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Effect of Soil Temperature on Vegetative and Reproductive Growth and Development in Three Spanish Genotypes of Peanut (*Arachis hypogaea* L.)

S. D. Golombek* and C. Johansen[1]

ABSTRACT

Extremes of soil temperature limit yield development of peanut. To obtain information relevant to improving yield by agronomic management and breeding, the influence of the soil temperature regimes (day/night) of 20/14 (T1), 26/20 (T2), 32/26 (T3), and 38/32 C (T4) imposed from the time of peg penetration into the soil until maturity on growth and development of three spanish genotypes of peanut (*Arachis hypogaea* L.) was investigated in a greenhouse. Soil temperature treatments were imposed by placing pots with individual plants in large temperature-controlled water baths. With increasing soil temperature from T1 to T3, leaves, stems and lateral roots became thinner. The leaf area increased from T1 to T3. The lateral root length increased up to maturity more at higher than at lower temperatures. The number of mature pods per plant, mature single seed mass, and therefore mature total seed mass per plant were highest at the intermediate temperature regimes, less at the warmest, and lowest at the coldest treatment. In early reproductive stages, pod inititation rate increased with decreasing soil temperature. Total pod growth and development of mature pods was lowest in T1, although pod initiation was high. Suboptimal soil temperatures slowed pod filling and maturation. At T4, one reason for the lower mature pod number compared to the intermediate temperature treatments seems to be the low pod initiation rate at early reproductive stages. These responses to temperature suggest agronomic management and genetic options for increasing yield at nonoptimal soil temperatures, such as irrigation during pod initiation stage when soil temperatures are high.

Key Words: Agronomic management, groundnut, pod initiation rate, yield.

To facilitate peanut breeding and improve field management, more information about the effects of environmental factors on growth of the peanut (*Arachis hypogaea* L.) plant and partitioning to the pods is essential. When water is nonlimiting, temperature and photoperiod are the major climatic factors affecting growth of peanut (Nigam *et al.*, 1994). For the peanut crop with its subterranean fruiting habit, soil temperature could have a major influence on reproductive growth and development. It is evident that extremes of soil temperature limit reproductive growth and yield of peanut (Ono, 1979; Ong, 1986). Studies of effects of air temperature on peanut are most commonly reported, but information about the effect of soil temperature is comparatively sparse (Cox, 1979; Leong and Ong, 1983; Nigam *et al.*, 1983).

The optimum temperature range for germination of peanut is 27-30 C (Fortanier, 1957; Bolhuis and De Groot, 1959). During the early stages of growth, the optimum shoot growth of the spanish cultivar Comet occurred at soil temperatures between 31 and 37 C, whereas optimum root growth occurred between 25 and 31 C (Ahring *et al.*, 1987). Suzuki (1966) found that the stem length and root weight increased with increasing soil temperature from 20 to 30 C. To our knowledge, no further information is available on the influence of root temperature on the vegetative growth of peanut.

The time between peg penetration into the soil and swelling of the ovaries of spanish and virginia genotypes was the shortest (2 d) at a podding zone temperature of

[1]Inst. for Plant Genetic and Crops Research, Corrensstr. 3, 06466 Gatersleben, Germany (e-mail: golombek@ipk-gatersleben.de) and International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, Andhra Pradesh 502 324, India (e-mail: C.Johansen@cgnet.com), respectively.

*Corresponding author.

32 C, increased to 5 and 7 d at 23 or 39 C, and took 2 wk at 15 C (Ono, 1979). A decrease in temperature from about 28 to about 22 C in the fruiting zone layer of the soil resulted in an increase in total as well as mature pod number at maturity (Dreyer *et al.*, 1981; Sanders and Blankenship, 1984), but no differences in total pod number were measured between 27 and 37 C (Dreyer, 1980). The growth rate per single pod of a spanish genotype increased with increase in pod zone temperature from 23 to 34 C (Dreyer *et al.*, 1981). Dreyer (1980) and Sanders *et al.* (1986) found an increase in the percentage of mature pod number with increasing pod zone temperature from 23 to 29 C.

