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Effect and interaction of temperature and photoperiod on growth and partitioning in three groundnut (*Arachis hypogaea* L.) genotypes[1]

By S N NIGAM, R C NAGESWARA RAO, J C WYNNE*, J H WILLIAMS**, M FITZNER* and G V S NAGABHUSHANAM

International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, Andhra Pradesh 502 324, India
**North Carolina State University, Raleigh, NC 27607, USA*
***ICRISAT Sahelian Center, BP 12404, Niamey (via Paris), Niger*

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Summary

Effect of temperature and photoperiod and their interaction on plant growth and partitioning of dry matter to pods was examined in three selected groundnut genotypes *viz.*, TMV 2, NC Ac 17090 and VA 81B. The genotypes were grown in six walk-in growth chambers which were programmed to simulate three temperature regimes (22/18°C, 26/22°C and 30/26°C day/night) each under long (12 h) and short (9 h) photoperiods. The plant growth rates and partitioning of dry matter to pods were estimated on a thermal time basis.

Plant growth rate (PLGR) was significantly influenced by temperature, photoperiod and genotype, whereas pod growth rate (PDGR) was influenced primarily by temperature and genotype. The interaction of genotype with photoperiod and with temperature was significant for both PLGR and PDGR. For example, at the 22/18°C temperature regime, VA 81B had a high PDGR, while NC Ac 17090 did not even initiate pod growth. The partitioning of dry matter to pods (Pf) was also significantly influenced by photoperiod, temperature and genotype, and significant interactions were found. Photoperiod did not significantly affect Pf under the low temperature regime, but at higher temperatures, partitioning to pods was significantly greater under short days. Pf of VA 81B was relatively insensitive to photoperiod compared with the other two genotypes. The study provided evidence of genotypic variability for photoperiod × temperature interactions which could influence adaptation of groundnut genotypes to new environments.

Key words: Groundnut, plant growth rate, pod growth rate, partitioning, photoperiod, thermal time

Introduction

Variability among groundnut (*Arachis hypogaea* L.) genotypes in their response to climatic conditions has great significance in determining their adaptation. Groundnut genotypes selected for high yield at one location may have unpredictable performance when moved to locations with differing environmental regimes due to genotype × environment interactions (Branch & Hildebrand, 1989). When availability of water is non-limiting,

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temperature (Leong & Ong, 1983) and photoperiod (Witzenberger, Williams & Lenz, 1985; Bell, Bagnall & Harch, 1991*a*) are the major climatic factors which influence the performance of groundnut genotypes.

Traditionally, determination of the photoperiod effect on plant species has been based on the time taken for initiation of flowering. In this sense, the groundnut has been considered as insensitive to photoperiod (Evans & King, 1975; Bunting, Gibbons & Wynne, 1985; Summerfield & Roberts, 1985). Photoperiod, however, was shown to have a profound effect on reproductive development in groundnut (Wynne, Emery & Downs, 1973; Wynne & Emery, 1974; Ketring, 1979; Emery, Sherman & Vickers, 1981), and the genotypes varied in their sensitivity to photoperiod (Witzenberger *et al.*, 1985; Bagnall & King, 1991*a*,*b*; Bell *et al.*, 1991*a*). Witzenberger *et al.* (1985) observed variability among groundnut genotypes for photoperiod response in yield and seed grades under field conditions. Flohr, Williams & Lenz (1990) observed that in a photoperiod sensitive genotype, NC Ac 17090, the long day treatment increased the thermal time for initiation of each peg and for each pod to mature, which resulted in a reduction in partitioning of dry matter to reproductive structures.

Temperature has been shown to influence rate of plant development primarily (Leong & Ong, 1983; Bagnall & King, 1991*a*) as well as reproductive growth (Cox, 1979). In a study involving a limited number of groundnut genotypes, the base temperature below which there was no development varied between 8°C and 11°C (Leong & Ong, 1983).

