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Photosynthetic and Respiratory Characteristics of Peanut Cultivars Adapted to Varying Night Temperatures[1]

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ABSTRACT

Relatively mild night temperatures can reduce leaf carbon dioxide exchange rates (CER) and dry matter (DM) accumulation in peanut (*Arachis hypogaea* L.). To investigate differences among cultivars in response to long-term exposure to a range of night temperatures, three peanut cultivars (OAC Ruby, Chico, and Early Bunch) with known differences in chilling sensitivity were grown in controlled-environment cabinets at the University of Guelph, Ontario. Effects of long-term exposure to night temperatures from 9 to 20 C were assessed in terms of leaflet and whole plant CER, DM accumulation, and phenological development. Effects of night temperature on rate of phenological development and DM accumulation were consistent with differences in accumulation of degree-days. Cultivars did not differ in daytime leaf CER response to all night temperatures except 9 C, at which CER for OAC Ruby was higher than for Early Bunch or Chico. CER in the 9 C treatment was 92% of the CER at 20 C for OAC Ruby and 80% for Early Bunch and Chico. Continuous exposure to night temperatures of 10 C reduced CER sensitivity to low daytime temperature in OAC Ruby, but Early Bunch was unaffected. Specific respiration rates were higher for plants of OAC Ruby than Early Bunch in the 10 C treatment, with indications that these differences were due to increased maintenance requirements. The ability of OAC Ruby to adapt to cool-night conditions may have a significant impact on crop performance in cooler environments.

Key Words: Peanut, photosynthesis, respiration, adaptation, night temperature, chilling.

Plants originating from tropical and subtropical parts of the world typically show dramatic reductions in growth and survival upon exposure to low (chilling) temperatures that are still well above freezing (e.g., 10 to 12 C) (Lyons, 1973; Hällgren and Öquist, 1990). However, within these broad geographic regions, species can occur within a wide diversity of habitats (e.g., at varying altitudes) which may result in considerable genotypic diversity in traits like photosynthetic capacity and photosynthetic temperature adaptation (Slatyer and Ferrar, 1977; Berry and Björkman, 1980; El-Sharkawy *et al.*, 1992). In addition, numerous species cope with marked seasonal and diurnal temperature fluctuations within a given habitat by exhibiting photosynthetic temperature acclimation (Öquist, 1983; Veres and Williams, 1984) or some degree of hardening response (Öquist and Martin, 1986; Grantz, 1989). However, not all chilling-sensitive plants show a chill-hardening capacity (Bauer *et al.*, 1985; Wolfe, 1991) and those that do often show only a marginal decrease in sensitivity to chilling temperatures (Öquist and Martin, 1986).

Peanut (*Arachis hypogaea* L.) is a tropical legume crop grown under a wide range of environmental conditions, although predominantly in tropical and subtropical regions. However, even in these environments, crops are often exposed to large diurnal and seasonal temperature variations (Lawn and Williams, 1987). The crop is extremely frost sensitive, and reported optimum temperatures for growth and photosynthesis range from 25 to 35 C and 20 to 30 C, respectively (Ketring *et al.*, 1982). Recent studies (Bell *et al.*, 1992, 1993, 1994b) have shown strong correlations among rate of dry matter (DM) accumulation, leaf carbon dioxide exchange rate (CER), and night temperatures. Both radiation use efficiency and CER were shown to decline linearly as minimum temperatures decreased from 20 to 9 C, although cultivar variation in CER sensitivity also was indicated, especially when plants were acclimated to fluctuating day/night temperatures under ambient conditions (Bell *et al.*, 1994b).

Bell *et al.* (1994b) reported relative cultivar response

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to a range of night temperatures in terms of leaflet gas exchange parameters for unhardened plants. The objectives of these studies were also to assess relative cultivar performance, but under conditions of continous exposure to a range of night temperatures and in terms of both leaf and whole plant carbon balance and DM production.

Materials and Methods

Cultural Details. Two experiment series were conducted during the spring and summer of 1992 at Guelph, Ontario. In each experiment peanut seedlings were grown in free-draining pots containing a mixture of fine grade vermiculite and topsoil (0-10 cm) of a Fox loamy sand (50:50, v:v). Pot size varied with experiment and with sampling objectives, so that pots contained either 8.5 or 1.5 kg of the air-dry potting mixture. Soil in each pot was fertilized with a complete fertilizer mix to ensure nutrients were not limiting (Bell *et al.*, 1994b) and inoculated with the commercial strain of *Bradyrhizobium*. Three peanut cultivars of varying origin, botanical type and chilling sensitivity (Bell *et al.*, 1994b) were used in these experiments. These were the very early maturity spanish cv. Chico and the early maturity virginia cv. Early Bunch and valencia cv. OAC Ruby, with the latter subsequently referred to as Ruby.

