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Effect of separate pod and root zone temperatures on yield and seed composition of three Spanish cultivars of groundnut (*Arachis hypogaea* L)

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Abstract: The effect of separate pod and root temperature regimes (all four combinations of 28/22 and 40/34 °C day/night temperature), imposed from the time of peg penetration until harvest, on yield and seed composition of three Spanish genotypes of groundnut (*Arachis hypogaea* L) was investigated. A decrease in pod temperature from 40/34 to 28/22 °C increased yield and oil, starch and protein mass per plant irrespective of root temperature. Additionally, a reduction in pod temperature decreased protein concentration and increased the sum of oil and starch concentration at a root temperature of 28/22 °C, whereas at a root temperature of 40/34 °C a decrease in pod temperature increased protein concentration. Root temperature reduction diminished oil concentration of genotypes AH 6179 and TMV 2 at a pod temperature of 40/34 °C. A decline in pod temperature affected fatty acid composition through a decrease in palmitic acid irrespective of root temperature and an increase in linoleic acid at a root temperature of 28/22 °C. A root temperature effect on fatty acid composition was not detected. It is concluded that field management practices and choice of genotype can influence groundnut yield and seed composition through effects on pod and root temperature.

Keywords: groundnut; pod temperature; root temperature; seed composition; oil; fatty acid composition; starch; protein; total soluble sugar; yield

INTRODUCTION

In recent studies, marked effects of soil temperature on seed composition of groundnut (*Arachis hypogaea* L) have been found.[1] To obtain information about possible favourable agronomic practices and breeding strategies, knowledge of the separate effects of pod and root temperature on seed quality is needed. This is because of different spatial distribution of pods and functioning roots in the soil, and their consequent exposure to different temperatures depending on the soil depth. We are unaware of previous studies which have tried to differentiate the effects of pod and root temperatures in groundnut.

The podding depth in groundnut varies with soil physical characteristics but is normally between 3 and 6 cm. However, in some genotypes the podding depth can extend from 6 to 13 cm (Wright GC, personal communication). Similarly, the root distribution in the soil profile depends on the genotype[2] and soil characteristics, but major root activity in the reproductive stage is normally deeper than podding depth, where soil temperatures would be different. Knowledge of the effects of pod and root temperature on yield and seed quality could provide information for the choice of genotypes and breeding strategies to select appropriate podding depth and root distribution for improved and/or stabilised yield and seed quality under soil temperature extremes. Soil temperature in the top layers of the soil, especially in the podding zone, varies by field management practices such as irrigation, straw or polyethylene mulching, shading (eg by mixed cropping) and adjusting the sowing date. Pod temperature can also be affected by breeding genotypes with an altered podding depth.

The influence of pod and root temperature on the dry matter accumulation of seeds depends on the temperature effect on source strength, sink activity of the seeds, activity of other sinks and the energy demand of the seed for maintenance, growth and accumulation of storage compounds. Maintenance respiration can increase with increasing temperature[3] but may also be insensitive to temperature in the long term.[4] In the groundnut genotypes used in the presently described experiment, optimum soil temperatures for 100-mature seed mass and yield per plant were in the range 26/22–32/26 °C (day/night).[1,5]

Temperature has been found to affect oil and protein concentration of seeds of several species,

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depending upon the combination of genotype and investigated temperature regime. The oil concentration decreased,[6] did not alter[7] or increased[7–11] with decreasing temperature. Similarly, the protein concentration was reduced[1,7,8] or increased[8] when the temperature was lowered.