More detailed information about the influence of soil temperature on the development of peanut yield is necessary to define breeding objectives and guide the choice of planting location, sowing date, and crop management. Also, it would be useful to have indications as to which processes governed by soil temperature regimes might need genetic enhancement. Therefore, the objective of the present study was to examine the influence of soil temperature from the time of peg penetration until maturity on the vegetative and reproductive growth and development.

Materials and Methods

The experiment was conducted twice in a greenhouse at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, near Hyderabad, India (17 30'N, 78 16'E). Exp. 1 was conducted from 4 Aug. to 28 Oct. 1993, and Exp. 2 from 15 Nov. 1993 to 3 March 1994. The peanut genotypes used in this experiment belong to subsp. *fastigiata* var. *vulgaris* (spanish type) and were TMV 2, AH 6179 and Comet. The genotypes were selected because they have similar time to flowering and maturity, 100-seed mass, number of seeds per pod, and leaf shape according to tests in several locations. TMV 2 is commonly grown in India, AH 6179 has performed relatively well in the hot environment at the ICRISAT Sahelian Center, Niger (J. H. Williams, 1993, pers. commun.), and Comet produced a relatively high yield in comparison with other cultivars grown in the relatively cool climate of Ontario, Canada (Roy *et al.*, 1980; Court *et al.*, 1984). Because statistical analysis revealed no genotypic differences regarding the treatment effect on the measured parameters, only the means of genotypes are presented.

Individual plants were grown in 7-L containers (height: 21 cm; upper diam.: 19 cm; lower diam.: 14 cm) with a 4:2:1 mixture of Alfisol soil, sand (2.0-0.02 mm), and vermiculite. The rooting medium was inoculated with *Bradyrhizobium* (strain NC 92). Single superphosphate was applied to increase phosphorus availability to 20 ppm Olsen-available P. All other nutrients were in the optimal range: 20.2 ppm available N, 574 ppm total N, 121 ppm available K, 280 ppm Mg, 1694 ppm Ca, 1.16 ppm DTPA extractable Zn, 35.2 ppm DTPA extractable Mn, and 1.54 ppm DTPA extractable Cu. Irrigation was applied twice daily to maintain the soil medium near field capacity [9.3 % (w/w)]. Soil temperature treatments (day/night) of 20/14 (T1), 26/20 (T2), 32/26 (T3), and 38/32 C (T4) with a 12-hr 'day' period and a 12-hr 'night' period were imposed by placing all pots of a temperature treatment in a large temperature-controlled water bath. Before starting the experiment, the effect of the water bath temperature on the soil temperatures at four positions within containers without plants (5 and 15 cm depth, in the middle and 3 cm from the edge of the pot) was analysed. During the whole temperature course no temperature difference between these four positions in the pot was detected. The temperature of the water was constantly monitored by thermocouples which were connected to electromagnetic relays, which switched heaters or coolers on or off according to the measured temperature, such that the water bath temperatures were maintained with an accuracy of ± 0.3 C. The transition time between day and night temperature was approximately 2 hr. In the greenhouse, the air temperature range was 24-35 C during the day and 20-27 C during the night. The relative humidity within the canopy was not measured. Because of the small size of the installations for regulation of root temperature (1.82,0.91 cm) and the permanent air circulation in the greenhouse due to air temperature control, only slight variations in air humidity between the treatments was assumed. The stem temperature at a height of 5 cm was measured with an infrared thermometer. No differences were measured between the temperatures of stems at 5 cm height of plants exposed to different soil temperatures (data not shown).