Large pots were sown at five seeds per pot and emerging seedlings thinned to leave three healthy, established plants, while small pots were sown at three seeds per pot and emerging seedlings thinned to one healthy established plant. All pots were kept in controlled-environment growth rooms at 25/20 C (day/night) temperatures until seedlings emerged. Pots then were allocated randomly to the various night temperature treatments in respective controlled-environment growth cabinets. In growth cabinets, plants were grown under a photosynthetic photon flux density (PPFD) of 550 to 600 μmol $m^{-2}sec^{-1}$ at the top of the canopy, 70% relative humidity, and ambient CO_2 levels ranging from 320 to 380 mL L^{-1} during a 24-hr period. Daytime temperatures of 28 ± 1.5 C were imposed during a 16-hr photoperiod.

Experiment 1 was undertaken to assess effects of continuous exposure to various night temperatures on plant growth and DM accumulation and leaflet CER at a single daytime temperature. Experiment 2 was undertaken to determine responses to daytime temperature of whole plant CER, rates of CO_2 efflux in the dark and leaflet chlorophyll content of plants adapted to 20 or 10 C night temperatures.

Experiment 1. Four growth cabinets were randomly allocated to night temperature treatments of 20 ± 1.2, 15 ± 1.0, 12 ± 0.7, and 9 ± 0.5 C in combination with daytime temperatures of 28 ± 1.5 C. All cabinets were adjusted so that temperatures were raised to 20 C for at least 30 min at the end of the 8-hr dark period, prior to illumination and the onset of the daytime temperature regime. Each cabinet contained 10 large pots of each cultivar, with all pots re-randomized twice each week. Temperature treatments were re-allocated to different cabinets in three separate replications of the experiment. A split plot design with three replicates was used to analyze all data, with night temperature treatments as main plot effects, cultivars as subplot effects, and individual pots treated as samples.

Phenological development was recorded during the course of the experiment using means from observations of six plants per treatment. The rate of vegetative development was assessed from the rate of appearance of nodes on the main axis (V-stages) (Boote, 1982). Time to first flower (50% of plants with at least one flower) also was assessed. Both parameters were related to accumulated degrees-days, with a base temperature of 13 C assumed for both processes (Leong and Ong, 1983; Bell *et al.*, 1991).

Beginning at 18 to 20 d after emergence (DAE), leaf CER measurements were made on three occasions at weekly intervals, beginning approximately 4 hr into the photoperiod. The sampling order was randomized to minimize any effects of measurement time on leaf CER, and care was taken to ensure uniform PPFD (650 ± 15 μmoles $m^{-2}sec^{-1}$), air temperature (29.5 ± 1.0 C), and ambient CO_2 (330 ± 15 mL L^{-1}) levels during the measurement sequence. Leaflet CER was measured on single leaflets from youngest fully expanded leaves of either the main stem or primary laterals. Each leaflet was briefly enclosed in a 0.25-L portable chamber system (Model 6200, Li-Cor Inc., Lincoln, NE) during measurement, with calibration and measurement details similar to those reported elsewhere (Bell *et al.*, 1994b). Values of leaflet CER, stomatal conductance, and intracellular CO_2 concentration were determined using standard procedures for the Li-Cor 6200 system. After CER measurement, leaflet laminae were harvested and leaflet area determined with a planimeter (LI-3100, Li-Cor Inc., Lincoln, NE). Leaflets then were dried at 80 C and weighed for determination of specific leaf weight (SLW, g m^{-2}).

Four pots of each cultivar were harvested immediately after the first and third CER samplings (Harvest 1 and Harvest 2, H1 and H2) and total leaf area, and leaf, stem and root dry weights were determined. Leaf samples from H2 were ground and analyzed for N content by Kjeldahl analysis, and for concentrations of C (combustion at 1350 C) and ash (residual after combustion at 500 C).

On two occasions immediately after the final CER measurement but preceding H2 in Rep. 1 and Rep. 2, rates of CO_2 efflux in the dark by young, fully expanded leaflets were determined with a Li-Cor 6200 system. All measurements were made from 1 to 2 hr after the beginning of the night period and at the respective night temperatures for the 20, 15, and 12 C treatments.