The conversion of sucrose to starch in the kernels of wheat and barley is impaired at high temperatures.[12,13] For wheat it was demonstrated that reduction of starch synthesis by high temperature can almost wholly be accounted for by reduced activity of soluble starch synthase.[12] Increasing temperatures above 20 °C in wheat and 30 °C in maize resulted in a reduction of the activity of soluble starch synthase in the kernels.[14]

The sugar concentration is affected by several interacting processes such as respiration, starch metabolism, sink–source relationship, etc. In soybean seeds the sucrose concentration decreased by more than 50% with an increase in temperature from 18/13 to 33/28 °C (day/night) during seed development, whereas stachyose was only slightly reduced and the other sugars remained unchanged.[15] Similarly, the sugar concentration of groundnut seeds was reduced by approximately 30% with increasing mean soil temperature from 21.7 to 28.8 °C.[16]

The fatty acid composition of the oil is of considerable importance in commercial oilseed species. In several species a marked effect of the temperature during seed development on the fatty acid composition of the seed oil was observed. Investigations on the effect of temperature on fatty acid composition of seed oil were mainly conducted in the range 10–33 °C. In three groundnut cultivars an increase in soil temperature from 20/14 to 32/26 °C (day/night) resulted in an increase in oleic acid and a decrease in linoleic acid of the seed oil.[1] Also, in other species such as soybean and linseed,[8,17] safflower,[18] sunflower[19] and flax[20] an increase in temperature within the range 10–33 °C caused an increase in oleate and a decrease in polyunsaturated fatty acids (linoleate or linolenate),. This temperature effect on oleic acid and polyunsaturated fatty acids is ascribed to the temperature sensitivity of desaturating enzymes, as eg has been shown for sunflower[21] and soybean.[22] The respective proportions of the saturated fatty acids 16:0 and 18:0 in the seed oil of several species were not altered or only slightly increased with increasing temperature within the range 10–33 °C.[8,9,11,17–19] Increasing temperature during seed maturation often results in a less unsaturated oil owing to an increase in oleate combined with a decrease in polyunsaturated fatty acids and a slight increase or no alteration in the saturated fatty acids 16:0 and 18:0 at increasing temperature.

To understand better the effects of pod and root temperature on groundnut seed development, a study under controlled conditions was undertaken whereby separate temperature regimes were applied to root systems and developing pods of three groundnut cultivars. Effects of all combinations of a moderate (28/22 °C day/night) and a high (40/34 °C day/night) pod and root temperature regime on yield and seed quality of groundnut were investigated.

EXPERIMENTAL

Materials

The experiment was conducted twice in a greenhouse at ICRISAT, Patancheru, near Hyderabad, India (17°30′N, 78°16′E). Experiment 1 was conducted between 13 February and 23 May 1995 and Experiment 2 between 19 July and 21 October 1995. The groundnut genotypes Comet, TMV 2 and AH 6179 used in this experiment belong to subsp *fastigata* var *vulgaris*. The genotypes have a similar time to flowering and maturity and a similar 100-seed mass. TMV 2 is a commonly grown cultivar in India. AH 6179 performs relatively well in the hot environment of ICRISAT Sahelian Center, Niger (Williams JH, personal communication). Comet produced a high yield in comparison with other varieties in the relatively cool climate of Ontario, Canada.[23,24]

Single groundnut plants were grown in a facility which allows pods and roots to grow in separate compartments.[25] The soil temperature of the pod and root compartments was controlled separately by water baths surrounding the compartments. Day/night temperature regimes of 28/22 and 40/34 °C within a 12 h ‘day’ and 12 h ‘night’ period were imposed separately on the pod and root compartments in all four combinations of these temperature regimes (see Tables 1–4). The temperature transition between the ‘day’ and ‘night’ period occurred mainly within 2 h, and the final set temperature was reached within 5 h. This soil temperature course simulates natural conditions better than a sudden temperature change. After reaching the set ‘day’ or ‘night’ temperature, the temperatures in the 40/34 °C treatment ranged between the set temperature and 0.6 °C less (root compartment) or 0.8 °C less (pod compartment). The fluctuations within the 28/22 °C treatment were ±0.3 °C in the root compartment and ±0.6 °C in the pod compartment. The air temperature ranged between 24 and 35 °C during the day and between 20 and 27 °C during the night.