Until the start of the treatments, the plants were grown outside of the water baths in the greenhouse. Fifty percent emergence was observed at 7 d after sowing (DAS). When the pegs started entering the soil (42 DAS in all cultivars in Exp. 1; 53 DAS in all cultivars in Exp. 2), uniform plants were selected and subjected to temperature treatments which continued until the final harvest. The following harvests of the plants were conducted: harvest 1 at 74 DAS in Exp. 2 (during pod enlargement stage); harvest 2 at 64 DAS in Exp. 1 and 88 DAS in Exp. 2 (during pod filling stage), and harvest 3 at 86 DAS in Exp. 1 and 109 DAS in Exp. 2 (maturity). Harvest 1 was omitted in Exp. 1 because of the occurrence of bud necrosis disease and removal of affected plants at an early stage.

After harvest, the plants were separated into individual plant parts. Maturity was determined by the hull-scrape method (Williams and Drexler, 1981). The leaf area was determined using a LI-COR 3100 leaf-area meter (LI-COR, Lincoln, NE). The root length was measured by a root length scanner (Comair, Commonwealth Aircraft Corp. Ltd., Melbourne, Australia). The dry mass of the plant parts was measured after drying for 48 hr at 60 C.

The experimental design was a split plot with four replications in which the soil temperatures were the main plots and the genotypes within the harvest dates were the subplots. Treatments were compared by analyses of variance using Standard-ANOVA of the Genstat 4.01 package (Genstat 4.01, 1977). Correlation coefficients were calculated with Genstat 4.01 (1977).

Results and Discussion

Vegetative Growth. With increasing soil temperature from T1 to T3, dry mass per length (stems, lateral, and tap root) or area (leaves) of all vegetative plant organs became less, but there were no differences between T3 and T4 treatments. This is reflected in the response to soil temperature of specific leaf area, specific stem length (length/stem dry mass), and specific lateral root length (length/lateral root dry mass) (Fig. 1a,c,e). The correlation coefficient was r = 0.88 for specific leaf