Experiment 2. Fourteen small (1.5 kg) pots of Ruby and Early Bunch were grown in growth cabinets at night temperatures of either 20 ± 1.2 or 10 ± 0.8 C from seedling emergence until first flower appearance. Plants were then placed in whole-plant chambers within a controlled-environment cabinet to determine both CO_2 efflux rates in the dark (four plants/treatment) and whole-plant CER-temperature response (six plants/treatment). Details of chamber characteristics have been reported by Pararajasingham and Hunt (1991). Briefly, the enclosures represented a partially closed system in which the gas circuit was closed only during the actual measurement. The root compartment was separated from the top compartment and not included in any measurements of gas exchange. Copper-constantan thermocouples introduced into each compartment were used to sense circulating air temperature, and chambers were arranged such that PPFD of 610 ± 10 μmol $m^{-2}sec^{-1}$ was incident at the top of the canopy in each of the four chambers within the cabinet.

The efflux rate of CO_2 from shoots was measured as the rate of increase in CO_2 concentration of the circulating air with time in the dark, with observations made at temperatures of 19.7 ± 0.2 and 11.2 ± 0.1 C. Four plants were measured from each of the 20 and 10 C treatments of Ruby and Early Bunch so that each cultivar-night temperature

combination was measured in each of the four chambers used in the experiment. Measurements were made 4 to 6 hr after the beginning of the photoperiod on each day, with plants allowed 1 hr in the dark to equilibrate to the new temperature prior to measurement. Measurements of CO_2 concentration were made with the infra-red gas analyzer of the Li-Cor 6200, with determinations made every second for 120 sec, and means recorded every 30 sec. At the end of the measurement period, plants were carefully harvested at ground level, washed, separated into leaf and stem components, and oven-dried at 80 C. Samples subsequently were weighed and ground for determination of C and ash contents. The methodology was similar to that in Exp. 1. The means of CO_2 measurements/L of system volume were regressed against time and the slope ($\mu L\ CO_2\ L^{-1}sec^{-1}$) was converted to mg CO_2 $plant^{-1}hr^{-1}$.

Whole-plant CER (roots excluded) was determined by methods similar to that used for CO_2 efflux rate, with observations made at 5-8 C intervals between approximately 12.5 and 34 C. Measurements were always begun at the highest temperature. Each chamber was opened to allow free air circulation during a 1-hr equilibration to each new air temperature before the system was closed for a measurement. Measurements of CO_2 concentration were made for 40 s, with means recorded every 10 sec. The rate of change in CO_2 concentration with time was expressed as mg CO_2 $plant^{-1}hr^{-1}$. At the end of the assessment period, plants were harvested and separated into leaf and stem components. Leaf area per plant was determined using a planimeter, and plants were dried at 80 C, weighed and ground for analysis of N, C, and ash contents.

Estimates of leaf chlorophyll content were made with the SPAD-502 portable chlorophyll meter (Minolta Corp., Ramsay, NJ) on leaflets similar to those used in CER measurement. The methodology used to collect leaf chlorophyll data has been reported in detail in Dwyer *et al.* (1991). Briefly, two estimates of chlorophyll content were made with a single SPAD-502 meter on the fully expanded terminal leaflets on a selected branch and averaged. Eight separate determinations were made on different plants of each cultivar in each temperature treatment, with the meter rezeroed every 10 samples. Due to a lack of information on the relationship between meter readings and actual leaf chlorophyll content in peanut and the reported variation in calibrations between species (Marquardt and Lipton, 1987), treatment comparisons were made on actual meter readings rather than estimated leaf chlorophyll content.

Data Analysis and Calculations. Analyses of variance using the GLM procedure of SAS (1985) were undertaken on destructive harvest, leaf chlorophyll, and leaf CER data. Destructive harvest data were analyzed as a split plot design with three replicates, night temperatures as main plots, cultivars as subplots, and four samples per replicate. Homogeneity of error variance, indicated by a nonsignificant Bartlett's test between harvest times for the 20, 15, and 12 C treatments, allowed a pooled analysis of variance to be undertaken with harvest times as sub-sub plots. Similar pooled analyses were undertaken for leaf analytical data, leaflet CER (all four night temperature treatments), and dark CO_2 efflux rates (the latter converted to specific rates to account for differences in SLW among treatments).

Data on whole plant CER-temperature response was complicated by plant-to-plant variation in leaf area and chamber-to-chamber variation in actual air temperature. The CER-daytime temperature response for each plant in each treatment, therefore, was analyzed by the REG procedure of SAS (1985). Models with both linear and quadratic components of temperature successfully accounted for most of the variation in whole-plant CER (R^2 = 0.81 to 0.95). Values of CER_{max} for each plant were used to convert absolute CER values (mg CO_2 $plant^{-1}hr^{-1}$) at each recording temperature to relative CER (i.e., relative CER = measured CER/CER_{max}). Relative CER (RCER) values for all plants in each night temperature treatment then were pooled and an RCER-daytime temperature response was determined for each treatment using the REG procedure of SAS. A similar approach has been used to standardize data for a given treatment imposed across a range of sites with differing absolute yield potential (Strong, 1981).