The root compartment was filled with sand (particle size 1–2 mm) to facilitate aeration, and air was pumped through the compartment once daily for 15 s. The sand in the root compartment was inoculated with *Bradyrhizobium*. The root compartment was watered daily with modified Broughton’s solution[26] containing (mM) 1 $CaCl_2$, 0.5 KH_2PO_4, 0.25 $MgSO_4$, 0.25 K_2SO_4 and (μM) 10 FeEDTA, 2 H_3BO_3, 1.5 $MnSO_4$, 0.5 $ZnSO_4$, 0.2 $CuSO_4$, 0.1 $CoSO_4$, 0.1 Na_2MoO_4. The pod compartment was filled with a 4:2:1 mixture of Alfisol soil, sand and vermiculite. This soil mixture was watered daily to approximate field capacity of 9.3%.

When the pegs started entering the soil (40 days after sowing (DAS) in all cultivars in Experiment 1 and 34 DAS in all cultivars in Experiment 2), the temperature treatments were initiated and continued until harvest (100 DAS in Experiment 1 and 94 DAS in Experiment 2).

Pod maturity was determined by the hull-scrape method.[6] The 100-seed mass was calculated from the seed number and seed mass of each individual plant. Mature seeds were freeze-dried, ground into a meal using a Waring blender, defatted and stored at 0–4 °C for further analysis. The 100-seed mass, chemical composition and fatty acid composition of the mature seeds of each individual plant of the experiment were determined.

Chemical composition

Nitrogen concentration was determined using a Technicon autoanalyser.[27] A factor of 5.46 was used for converting the nitrogen into crude protein concentration. Oil was determined by extracting the groundnut meal with *n*-hexane in a Soxhlet apparatus.[28] Total soluble sugars in groundnut meal were extracted with hot 80% aqueous ethanol and determined according to the procedure of Dubois *et al.* [29] Starch was determined by hydrolysing the meal with amyloglucosidase enzyme[30] and analysing the sugars in the hydrolysate according to the procedure of Dubois *et al.* [29]

Fatty acid composition

Fatty acid methyl esters (FAMEs) of hexane extracts were prepared using 14% (w/v) boron trifluoride in methanol[31] and analysed according to the method of Mercer *et al*[32] with the following modifications. Gas chromatography analysis was performed on a Shimadzu model GC-9A gas chromatograph (Shimadzu Corp, Tokyo, Japan) fitted with a flame ionisation detector and a glass column (210 mm × 3 mm id) packed with Altech CS-10 W-AW (80–100 mesh) (Altech Associates, Deerfield, IL, USA). The carrier gas helium was maintained at a flow rate of 50 ml min^{-1}. The temperatures of the injector and detector were maintained at 250 and 300 °C respectively. The column temperature was held at 190 °C for 4 min initially, programmed to increase from 190 to 250 °C at 10 °C min^{-1}, then held at 250 °C for 2 min. Peaks were identified using standard FAMEs and quantified using methyl heptadecanoate (17:0) as internal standard.

Statistical analysis

The experiment used was a completely randomised design. The statistical analysis was performed using the GLM procedure of the Statistical Analysis System,[33] and the comparison of means was conducted using the Tukey–Kramer test.

RESULTS AND DISCUSSION

100-Mature seed dry mass and yield

The effect of the temperature treatment on 100-seed mass, number of seeds per plant and seed yield per plant was not modified by the cultivar (*F*-test; Table 1). The 100-seed mass increased when pod temperature was decreased to 28/22 °C at a root temperature of 28/22 °C. A lower root temperature had no effect on the 100-seed mass at a pod temperature of 40/34 °C. Therefore pod temperature seems to be of importance for the development of a desirable high 100-seed mass for confectionary use. Mature seed number per plant was not significantly affected by the temperature treatment. The yield per plant increased when the pod temperature was lowered independently of root temperature, mainly owing to the temperature effect on individual seed mass, whereas the root temperature had no effect on the yield. This result is of importance for agricultural practice. In these experiments the adaptation of the cultivars to environments of contrasting temperature regimes was not reflected by the effect of pod or root temperature on yield. This might be partly due to the experimental variation of only pod and root temperature, but not air temperature to which the varieties might be adapted too.