Photoperiod interactions with other environmental factors are not uncommon in grain legumes (Lawn & Williams, 1987; Roberts & Summerfield, 1987). There is, however, very little information on photoperiod × temperature interaction in groundnut, although some workers have demonstrated genotype × photoperiod interactions (Wynne *et al.*, 1973) or genotype interactions with a particular environmental factor such as low irradiance (Bagnall & King, 1991*b*). Consideration of these responses in breeding strategies is important for improving the general or specific adaptability of genotypes developed in crop improvement programmes.

The objective of the present study was to examine the effect of photoperiod and temperature on the reproductive growth and development of three diverse groundnut genotypes having differing seed size and maturity.

Materials and Methods

Of the three groundnut genotypes included in the study, earlier work showed that the Indian cultivar, TMV 2, was insensitive, while the germplasm accession, NC Ac 17090, was sensitive to photoperiod (Flohr *et al.*, 1990). The reaction of the US cultivar, VA 81B, to photoperiod was not known (Table 1).

The study was conducted in the Phytotron unit of the Southeastern Plant Environment Laboratory, North Carolina State University, Raleigh, North Carolina, USA. Six walk-in growth chambers were programmed to simulate three temperature regimes under each of the two photoperiod treatments described below:

Photoperiod

LD 9 h of artificial illuminance (photosynthetic photon flux density of 598 μmol m^{-2} s^{-1}) + 3 h of low intensity light (44 μmol m^{-2} s^{-1}) in the middle of the dark period (11 pm – 2 am) to simulate long-day effects (Wynne *et al.*, 1973).

Table 1. *Description of the three groundnut genotypes used in the study*

Genotype	Origin	Classification	Relative maturity	Seed size
TMV 2	India	*A hypogaea* subsp *fastigiata* var *vulgaris*	Early	Small
NC Ac 17090	Peru	*A hypogaea* subsp *fastigiata* var *fastigiata*	Medium	Medium
VA 81B	USA	*A hypogaea* subsp. *fastigiata* var *vulgaris*	Late	Large

* Including seed mass as quantification

SD 9 h of artificial illuminance (photosynthetic photon flux density of 598 μmol m^{-2} s^{-1}) to simulate short-day conditions.

Temperature regimes

T_1 22/18°C (day/night)
T_2 26/22°C (day/night)
T_3 30/26°C (day/night)

The relative humidity in chambers was maintained at about 70% and the CO_2 levels were held at approximately 400 ppm during the course of the study.

Each genotype was sown in four pots. Three healthy seeds of each genotype with similar mass were planted at 4 cm depth in each plastic pot (25.4 cm diameter) filled with Jiffy Mix and gravel (1:2). Pots were completely randomised in the programmed growth chambers and watered with modified Hoagland's solution (Downs & Thomas, 1983) at 2-day intervals. After emergence, only the most vigorous seedling in each pot was retained. At the peak flowering stage, gypsum, at a rate equivalent to 450 kg ha^{-1}, was mixed in the top soil of each pot.

A few extra pots of each genotype, kept at 26/22°C temperature regime, were used to observe maturity of the pods and determine the time for final harvest (Table 2). The time taken by the genotypes to mature at 26/22°C regime was used as the basis for calculating the thermal time (measured in degree days, °Cd), T, required by each genotype for harvest under the other two temperature regimes. T was calculated as $T = E(T_i - T_b)$ where, T_i is the mean daily temperature on day i and T_b is the base temperature, taken as 10°C for groundnut (Mohamed, 1984). Subsequently, phenological observations made during the growing period allowed base temperature to be re-computed for each genotype (presented

Table 2. *Estimated base temperature and growth duration and equivalent thermal time (°C days, given in brackets) for the three groundnut genotypes grown at three temperature regimes*

		Duration in days and thermal time		
Genotype	Estimated base temperature (°C)	T_1 22/18 (°C)	T_2 26/22 (°C)	T_3 30/26 (°C)
TMV 2	13 29	154 (1033)	110 (1178)	86 (1266)
NC Ac 17090	12 54	161 (1202)	115 (1318)	90 (1391)
VA 81B	11 65	182 (1520)	130 (1605)	101 (1651)

in Results). The revised thermal time computations were used for estimation of growth parameters. The experiment was run in two cycles. The data were analysed using PROC GLM procedure of SAS (Anon., 1985) with runs treated as replicates.