Data on whole-plant CO_2 efflux measurements required similar treatment, although the temperature variation from chamber to chamber was less than for CER determinations. Individual plant CO_2 efflux data were converted to specific rates (i.e., mg CO_2 g^{-1} DM hr^{-1}) and analyzed for each cabinet temperature (i.e., 19.7 and 11.2 C) with the GLM procedure of SAS. Chamber air temperature was used as a covariate in the analysis.

Stahl and McCree (1988) used the following equation to describe the C balance over a given time interval:

$$NET = Yg\ (GROSS - m\ BIOMASS), \qquad [Eq.\ 1]$$

where NET and GROSS are the net and gross gain in C, respectively, *Yg* is the yield of growth parameter (g C retained per g C assimilated), and *m* is the maintenance respiration coefficient (mg C respired per g C in existing biomass). Whole-plant CER (mg CO_2 $plant^{-1}$ hr^{-1}) and respiration rates (mg CO_2 g^{-1} DM hr^{-1}) at a single temperature were derived from the CER-temperature and CO_2 efflux-temperature relationships indicated earlier, and expressed in units of mg C $plant^{-1}hr^{-1}$ for plants with leaf area and DM equal to the mean for each cultivar and temperature regime. Values of whole-plant CER represented NET (Eq. 1), while GROSS was calculated as the sum of whole-plant CER plus dark respiration. The temperature chosen was 22 C, so CER rates were near the maximum and no extensive extrapolation of respiration data was necessary.

Analytical data for whole-plant C and ash contents were used to estimate reciprocal production values (PVI; g glucose required g^{-1} DM synthesized) as outlined by Vertregt and Penning de Vries (1987). The relationship between PVI and biomass carbon was investigated for plants from two harvests taken 7 d apart (i.e., immediately prior to whole plant CO_2 efflux measurements and 5 d after completion). Reciprocal production values decreased significantly as biomass carbon increased; thus PVI, C content, and plant DM from each harvest was used to calculate PVI and C content of new DM synthesized during the 7-d period. The relative carbon concentrations of this new DM and of glucose were used to convert PVI of new DM (g glucose g^{-1} DM) to *Yg* (g C g^{-1} C). By using these derived Yg values, Equation 1 could then be solved to provide an estimate of the maintenance respiration coefficient *(m)*.

Estimates of *m* were also derived from specific CO_2 efflux data for fully expanded leaflets with the assumption that, as tissue was no longer growing, growth respiration was absent and total respiration was attributable to maintenance (Amthor, 1989).

Results

All cultivars showed strong responses to night temperature in all growth components except the proportion of total DM allocated to root growth and between leaves and stem at H1. (Table 1). Effects of treatments at both H1 and H2 were similar, although the magnitude of differences among cultivars and temperature regimes was greater at H2. Cultivars behaved similarly in response to reduced night temperature in that production of leaf area and total DM fell sharply, while SLW and SLN increased. Data for the ratio of leaf:stem DM, especially at H2, indicate that unlike the proportion of total DM allocated to roots, distribution of DM between above-ground components was sensitive to night temperature (Table 1). All cultivars showed a linear decline in the leaf:stem DM ratio with increasing thermal time (R^2 = 0.78 to 0.79), with the rate of decline significantly less in Chico (b = -0.0034±0.0005 degree-day^{-1}) than in Ruby or Early Bunch (pooled b = -0.0044±0.0005 degree-day^{-1}); thus the differences in leaf:stem DM ratio were attributable to differing rates of accumulation of thermal time.

Cultivars differed significantly in both rate of vegetative development and thermal time required for flowering, although neither parameter was affected by temperature treatment. Chico showed a more rapid rate of V stage accumulation (b = 0.026±0.001 degree-day^{-1}) than Ruby and Early Bunch (pooled b = 0.024±0.001 degree-day^{-1}). Chico also required less time to flower (207.9±9.4 degree-days) than Early Bunch (299.3±17.8 degree-days). The differences between Chico and Ruby (219.3±12.2 degree-days) were not statistically significant (P<0.05). These differences resulted in Chico flowering 0.8 and 1.2 calendar days earlier than Ruby and 7.1 and 9.4 calendar days sooner than Early Bunch in the 20 and 9 C night treatments, respectively.