The lower seed yield per plant at a pod temperature of 40/34 °C compared to the pod temperature of 28/22 °C could be due to increased carbon loss by respiration and/or reduced sink activity of the seeds. Sink strength[3] and respiration can be influenced by temperature, but maintenance respiration is not necessarily enhanced with increasing temperature in the long term.[4]

Chemical composition

The seed oil concentration at 40/34 or 28/22 °C soil temperature (pod and root temperature) was similar (Table 2). In another study at a lower soil temperature range (20/14–26/20 °C) the oil concentration of the same genotypes increased with increasing soil temperature.[1] However, in the present experiments the combination of 40/34 and 28/22 °C pod or root temperature had an effect on seed oil concentration, and there were significant differences between the genotypes in this regard (Table 2). Whereas in Comet the temperature treatment was without effect on oil concentration, in TMV 2 and AH 6179 a reduction of root temperature at a pod temperature of 40/34 °C diminished the oil concentration. Pod temperature affected the oil concentration only in TMV 2 at a root temperature of 28/22 °C: the oil concentration increased with decreasing pod temperature.

The better performance of AH 6179 in hot environments and Comet in relatively cold environments is reflected by the ability of AH 6179 to accumulate a higher oil concentration at the soil temperature (pod and root temperature) of 40/34 °C compared to Comet (Table 2).

The temperature effect on the concentration of starch, protein and total soluble sugars, the sum of the concentrations of oil and starch, and the ratio of total soluble sugars to starch was not significantly affected by cultivar (*F*-test; Table 2). Starch concentration decreased by an increase in pod temperature at a root temperature of 28/22 °C and was unaffected by an increase in root temperature at a pod temperature of 28/22 °C. Sucrose accounts for around 90% of the total sugars of groundnut seeds.[16,34] Therefore the increase in the ratio of total soluble sugars to starch with an increase in pod temperature at a root temperature of 28/22 °C could be an indication of reduced metabolisation of sucrose into starch. This could be due to a diminished activity of soluble starch synthase in the seeds with increasing temperature, as observed in maize, barley and wheat kernels.[12,14] A reduced conversion of sucrose into starch could account for the lower starch concentration at the higher pod temperature for the 28/22 °C root treatment.

The protein concentration was similar at 40/34 or 28/22 °C soil temperature (pod and root temperature) but was affected by the combination of 40/34 and 28/22 °C pod or root temperature (Table 2). A decrease in pod temperature lowered the protein concentration at a root temperature of 28/22 °C, whereas it increased protein concentration at a root temperature of 40/34 °C. Root temperature did not affect protein concentration at a pod temperature of 28/22 °C, whereas a decrease in root temperature increased the protein concentration at a pod temperature of 40/34 °C. From the nutritional point of view a high protein concentration is desirable. For protein synthesis, developing legume seeds import nitrogen mainly in the form of amides.[35] For the subsequent metabolisation of amides to amino acids, carbon skeletons are necessary. There is evidence that carbon partitioning is controlled in response to nitrogen availability.[36] It is remarkable that the only temperature effect on the sum of oil and starch concentration was a decrease with decline of pod temperature from 40/34 to 28/22 °C at a root temperature of 28/22 °C, which was accompanied by an increase in protein concentration. The plants exposed to 40/34 °C pod temperature and a root temperature of 28/22 °C had the highest nitrogen fixation per plant of all treatments. This was higher than for the 28/22 °C soil temperature (pod and root temperature) treatment and much higher than for the treatments with high root temperature (data not

Table 1. Effect of pod and root temperature on yield and yield components of groundnut[a]