Observations

Days to emergence and first flower appearance were recorded. At the end of the predetermined thermal time, plants were carefully harvested along with roots and separated into leaves, stems, pods and roots. Leaf area was measured on a sub-sample of leaves using a leaf area meter (Licor-3100[1]). The dry weights of leaf sub-samples, remaining leaves, stems and roots were determined separately after oven-drying the samples at 70°C for 24 h. The leaf area per plant was determined using specific leaf weight of the leaf sub-sample and dry weight of the remaining leaves. After initial sun-drying for 2 weeks, pods were oven-dried at 33°C for 48 h to ensure uniformity in drying before weighing.

Total dry matter (including roots) on a single plant basis was calculated after adjusting for the high energy content in pods using a factor of 1.65 (Duncan, McCloud, McGraw & Boote, 1978).

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Calculation of growth rates and partitioning

Plant growth and pod growth rates and partitioning were calculated on a thermal time basis by modifying the non-destructive methodology described by Williams & Saxena (1991). This method allowed estimation of crop growth rates and partitioning using observations on time to emergence and flowering, and vegetative and pod yields at the final harvest. Expression of growth rates on a thermal time basis avoided confounding effects due to genotypic differences in duration, while examining photoperiod and temperature effects.

Briefly, the plant growth (PLGR) and pod growth rates (PDGR) were calculated as:

$$PLGR\ (mg\ pl^{-1}\ °Cd^{-1}) = TDM/(Th - Te)$$

$$PDGR\ (mg\ pl^{-1}\ °Cd^{-1}) = PDM/(Th - (Tf + Tp))$$

where,

TDM = adjusted total dry matter including roots
PDM = pod dry matter after adjusting for high energy content
Th = thermal degree days accumulated from sowing until final harvest
Te = thermal degree days accumulated from sowing until emergence
Tf = thermal degree days accumulated until the first flower appearance, and
Tp = thermal degree days between flowering and initiation of pod set (taken as 10 days for the genotypes tested in the present study).

Partitioning factor (proportion of dry matter partitioned into pods) was calculated as:

Pf = PDGR/PLGR

Results

The T_b was computed for each genotype, by regressing the rate of progression to first flowering against the mean temperature. The point at which the regression line intercepted the x axis (representing the mean temperature) was taken as T_b. The estimated T_b for TMV 2, NC Ac 17090, and VA 81B were 13.3°C, 12.5°C and 11.6°C, respectively (Table 2).

[1]Mention of commercial products or companies does not imply endorsement or recommendation by ICRISAT over others of similar nature

Table 3. *Mean squares for phenology, plant growth rate (PLGR), and partitioning coefficient (Pf) calculated on the basis of thermal time for three groundnut genotypes grown under two photoperiod and three temperature regimes*

Source of variation	df	Thermal time for Emergence	Thermal time for First flower	PLGR	PDGR	Pf
Rep (R)[1]	1	69.9	6408**	779.2	10.8	0.003
Temperature (T)[1]	2	365.2	1634*	3702**	1164.5**	0.372**
Photoperiod (P)[1]	1	61.8	4780**	8627**	0.0	0.369**
T × P[1]	2	78.9	1011	856	85.5	0.086*
R × T × P	5	517.9	278	212	78.5	0.012
Genotype (G)[2]	2	536.4**	11244**	2858**	832.3**	0.407**
T × G[2]	4	29.6	290	305**	196.8**	0.021*
P × G[2]	2	46.4	75	627**	157.1**	0.045**
T × P × G[2]	4	12.8	195	98	49.9	0.008
Error	12	27.5	165	60	17.0	0.006
CV (%)		8.9	3.5	11.2	18.4	18.7

*, ** = Significant at 5% and 1% probability levels, respectively.
[1] = Significance tested using Type III MS of R × T × P as an error term.
[2] = Significance tested using error MS.

The thermal time dependent parameters were calculated using the computed T_b's for each genotype.