Long-term exposure to differing night temperatures caused similar trends in daytime leaflet CER among cultivars, with lower night temperatures resulting in lower daytime CER (Fig. 1). There was, however, an apparent cultivar x night temperature interaction (significant at P<0.08). CER in Ruby was 3.5 to 5.4% lower than that in Chico or Early Bunch, respectively, under 20 C night temperatures, but was 10% higher than both cultivars under night temperatures of 9 C. The differences among cultivars were significant (at P<0.05) only at 9 C night temperatures. There was no consistent relationship between leaf chlorophyll content (indicated

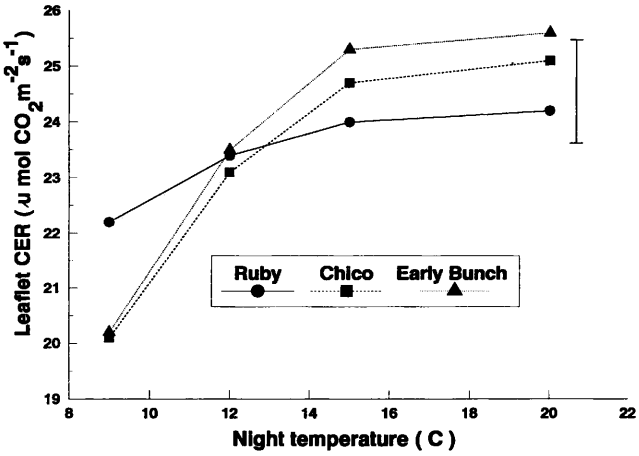

Fig. 1. Effects of long-term exposure to various night temperatures on CER of young, fully expanded leaflets measured during the day at 29.5±1.0 C with ambient CO_2 concentrations of 315±15 mL L^{-1} and 650±15 mmol m^{-2} sec^{-1} PPFD. Data are shown for the cultivars OAC Ruby, Chico, and Early Bunch, with vertical bar indicating an LSD (0.05).

Table 1. Dry matter (DM) and components and specific leaf nitrogen (SLN) of three peanut cultivars grown at four night temperatures, and assessed on two harvest dates (18 to 20 DAE, H1; 28 to 30 DAE, H2). Data are means of night temperature and cultivar treatments as temperature x cultivar interactions were not significant. Values of LSD (0.05) are shown for each harvest date (no. = 9 for H1, no. = 12 for H2).[a]

	H1					H2					
Variable	SLW	Leaf area	Leaf DM: stem DM	Total DM	Root DM: total DM	SLW	Leaf area	Leaf DM: stem DM	Total DM	Root DM: total DM	SLN
	g m^{-2}	cm^{2}plant^{-1}		g plant^{-1}		g m^{-2}	cm^{2}plant^{-1}		g plant^{-1}		g N m^{-2}
Night temp. (C)											
20	36.0	562	1.66	4.70	0.29	39.3	1750	1.07	16.6	0.19	1.43
15	40.9	417	1.88	3.90	0.31	46.6	1320	1.34	13.7	0.20	1.57
12	41.9	347	1.84	3.46	0.34	50.1	1030	1.55	10.9	0.19	1.66
9	ND	ND	ND	ND	ND	47.1	663	1.83	6.5	0.23	1.81
LSD (0.05)	2.2	147	NS	0.85	NS	2.5	159	0.22	2.6	NS	0.14
Cultivar											
OAC Ruby	42.1	478	1.65	4.81	0.33	51.5	1210	1.30	14.2	0.21	1.73
Chico	35.2	420	1.66	3.40	0.30	50.0	1120	1.36	10.2	0.20	1.54
Early Bunch	41.9	427	2.07	3.85	0.31	45.0	1250	1.67	11.3	0.19	1.62
LSD (0.05)	2.0	58	0.06	0.45	NS	1.9	114	0.07	1.3	NS	0.09

[a]ND = not determined.

by SPAD readings) and leaflet CER in response to night temperature (data not shown).

The effects of long-term exposure to night temperatures of 10 or 20 C on response of whole-plant CER to varying daytime temperatures were examined for Early Bunch and Ruby. Differences in leaf area plant^{-1}, both between and within temperature regimes, made comparisons of absolute values of whole-plant CER among treatments meaningless. Differences in temperature response between night temperature treatments were, therefore, examined in terms of relative CERs (RCER). Effects of daytime temperature on RCER of whole plants were examined with multiple regression techniques. Models incorporating linear and quadratic temperature components were able to account for much of the variation in RCER (Fig. 2; R^2 = 0.82 to 0.91).

The response of RCER to daytime temperature was not significantly different between Early Bunch grown at 10 and 20 C night temperatures or Ruby grown at 20 C night temperatures (Fig. 2). Ruby grown at 10 C night temperatures differed significantly from the other treatments due to an improved tolerance to low daytime temperatures. Optimum daytime temperature for CER of both cultivars grown under 20 C nights was near 24.5 C, with both cultivars showing RCER>0.9 in the range of 20 to 30 C. As daytime temperatures fell to 12.0 C (the limit of our data), RCER had fallen to 0.52 and 0.48 for Early Bunch and Ruby, respectively (Fig. 2). In contrast to the data recorded for Early Bunch, Ruby grown under 10 C nights showed a different CER response to daytime temperature than if grown under 20 C nights. Optimum daytime temperature fell to approximately 23 C, and RCER remained ≥ 0.9 between 16 and 31 C, a wider range than that shown in the 20 C treatment. Perhaps most important, however, was the significantly improved CER capacity at low daytime temperature, with RCER at 12.0 C still 0.70.