Genotype *Temperature treatment (°C day/night)*				
Pod	*Root*	*100-Mature seed mass (g)*	*Number of mature seeds per plant*	*Mature seed mass (g)*
Comet				
40/34	28/22	26.3aA	36.0aA	8.8aA
28/22	28/22	34.1bA	30.8aA	10.6aA
40/34	40/34	24.5aA	29.0aA	7.1aA
28/22	40/34	28.0aA	36.0aA	10.3aA
TMV 2				
40/34	28/22	27.4abA	25.8aA	7.1abA
28/22	28/22	33.0bA	37.5aA	12.6bA
40/34	40/34	23.6aA	24.9aA	6.1aA
28/22	40/34	29.0abA	35.1aA	9.8abA
AH 6179				
40/34	28/22	29.4aA	37.9aA	10.2aA
28/22	28/22	37.0bA	36.7aA	13.6bA
40/34	40/34	27.3aA	39.3aA	11.2aA
28/22	40/34	31.5abA	41.5aA	13.2aA
Ø SED		1.7	4.3	1.6
Mean[b]				
40/34	28/22	27.7ab	33.2a	8.7a
28/22	28/22	34.7c	35.0a	12.3c
40/34	40/34	25.1a	31.1a	8.2a
28/22	40/34	29.5b	37.5a	11.1bc
Ø SED		1.0	2.5	0.9
Significance of *F*-test[c]				
Temperature		***	NS	***
Temp × genotype		NS	NS	NS
Temp × experiment		***	NS	NS
Temp × gen × exp		NS	*	NS

[a] Means are significantly different at the $P < 0.05$ level if followed by different letters: comparison within a variety with lower-case letters; comparison within a temperature treatment with upper-case letters.

[b] Where the interaction with the experiment was significant (*F*-test), a box indicates that the same treatment grouping was found in both experiments.

[c] Asterisks denote significance at $*P < 0.05$, $**P < 0.01$ and $***P < 0.001$ levels; NS, not significant.

shown). Plants treated with 40/34 °C pod temperature and 28/22 °C root temperature also developed a lower seed mass per plant than plants exposed to moderate pod temperatures (Table 1). Because of the high nitrogen fixation and the relatively low seed mass production per plant, plants treated with 40/34 °C pod temperature and 28/22 °C root temperature had a relatively high ratio of nitrogen to carbon. This might have led to an increase in protein synthesis at the expense of oil and starch synthesis.

Oil, starch and protein mass per plant

Owing to the temperature effects on seed yield per plant (Table 1) and on chemical composition (Table 2), the temperature treatments had a significant effect on oil, starch and protein mass of the mature seeds per plant (Table 3). The effect of temperature on the amount of these seed components per plant was not modified by the cultivar ($P < 0.05$). Values of oil, starch and protein mass per plant were highest at the 28/22 °C soil temperature (pod and root) mainly because of the high mature seed mass production at that temperature (Table 1). A lower pod temperature increased the oil and starch mass per plant irrespective of root temperature (Table 3). The amount of seed protein per plant increased with decreasing pod temperature at a root temperature of 40/34 °C. On the other hand, the only effect of a reduction of root temperature was an increase in protein mass at a pod temperature of 40/34 °C.

Fatty acid composition

The temperature effect on fatty acid composition of the seed oil was not modified by the cultivar according to the *F*-test (Table 4). A decrease in pod temperature reduced palmitic acid (16:0) slightly, whereas root temperature was without effect on palmitic acid. Palmitic acid in the seed oil was also slightly reduced by lowering the soil temperature in the groundnut genotypes AH 6179 and TMV 2.[1] This is in agreement with the effect of a decrease in plant temperature in sunflower,[19] flax,[9] white mustard and rape.[11] How-

Table 2. Effect of pod and root temperature on chemical composition of mature groundnut seeds (per cent dry mass)[a]