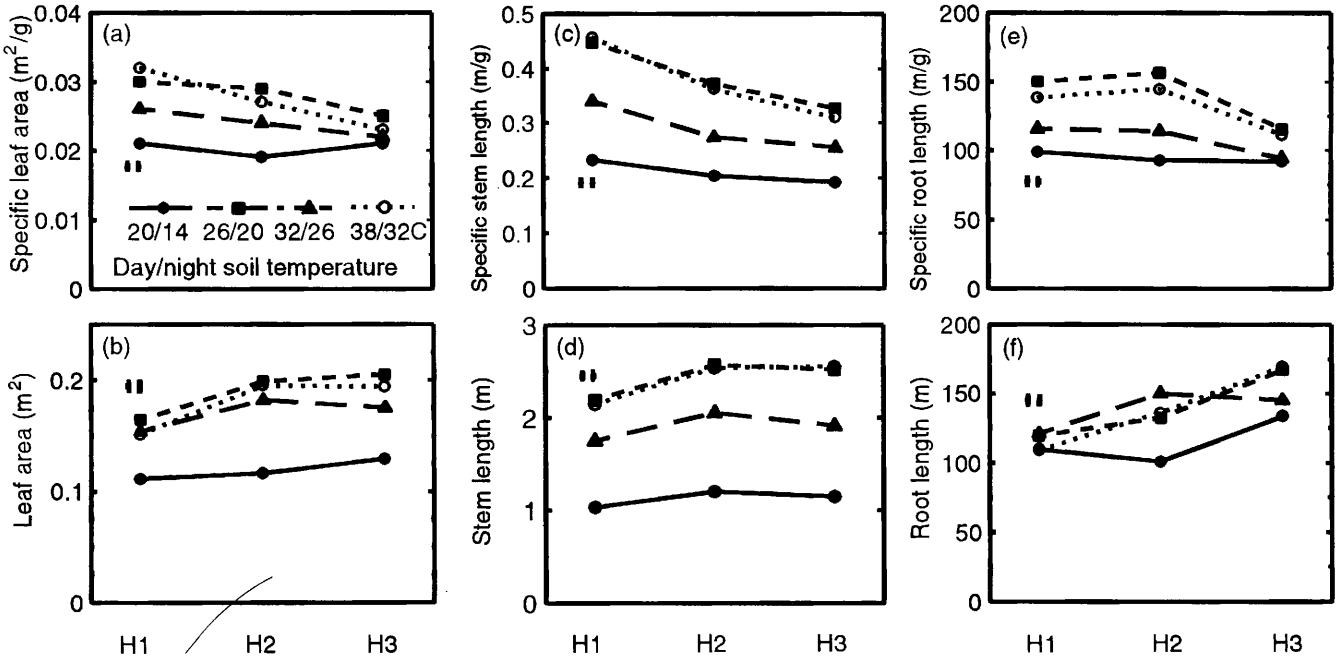

Fig. 1. Effect of soil temperature (20/14, 26/20, 32/26, 38/32) on (a) specific leaf area, (b) leaf area per plant, (c) specific stem length, (d) stem length, (e) specific lateral root length and (f) root length per plant. Results presented for Exp. 2, harvest 1 (H1): 74 DAS, harvest 2 (H2): 88 DAS, harvest 3 (H3): 109 DAS. The left vertical bar represents S.E. for comparison of means within a harvest, the right for comparison of means within a temperature treatment (DF=6).

area and specific stem length, r =0.71 for specific leaf area and specific root length, and r =0.61 for specific stem length and specific root length (Exp. 2). The effect of soil temperature on the length or area per dry mass became less as plants aged (Fig. 1a,c,e).

The leaf and stem mass at harvests 2 and 3 increased from T1 to T2 and was not changed up to T4 (Fig. 2). The development of leaf area, a major factor determining the photosynthetic capacity of the plant, was enhanced at harvests 2 and 3 with increasing soil temperature from T1 to T3 (Fig. 1b). The increase in leaf area per plant due to soil temperature treatment resulted from an increase in leaf dry mass (Fig. 2) as well as specific leaf area (Fig. 1a). With increasing leaf area from T1 to T3 the number of leaves per plant and the average single leaf area increased (Table 1). The number of branches (data not shown) was not influenced by the treatment, but the stem length increased from T1 to T3 and remained unaltered to T4 (Fig. 1d).

The total root mass was greater at the lower than at the higher temperatures because the tap root mass was greater in all investigated stages and the lateral root mass in the early reproductive stages (Fig. 2). At maturity there were no treatment differences in lateral root mass. The nodule mass increased until maturity. From T1 to T2 the nodule mass declined but it increased from T3 to T4.

The specific leaf area has been shown to decline in response to low ambient temperatures in many species (Charles-Edwards, 1982; Charles-Edwards *et al.*, 1983). In peanut, Nageswara Rao and Wright (1994) observed a lower specific leaf area of plants grown at lower ambient minimum temperatures. Bagnall *et al.* (1988) reported a higher specific leaf area of leaves exposed to 20 C compared to leaves exposed to 30 C. Similarly, a decline of specific root length with decreasing soil temperature has been reported often for other plant species (Bowen, 1991).

The specific root length was more in the warmer compared to the cooler treatments at all investigated stages (Fig. 1e). The lateral root mass increased more over time in the higher temperature treatments (Fig. 2). This led to a greater increase in root length from harvests 1 to 3 at the warmer temperatures than it did at the cooler temperatures (Fig. 1f). The development of a greater root length with increasing soil temperature may be important for the supply of the increasing shoot mass with water, nutrients, and phytohormones and may eventually contribute to enhanced shoot growth (Atkin *et al.*, 1972; BassiriRad *et al.*, 1991).

Reproductive Growth. The effect of soil temperature on yield development results from soil temperature effects on pod initiation rate, pod growth, and pod maturation. An adequate pod initiation rate in early, but not late, reproductive stages is an important precondition for the development of mature pods. The pod inititation rate in early reproductive stages increased with decreasing soil temperature as is reflected in the increased number of pods and subterranean pegs with decreasing soil temperature during the first two investigated stages (Fig. 3). The total pod growth was lowest in T1 (Fig. 2), although pod initiation was high (Fig. 3). This might be due to a low single pod growth in T1. Ono *et al.* (1974) observed an increase in single pod growth rate from 15-17 to 31-33 C.