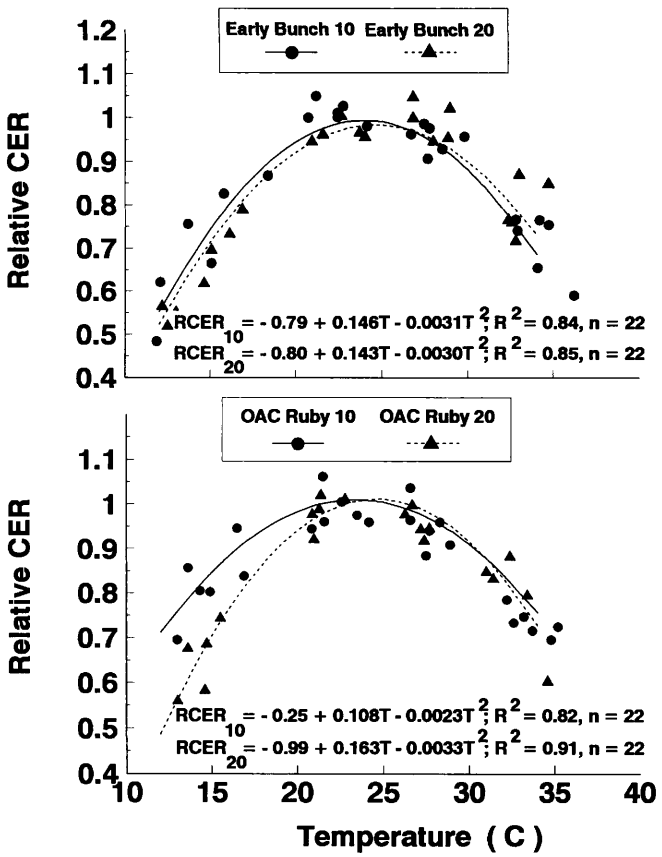

Fig. 2. Relationships between relative whole plant CER and daytime air temperature for two peanut cultivars grown exclusively under 10 C or 20 C night temperatures. Data are shown for (a) Early Bunch and (b) OAC Ruby. Equations describing relationships are shown, with the relationship for OAC Ruby at 10 C significantly different to all others (P<0.05).

Specific respiration rates of whole plant above-ground DM (Table 2) were significantly greater for Ruby than for Early Bunch. Although specific respiration rates of plants of Ruby acclimated to 10 C nights were higher than for plants at 20 C, the difference was not statistically significant. Similar data for leaf specific respiration rates (Table 3) showed no differences between Ruby and Early Bunch in plants acclimated to 20 C and measured near that temperature, but differences became increasingly apparent as the night temperature at which plants were acclimated declined.

Measurement temperature effects on whole-plant specific respiration rates showed Q_{10} ranging from 1.77±0.23 to 2.07±0.27 and a mean Q_{10} across all treatments of 1.95, very similar to the expected value of 2.0 (Johnson and Thornley, 1985; Amthor, 1989).

Carbon and ash concentration for whole plants of Ruby and Early Bunch showed no significant effects of cultivar or temperature regime. Values did differ significantly with time, with whole-plant carbon content falling from 438±6 to 423±5 mg g^{-1} DM and ash content rising from 109±4 to 133±8 mg g^{-1} DM between 25 and 32 DAE. Pooled reciprocal production values (PVI) of 1274±11.7 and 1192±9.2 mg glucose g^{-1} DM were obtained for the early (25 DAE) and late (32 DAE) harvests, respectively.

Actual mean plant DM data, derived values of gross input, net gain and Yg, and estimates of the maintenance coefficient *m* (mg C g^{-1} C hr^{-1}) are shown in Table 4. Ruby and Early Bunch showed similar *m* values in the 20 C night temperature treatment, but *m* of Ruby acclimated to 10 C nights was 85% greater than Ruby in the 20 C treatment and 250% greater than *m* of Early Bunch in the corresponding treatment.

Carbon and ash concentrations of fully expanded leaflets did not differ among temperature treatments, and

Table 2. Dry matter (DM), nitrogen concentration (N), and specific respiration rate of whole plants (no. = 4) of Ruby and Early Bunch grown at 20 or 10 C night temperatures.