Genotype Temperature treatment (°C day/night)							
Pod	Root	Oil	Starch	Oil + starch	Protein	Total soluble sugars	Total soluble sugars/starch
Comet							
40/34	28/22	47.6aA	7.9aA	55.5aA	28.5bA	3.0bAB	0.37bA
28/22	28/22	49.5aA	9.4aA	58.9bA	25.1aA	2.5aA	0.27aA
40/34	40/34	48.9aA	8.7aA	57.6abA	24.8aA	3.2aA	0.38bA
28/22	40/34	50.3aA	9.5aA	59.7bA	24.9aA	2.6aA	0.28aA
TMV 2							
40/34	28/22	45.8aA	8.1aA	53.9aA	30.0bA	3.0aB	0.38bA
28/22	28/22	49.0bA	8.9abA	57.9bA	26.1aA	2.7aA	0.31aA
40/34	40/34	49.5bAB	8.0aA	57.5bA	25.7aA	2.9aA	0.37bA
28/22	40/34	48.7abA	9.8bA	58.5bA	26.9abA	2.8aA	0.28aA
AH 6179							
40/34	28/22	48.7aA	7.6aA	56.3aA	29.2bA	2.4abA	0.32bA
28/22	28/22	49.5abA	9.8abA	59.2bA	25.9abA	2.3aA	0.24aA
40/34	40/34	52.2bB	8.5abA	60.7bB	23.7aA	2.9bA	0.35bA
28/22	40/34	49.4abA	9.8bA	59.2bA	26.4abA	2.4abA	0.25aA
Ø SE		0.9	0.5	1.0	0.9	0.2	0.02
Mean[b]							
40/34	28/22	47.4a	$\boxed{7.9a}$	55.2a	29.2c	2.8bc	$\boxed{0.36b}$
28/22	28/22	$\boxed{49.3b}$	$\boxed{9.4b}$	58.7b	25.7ab	$\boxed{2.5a}$	$\boxed{0.27a}$
40/34	40/34	$\boxed{50.2b}$	8.4a	59.6b	24.7a	3.0c	0.37b
28/22	40/34	$\boxed{49.5b}$	$\boxed{9.7b}$	59.2b	26.1b	$\boxed{2.6ab}$	$\boxed{0.27a}$
Ø SE		0.5	0.3	0.6	0.5	0.1	0.01
Significance of *F*-test[c]							
Temperature		***	***	***	***	***	***
Temp × genotype		*	NS	NS	NS	NS	NS
Temp × experiment		**	*	NS	NS	***	***
Temp × gen × exp		NS	*	NS	NS	NS	NS

[a] Means are significantly different at the $P < 0.05$ level if followed by different letters: comparison within a variety with lower-case letters; comparison within a temperature treatment with upper-case letters.

[b] Where the interaction with the experiment was significant (*F*-test), a box indicates that the same treatment grouping was found in both experiments.

[c] Asterisks denote significance at *$P < 0.05$, **$P < 0.01$ and ***$P < 0.001$ levels; NS, not significant.

Table 3. Effect of pod and root temperature on amount of oil, starch and protein in mature seeds per plant[a]

Genotype Temperature treatment (°C day/night)		Seed oil per plant	Seed starch per plant	Seed protein per plant
Pod	Root	(g)	(g)	(g)
Comet				
40/34	28/22	4.52aA	0.75aA	2.71aA
28/22	28/22	5.25aA	1.01aA	2.70aA
40/34	40/34	3.48aA	0.62aA	1.78aA
28/22	40/34	5.24aA	0.96aA	2.56aA
TMV 2				
40/34	28/22	3.28aA	0.60aA	2.12abA
28/22	28/22	6.20bA	1.09bA	3.32bA
40/34	40/34	3.37aA	0.53aA	1.69aA
28/22	40/34	4.75abA	0.95abA	2.63abA
AH 6179				
40/34	28/22	5.44aA	0.85aA	3.25aA
28/22	28/22	6.71aA	1.32aA	3.52aA
40/34	40/34	5.87aA	0.95aA	2.68aA
28/22	40/34	6.52aA	1.30aA	3.50aA
Ø SE		0.8	0.15	0.42
Mean				
40/34	28/22	4.41a	0.73a	2.69b
28/22	28/22	6.05bc	1.14b	3.18b
40/34	40/34	4.24a	0.70a	2.04a
28/22	40/34	5.50b	1.07b	2.90b
Ø SE		0.5	0.08	0.24
Significance of *F*-test[b]				
Temperature		***	***	***
Temp × genotype		NS	NS	NS
Temp × experiment		NS	NS	NS
Temp × gen × exp		NS	NS	NS