The number of mature pods was highest in the inter-

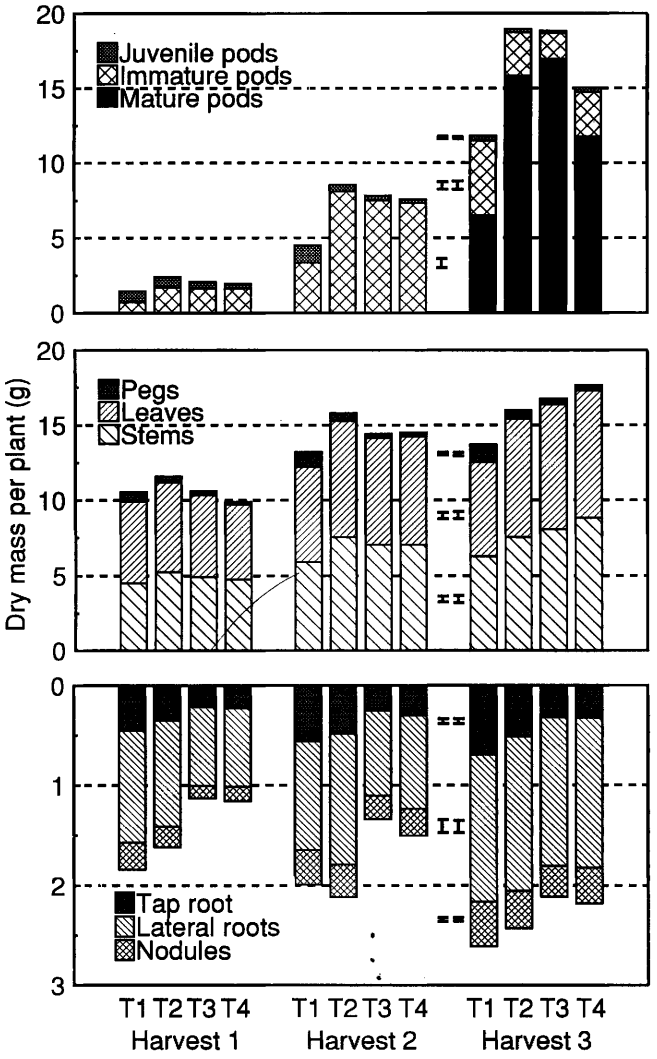

Fig. 2. Effect of soil temperature (T1=20/14, T2=26/20, T3=32/26, T4=38/32 C day/night soil temperature) on dry mass of different plant parts (Exp. 2, harvest 1: 74 DAS, harvest 2: 88 DAS, harvest 3: 109 DAS). The left vertical bar represents S.E. for comparison of means within a harvest, the right for comparison of means within a temperature treatment (DF=6).

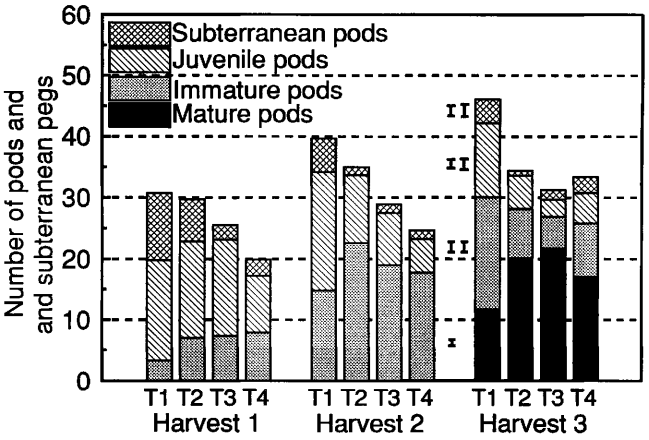

Fig. 3. Effect of soil temperature (T1=20/14, T2=26/20, T3=32/26, T4=38/32C day/night soil temperature) on number of pods and subterranean pegs (Exp. 2, harvest 1: 74 DAS, harvest 2: 88 DAS, harvest 3: 109 DAS). The left vertical bar represents S.E. for comparison of means within a harvest, the right for comparison of means within a temperature treatment (DF=6).

mediate soil temperature treatments (Fig. 3). In T1 the number of mature pods was lowest compared to the other treatments, despite a high pod inititation rate because of the slow single pod growth. The warmest treatment produced fewer mature pods than did the intermediate temperatures; at least one reason seems to be the low pod initiation rate in the initial phases of pod development.