Cultivar	Night temp.	DM	N	Specific respiration measured at 11.2 C	Specific respiration measured at 19.6 C
	C	g plant^{-1}	%	mg CO_2 g^{-1} DM hr^{-1}	
Ruby	20	6.1±1.1	2.84±0.14	0.203±0.015	0.307±0.026
	10	4.2±0.7	2.92±0.11	0.216±0.015	0.368±0.025
Early Bunch	20	6.2±1.1	2.89±0.13	0.153±0.016	0.266±0.024
	10	3.9±0.6	2.89±0.14	0.161±0.014	0.259±0.025

Table 3. Nitrogen concentration (N), total respiration rates, specific leaf weights, and calculated specific respiration rates for 10 fully expanded leaves of Ruby and Early Bunch grown at 20, 15 and 12 C night temperatures.

Cultivar	Night temp.	Measurement temp.	N	Total respiration rate	Specific leaf weight	Specific respiration rate
	-------- C --------		%	mg CO_2 m^{-2} hr^{-1}	g m^{-2}	mg CO_2 g^{-1} DM hr^{-1}
Ruby	20	21.9±0.5	3.84±0.22	145.7±9.0	69.9± 6.0	2.08±0.09
Early Bunch	20		4.22±0.35	144.7±8.9	68.5 ±11.3	2.11±0.13
Ruby	15	16.7±0.4	3.62±0.34	89.3±6.5	74.1± 6.0	1.21±0.12
Early Bunch	15		4.17±0.24	76.1±4.6	74.1± 3.1	1.03±0.10
Ruby	12	12.5±0.2	3.60±0.15	80.9±4.0	74.1± 3.8	1.09±0.14
Early Bunch	12		4.21±0.15	62.4±6.4	76.8± 6.9	0.81±0.06

Table 4. Above-ground dry matter (DM), gross input and net gain, yield of growth, and derived values of the maintenance coefficient[a] for Ruby and Early Bunch peanut grown at 20 or 10 C night temperatures. Values calculated for plants at 22 C.

Cultivar	Night temp.	DM	Gross input	Net gain	Yg[b]	m[c]
	C	g $plant^{-1}$	mg C $plant^{-1}hr^{-1}$		g C g^{-1}C	mg C g^{-1}C hr^{-1}
Ruby	20	4.0±0.7	28.86	22.67	0.85	0.85
	10	2.7±0.6	20.06	14.89	0.86	1.59
Early Bunch	20	4.6±1.2	29.13	22.62	0.85	0.93
	10	3.1±0.9	21.57	17.58	0.84	0.45

[a]Derived from the C balance equation of Stahl and McCree (1988).
[b]Yg units are g C retained g^{-1} C assimilated.
[c]m units are mg C respired g^{-1} C in existing biomass.

pooled estimates of the C content of leaflets of Early Bunch (448 mg C g^{-1} DM) were not significantly different from Ruby (446 mg C g^{-1} DM). Estimates of m from fully expanded leaflets showed similar trends as those from whole plants, with no differences evident in 20 C plants (m = 1.27 and 1.28 mg C g^{-1} C hr^{-1} at 21.9 C for Ruby and Early Bunch, respectively). Values of m declined with declining measurement temperature, but the differences between Ruby and Early Bunch increased as night temperature decreased. Ruby grown under 15 C nights (m = 0.74 mg C g^{-1} C hr^{-1}, measured at 16.7 C) had an m that was 17% higher than Early Bunch, and Ruby grown under 12 C nights (m = 0.67 mg C g^{-1} C hr^{-1}) had an m 36% higher than Early Bunch.

Discussion

Plants of all cultivars had decreased rates of phenological development and DM accumulation when grown under low night temperatures (Table 1). Despite evidence of differences among unhardened plants of these cultivars in sensitivity to cool night temperatures (Bell *et al.*, 1994b), temperature x cultivar interactions were not significant for any growth component. The effects of temperature treatments on DM (Table 1) appeared to be due largely to effects on leaf area development rather than photosynthetic capacity of developed leaves (Fig. 1), with the exception of the 9 C treatment. Both slow leaf area development and restricted photosynthetic capacity reduced DM accumulation rates with 9 C nights.

Ruby produced more DM at each harvest; and, although leaflet CER was not generally different from that of either Early Bunch or Chico (except after 9 C nights), Ruby had higher net assimilation rates over all assessment periods (data not shown). This suggests greater CER per unit of total leaf area in Ruby plants, which could be due to better PPFD distribution within the canopy (Loomis and Williams, 1969; Fitter and Hay, 1987; Hay and Walker, 1989). While cultivar differences in PPFD distribution within canopies occur in field-grown peanuts (Bell *et al.*, 1993), we did not attempt to determine such differences in these studies.

