-16, lower seed dry weight was due solely to the effects of high temperature on total dry matter accumulation; high temperature did not affect dHI/dt. In contrast, in genotypes ICGV 86015 and ICGV 87282 both dry matter accumulation and dHI/dt were reduced, particularly in ICGV 87282. On the basis of responses of dry matter accumulation to high temperature, and allowing for differences in yield potential under optimum conditions, genotypes did not differ in tolerance. However, on the basis of partitioning to pods and seeds, genotypes 796 and 47-16 could be classified as moderately heat tolerant and ICGV 87282 as heat susceptible. These data therefore support the field-based classification of Greenberg et al. (1992) and show that there is genotypic variation in the ability of genotypes to maintain partitioning at high temperature in peanut. There was also some evidence from genotype ICGV 86015 that responses of pod and seed dHI/dt to high temperature may differ and this requires further investigation.

It is not clear what the physiological basis of heat tolerance is in the genotypes studied here, but is it associated with higher optimum temperatures for pollen germination and tube growth, better fruit set at high air temperature, better fruit growth at high soil temperature and better membrane integrity at high temperature (Craufurd et al., 2000; Kakani et al., 2000). The responses of flower production, pollen production, fruit set, or sink size to high temperature have been described and modeled by Vara Prasad et al. (1999, 2000). These effects of high temperature on a number of processes may be reflected in genotypic differences in the optimum temperature (Ismail and Hall, 1998), which for pod growth in peanut is comparatively low at 24°C (Cox, 1979).

Peanut growth simulation models, such as CROPGRO-peanut (Boote et al., 1998) or QNUT (Hammer et al., 1995) do not at present describe differential genotypic responses to high temperature. The data generated from this research clearly suggest that crop models need to take account of genotypic differences in the response of both pod and seed dHI/dt to temperature, as well as the effects of high temperature on the onset of pod and seed filling, if pod and seed yields are to be successfully simulated in warm environments. The CROPGRO-peanut model has a number of genetic coefficients and phase modifiers that describe and modify phase durations, and vegetative and reproductive attributes (Boote et al., 1998). The mechanistic CROPGRO model allows the input of genotype-specific traits to predict daily growth and development in response to environment, and allows a partitioning limit function that decreases partitioning to pods at high temperatures to be set (Boote et al., 1998). There is potential, therefore, to simulate genotypic variation in response to high temperature in CROPGRO by adding additional coefficients that describe the sensitivity or tolerance of genotypes to high temperature. The fact that dHI/dt was constant at optimum and high temperature for a particular genotype is also useful for less mechanistic models such as QNUT, as it is only necessary to track total crop mass and multiply by a daily value of dHI/dt to obtain seed mass. However, to simulate genotypic responses, the sensitivity of dHI/dt to temperature (and other factors such as photoperiod) has to be determined.

In summary, this research has shown that high air temperature reduces total dry matter accumulation and pod and seed dry weight. Pod and seed HI in peanut is linear at both optimum (day/night, 28/22°C) and high (38/22°C) temperatures. High temperature significantly delayed the start of pod and seed filling and reduced
dHI/dr in genotypes ICGV 86015 and ICGV 87282. The value of dHI/dr in genotypes 796 and 47-16, however, was not affected by high temperature. Genotypic variation in dHI/dr of pods and seeds at high temperature, which contributes to higher pod and seed yields, is therefore present in peanut.

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