Pod initiation during later reproductive stages between harvests 2 and 3 continued in the extreme temperature treatments, whereas it had ceased in the intermediate treatments (Fig. 3). The continuous high pod initiation in T1 until harvest might be due to the slow pod growth because it has been shown for peanut that an increase in pod mass has an inhibitory effect on further pod initiation (Har-Tzook and Goldin, 1967; Williams *et al.*, 1976). The cessation in pod initiation after harvest 2 in the intermediate treatments might have been caused by the high increase of pod dry mass. The increase in pod number in T4 also during later reproductive stages might have been caused by the lower pod mass increase compared to the intermediate treatments. The soil temperature effect on pod inititation rate resulted in the highest total pod number at maturity in the coldest treatment, but similar total pod number in the other temperature treatments (Fig. 3). Also, Dreyer *et al.* (1981) and Sanders and Blankenship (1984) found an increase in total pod number at maturity with a decrease in the fruiting zone temperature of the soil from about 28 to 22 C. In conformity with the results presented here, Dreyer *et al.* (1981) found no further difference in total pod number at maturity in the soil temperature range between 27 and 37 C.

As a consequence of the soil temperature effects on pod number and maturation, the developmental pod profile at maturity was most advanced in T2 and T3, followed by T4, and was much less advanced in the coldest treatment (Fig. 3). Similarly, Dreyer (1980) and Sanders *et al.* (1986) observed an increase in percentage of mature pod number with increasing pod zone temperature from 23 to 29 C.

The 100-mature seed mass was highest at the intermediate temperature treatments and lowest at the coldest treatment (Fig. 4). Because the maturity of the pods was determined by the hull-scrape method (Williams and Drexler, 1981) and all the pods selected as mature had a high shelling percentage (Table 1), differences in mature single seed mass were not the result incomplete maturation at the extreme temperature treatments.

As a consequence of the temperature effect on 100-mature seed (Fig. 4) as well as pod mass and developmental profile of the pods (Fig. 3), the mature pod and seed mass was highest at T2 and T3, lowest at T1, and intermediate at T4 (Fig. 2). Mature pod mass production was most efficient at the intermediate treatments and lowest at the coldest treatment, in view of the percentage of mature pods in the total pod mass (Fig. 2).

Table 1. Effect of soil temperature (T1=20/14, T2=26/20, T3=32/26, T4=38/32 C day/night) at different growth stages on several physiological parameters (Exp. 2). Standard errors (DF=6) are given for comparison of means within a harvest and within a temperature treatment (Temp.).

Physiological parameter	Harvest 1				Harvest 2				Harvest 3				SED	
	T1	T2	T3	T4	T1	T2	T3	T4	T1	T2	T3	T4	Harvest	Temp.
Leaves/plant (no.)	51	61	65	61	57	71	75	78	61	70	72	72	2.5	2.5
Avg area/leaf (cm^2)	22.3	25.5	25.3	25.2	20.8	26.1	27.3	25.3	21.4	25.2	28.9	27.0	0.8	0.8
100-Immature seed dry mass (g)	0.8	3.6	3.5	4.1	2.4	10.0	13.6	15.4	9.1	12.8	12.4	11.7	0.8	0.8
Shelling percentage:														
Immature pods	5.6	19.4	28.0	36.3	19.3	51.1	63.9	70.1	50.0	63.3	64.7	61.4	2.13	2.33
Mature pods	--	--	--	--	--	--	--	--	72.3	80.0	80.7	78.7	--	0.9