[a] Means are significantly different at the $P < 0.05$ level if followed by different letters: comparison within a variety with lower-case letters; comparison within a temperature treatment with upper-case letters.

[b] Asterisks denote significance at $*P < 0.05$, $**P < 0.01$ and $***P < 0.001$ levels; NS, not significant.

ever, temperature did not affect the palmitic acid concentration in the seed oil of some species such as soybean[8,15] and safflower.[18]

Pod and root temperature had no effect on stearic acid (18:0) or oleic acid (18:1). This result is consistent with previous investigations with the same groundnut genotypes, where decreasing soil temperature had no effect on stearic acid or oleic acid in the higher soil temperature range (32/26–38/32 °C day/night) but reduced both fatty acids in the lower soil temperature range (20/14–32/26 °C day/night).[1] In other investigations in dependence on genotype and temperature range, no temperature effect on stearic acid occurred, eg in seed oil of soybean,[8,15] or there was a slight reduction with decreasing temperature, eg in safflower,[18] sunflower,[19] flax[9] and linseed.[17]

Linoleic acid (18:2) was the only 18-C fatty acid that showed a response to temperature treatment. The linoleic acid percentage was lowered with a decrease in pod temperature at a root temperature of 28/22 °C. This was in accordance with a previous study, where within a soil temperature range between 32/26 and 20/14 °C (day/night) the reaction of linoleic acid was similar in the same groundnut genotypes.[1] The effect of pod temperature on fatty acid composition demonstrates that the linoleic acid as well as the palmitic acid fraction of groundnut seed oil can be affected by pod temperature independently of root temperature. At a pod temperature of 40/34 °C the root temperature did not affect linoleic acid.

Pod or root temperature had no effect on arachidic (20:0) and eicosenoic (20:1) acid concentration and no major effect on behenic (22:0) or lignoceric (24:0) acid concentration in the oil (data not shown).

The main effect of the temperature treatment on fatty acid composition of the oil was a reduction in 16:0 and an increase in 18:2 with decreasing pod temperature. In the plastids of developing oil seeds, 16:0 can be elongated to 18:0 and then desaturated to 18:1. The proportion of fatty acids in seed oil is predominantly influenced by enzymes regulating the relation of 16:0, 18:0 and 18:1 exported from the plastids and by enzymes which subsequently metabolise these fatty acids, eg 18:1 by desaturation to 18:2.[37] Therefore the opposite reaction of 16:0 and 18:2 content to pod temperature mirrors the effect of pod temperature on the activity of enzymes regulating the proportion of 16:0 and 18:1 out of the fatty acids exported from the plastids.

Mainly as a consequence of the reduction in 16:0 content and increase in 18:2 content with decreasing pod temperature, the content of unsaturated oil increased with decreasing pod temperature independently of root temperature. In most of the reported combinations of genotype and investigated temperature regimes the increase in seed oil desaturation with decreasing temperature was mainly due to a shift within the unsaturated 18-C fatty acids.[8,17–20,37] Also in groundnut a soil temperature reduction from 32/26 to 20/14 °C (day/night) increased the extent of unsaturation of the oil mainly because of a shift from 18:1 to 18:2,[1] whereas in the higher pod temperature regime of the presented experiment a decrease in pod temperature increased the unsaturation of the oil primarily owing to a shift from 16:0 to 18:2. An increase in the extent of unsaturation of lipids improves the nutritional quality of seeds and unheated oil, whereas a decrease improves oil stability and shelf-life of the groundnut products.