Relative sensitivities of leaf CER to chilling temperatures were similar for both acclimated and nonacclimated plants. Leaf CER for nonacclimated Ruby and Chico plants exposed to night temperatures of 9 C were reduced by 0 or 23%, respectively, after exposure for a single night and by 20 or 30%, respectively, after exposure for four consecutive nights (Bell *et al.*, 1994b). The response by Early Bunch was intermediate. After continuous exposure to nights of 9 C from emergence, differences in leaflet CER at similar high daytime temperatures were still evident among cultivars at 20 to 30 DAE. CER of Ruby was reduced to 92% and CERs of Chico and Early Bunch were reduced to approximately 80% of that in plants acclimated to nights of 20 C (Fig. 1). These reductions in leaflet CER under 9 C night temperatures were accompanied by reductions in stomatal conductance of 47% in Ruby and 73% in Early Bunch (Bell, 1993). While the percentage reduction in stomatal conductance greatly exceeded the percentage reduction in CER (Fig. 1), the reductions in stomatal conductance were similar to that recorded in unhardened plants by Bell *et al.* (1994b). Collectively, these results suggest that the ability of peanut cultivars to "harden" (i.e., adapt to cool night conditions during continual exposure) is minimal, with the possible exception of the relatively chill-tolerant cultivar Ruby.

Lower leaflet CER in cool night treatments occurred despite higher SLN, a factor often directly correlated with leaflet CER (Sinclair and Horie, 1989; Muchow, 1990; Sinclair *et al.*, 1993). Higher levels of leaf chlorophyll also occurred in cool-night plants (data not shown). These results, combined with evidence that chilling temperatures in the dark do not affect subsequent efficiency

of capture of excitation energy (Bell, 1993), suggest that CER limitations following cool night temperatures may result from effects on enzymatic processes in the dark reactions of photosynthesis. This area obviously requires further research.

Ruby exhibited an adaptation to low night temperature not seen in Early Bunch. CER sensitivity to low daytime temperatures was reduced in Ruby grown under low night temperatures (Fig. 2). The resulting flat temperature response over a broad temperature range is typical of species adapted to arctic or alpine ecosystems (Billings *et al.*, 1971; Tieszen *et al.*, 1981) or to environments where large diurnal temperature variations occur during the long days of summer (Veres and Williams, 1984; Öquist and Martin, 1986). While such a characteristic seems unexpected in peanut genotypes, its existence probably results from the supposed origins of *A. hypogaea* in the foothills of the Eastern Andes in northwest Argentina and south Bolivia (Smartt and Hymowitz, 1985), an area characterised by high altitudes and associated large diurnal temperature fluctuations. The greater CER stability in Ruby acclimated to 10 C nights, compared to Early Bunch, was associated with higher specific respiration (Table 2) and an apparently higher maintenance respiration coefficient (m) for both whole plants (Table 3) and leaves. The consistent difference between Ruby and Early Bunch in whole plant respiration (Table 2) probably was related in part to higher growth rates (Table 1) (McCree, 1970). Similarly, the difference in whole plant m may have been partially due to a greater sunlit leaf area [i.e., more photosynthetically active leaf to maintain (Penning de Vries, 1975; Amthor, 1989)]. However, there were consistent increases in m for whole plants (Table 3) or fully expanded, sunlit leaves when Ruby was grown under cool, rather than warm, night temperatures. These increases were not evident in Early Bunch. These data suggest adaptation by Ruby to cool-night conditions is associated with an increase in m. Although the mechanisms are not clear, specific respiration rates (Table 2) and estimates of m (Table 3) are consistent with an interpretation that cool-night adaptation in Ruby may involve an increase in rate of enzyme turnover or maintenance (Penning de Vries, 1975; Amthor, 1989).

There are advantages to incorporating an ability to adapt to a range of temperature conditions in peanut germplasm for use in subtropical and temperate regions. Growing seasons could be extended, particularly for the early part of the season, although frost occurrence and germinability in cool soils will continue to provide finite limitations to peanut growing seasons and locations (Lawn and Williams, 1987). While such adaptation may provide protection against periods of cooler weather which may occur at critical phenological stages during the season (e.g., pod addition), adaptation to cool temperatures early in the season may lower potential CER during the later part of the growing season when night temperatures are warmer (Bell *et al.*, 1994a). This would result in less efficient use of high incident PPFD and warm temperatures and may limit potential yields.

An aspect requiring further research is whether peanut cultivars can adapt to new temperature regimes occurring during the season and, if so, what is the extent of any such acclimation response. These factors will be especially important in cultivars which show some ability to adapt to cool night conditions during early growth. The ability to acclimate to changing conditions has been shown to depend strongly on species and growth stage (Öquist, 1983; Veres and Williams 1984), and would have a considerable impact on any benefits of cool night tolerance.

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