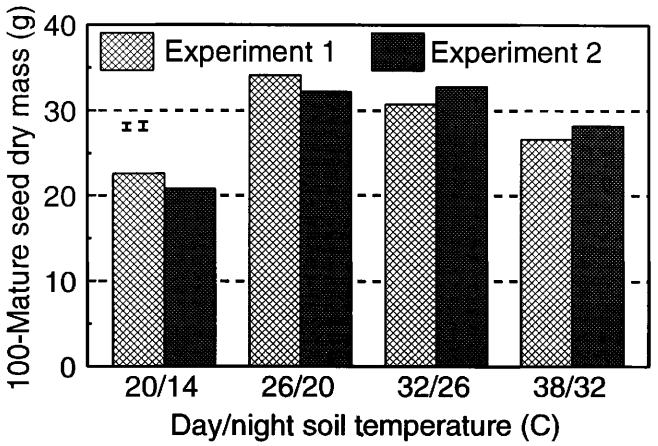

Fig. 4. Effect of soil temperature on average single mature seed dry mass. The left vertical bar represents S.E. for comparison of means of Exp. 1, the right for comparison of means of Exp. 2.

The comparatively low assimilating area at the coldest temperature regime could have contributed to the low final pod mass at T1 (Figs. 1b and 2). With an increase in soil temperature from T3 to T4, final pod mass, but not leaf area, decreased; the assimilating area at T4 was less efficient for pod mass production compared to T3.

An increase in pod yield of plants exposed to the lowest soil temperature, where mature pod number is proportionally less, cannot be achieved by extension of the filling period as peg deterioration commences soon after the earliest pods reach their maximum dry mass. Low temperatures during the pod filling stage limit yield formation and thus management to enhance soil temperature at this stage would be useful. This could be achieved by polythene mulching or adjustment of sowing date. Reduced pod yield at the highest temperature is attributable to low pod initiation rate at early reproductive stages, and thus a reduction in soil temperature at this stage should be beneficial. This could be achieved by irrigation or changed sowing date, or possibly by increasing plant density if other environmental factors such as soil moisture availability would allow a temperature reduction. Further experimentation to test these management options to alleviate adverse temperature effects would be useful. For genetic enhancement, an increased pod initiation rate in the early reproductive stages might be useful under high soil temperature conditions, and an enhanced single pod growth might be desirable under low soil temperature conditions. The knowledge of the influence of soil temperature on single mature seed size could improve peanut production for confectionary use by field management and appropriate choice of growing area and sowing date.

Comparison Between Experiments and Genotypes. The soil temperature effects discussed in this paper were generally similar in both experiments. The number of mature and immature pods as well as the single mature seed (Fig. 4) and pod mass were similar in both experiments, but the number of juvenile pods in Exp. 1 was higher than in Exp. 2. In Exp. 1, the top growth was more and the root growth was less than in Exp. 2. The growth differences between the experiments might have been due to the higher air temperature, mostly higher minimum temperatures, and higher relative humidity in Exp. 1 compared to Exp. 2. An increase in shoot growth and shoot/root ratio with increasing air temperature has been reported (De Beer, 1963; Cox, 1979). The fact that the genotypes responded similarly to the soil temperature treatments, although performing well in environments with extremely different temperatures, indicates that their performance in the extreme environments is not caused by their response to soil temperature.

Conclusions

Soil temperature had a marked effect on the vegetative and reproductive growth and development of three spanish genotypes of peanut. The highest mature pod production was observed at the soil temperature treatments 26/20 and 32/26 C, the lowest at 20/14 C, and intermediate at 38/32 C (day/night). This was primarily due to soil temperature effects on the processes of pod initiation rate, pod growth rate, and 100-mature seed mass. The pod initiation rate increased with decreasing soil temperature from T3 to T1, the pod growth rate was enhanced with increasing soil temperature from 20/14 to 26/20 C, and the 100-mature seed mass was highest at the

intermediate temperature treatments and lowest at the coldest treatment.

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