Implications for agricultural practice

The present study, comparing an optimum soil temperature for pod yield (28/22 °C) with a supra-optimal soil temperature for pod yield (40/34 °C), suggests several avenues for yield and quality improvement. Reduction of high soil temperature in the fruiting zone of the soil, through agronomic management or genotype selection for deeper podding, could increase the yield and the oil, starch and protein mass of the mature seeds per plant. Reduction of high pod

Table 4. Effect of pod and root temperature on fatty acid composition of oil of mature groundnut seeds (per cent of total fatty acids)[a]

Genotype Temperature treatment (°C day/night)						
Pod	Root	16:0[b]	18:0	18:1	18:2	Saturated/unsaturated fatty acids[c]
Comet						
40/34	28/22	15.8bA	2.4abA	40.8aA	34.3aA	0.32bA
28/22	28/22	13.5aA	2.9bA	40.1aA	36.9bA	0.29aA
40/34	40/34	16.2bB	2.2aA	39.2aA	35.4abA	0.32bA
28/22	40/34	13.4aA	2.9abA	40.1aA	36.8bA	0.29aA
TMV 2						
40/34	28/22	15.3bA	2.5aA	42.0aA	33.3aA	0.31bA
28/22	28/22	13.3aA	2.3aA	41.5aA	36.0bcA	0.28aA
40/34	40/34	15.0bA	2.4aA	41.0aA	34.8abA	0.30bA
28/22	40/34	12.9aA	2.5aA	40.5aA	37.1cA	0.27aA
AH 6179						
40/34	28/22	15.7bA	2.3aA	41.4aA	34.1aA	0.31bA
28/22	28/22	13.1aA	2.6aA	41.2aA	36.6bA	0.27aA
40/34	40/34	15.2bA	2.3aA	40.5aA	35.3abA	0.31bA
28/22	40/34	12.6aA	2.6aA	40.6aA	37.1bA	0.27aA
Ø SE		0.3	0.2	0.8	0.6	0.007
Mean[d]						
40/34	28/22	15.6b	2.4a	41.4a	33.9a	0.31b
28/22	28/22	13.3a	2.6a	40.9a	36.5b	0.28a
40/34	40/34	15.5b	2.3a	40.2a	35.2a	0.31b
28/22	40/34	12.9a	2.6a	40.4a	37.0b	0.28a
Ø SE		0.2	0.1	0.5	0.3	0.004
Significance of *F*-test[e]						
Temperature		***	*	*	***	***
Temp × genotype		NS	NS	NS	NS	NS
Temp × experiment		*	NS	***	***	*
Temp × gen × exp		NS	NS	NS	NS	NS

[a] Means are significantly different at the $P < 0.05$ level if followed by different letters: comparison within a variety with lower-case letters; comparison within a temperature treatment with upper-case letters.

[b] Figure before colon indicates the number of carbon atoms. Figure after colon is the number of double bonds in the fatty acid chain.

[c] Measured saturated fatty acids: 16:0, 18:0, 20:0, 22:0, 24:0. Measured unsaturated fatty acids: 18:1, 18:2, 20:1.

[d] Where the interaction with the experiment was significant (*F*-test), a box indicates that the same treatment grouping was found in both experiments.

[e] Asterisks denote significance at $^{*}P < 0.05$, $^{**}P < 0.01$ and $^{***}P < 0.001$ levels; NS, not significant.

temperature could increase the sum of oil and starch concentration and decrease protein concentration at a moderate root temperature, and increase protein concentration at a high root temperature. Reduction of high pod temperature could influence fatty acid composition through an increase in linoleic acid and a decrease in palmitic acid concentration and could lead to an increase in the extent of unsaturation of the seed oil. Root temperature in deeper soil layers can be influenced by agricultural practices such as sowing date, growing location and choice of a genotype with a particular root distribution pattern. Reduction of high root temperature could increase the protein mass per plant if pod temperature is high.

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