Days to emergence and flowering

Thermal time for emergence (mean = 59 ± 2.1°Cd) was significantly influenced by genotype ($P < 0.01$, Table 3). In terms of calendar time, however, the time taken for emergence was shortened from 8 days at T_1 regime to 3 days at T_3 regime (Table 4).

Table 4. *Influence of temperature and photoperiod on days after sowing to emergence (TE) and first flower appearance (TF) in three groundnut genotypes*

Genotype		T_1 (22/18°C) LD	T_1 (22/18°C) SD	Temperature T_2 (26/22°C) Photoperiod LD	Temperature T_2 (26/22°C) Photoperiod SD	T_3 (30/26°C) LD	T_3 (30/26°C) SD
TMV 2	TE	8.0	8.5	5.0	5.6	3.0	3.1
	TF	48.5	52.5	32.0	33.2	21.7	23.2
NC Ac 17090	TE	8.0	8.2	5.1	5.5	3.1	3.2
	TF	45.4	53.6	30.5	32.5	21.9	22.0
VA 81B	TE	8.0	9.1	5.2	5.9	3.5	3.5
	TF	44.6	49.7	33.1	34.2	23.6	23.7

		TE	TF
SED for temperature and photoperiod means	(df = 5)	1.98	2.59
SED for genotype means	(df = 12)	0.29	1.35
SED for temperature mean at the same level of photoperiod and genotype		1.63	1.86
SED for photoperiod mean at the same level of temperature and genotype		1.63	1.86

The thermal time required for first flower appearance varied significantly with temperature ($P < 0.05$), photoperiod ($P < 0.01$), and genotype ($P < 0.01$, Table 3). The interactions of temperature, photoperiod and genotypes, however, were not significant (Table 3). In the SD and T_1 regime, flowering was delayed by 4 days in TMV 2, 5 days in VA 81B, and by 8 days in NC Ac 17090 compared with LD, but the difference between LD and SD for time to flowering was minimised as the temperature increased (Table 4).

Plant growth rate

The PLGR was significantly influenced by temperature ($P < 0.01$), photoperiod ($P < 0.01$) and genotype ($P < 0.01$, Table 3). Among interactions, temperature × genotype and photoperiod × genotype were significant ($P < 0.01$), while the temperature × photoperiod was not.

There was a trend for decline in the mean PLGR with the rise in temperature. The PLGR declined form 87.5 mg pl^{-1} $°Cd^{-1}$ at T_1 to 52.4 mg pl^{-1} $°Cd^{-1}$ at T_3. Plants in LD had significantly greater PLGR (84.8 mg pl^{-1} $°Cd^{-1}$) than that of under SD (53.8 mg pl^{-1} $°Cd^{-1}$). Among genotypes, NC Ac 17090 had the highest PLGR (83.3 mg pl^{-1} $°Cd^{-1}$) while VA 81B had the lowest (52.7 mg pl^{-1} $°Cd^{-1}$).

The PLGR was consistently greater in LD than in SD at all temperature regimes in all genotypes (Fig. 1). However, the differences due to photoperiod were significant only at T_2 and T_3 in TMV 2 and NC Ac 17090.

Pod growth rate

Since the time taken from the first flower appearance to pod initiation (Tp) was not recorded in the present study, a thermal time equivalent of 10 days (deduced from earlier works of Williams, Wilson & Bate, 1975; Cox, 1979) was assumed as the time taken from flowering to pod initiation. It is possible that the thermal time required from flowering to pod initiation may vary among genotypes. However, genotypic variation in this fraction of thermal time (Tp) in the total thermal time (Th) would be relatively small, thus the variation in Tp may only alter the pod growth rate marginally.

Temperature and genotype had a significant effect ($P < 0.01$) on PDGR (Table 3) but there was no overall effect of photoperiod although temperature × genotype ($P < 0.01$) and photoperiod × genotype ($P < 0.01$) interactions for PDGR were significant.

In all genotypes, the highest PDGR was in the T_2 regime (Fig. 2) and it declined both at the lower and higher temperatures. Genotypes varied also with VA 81B producing the highest (30.9 mg pl^{-1} $°Cd^{-1}$) and NC Ac 17090 the lowest (14.2 mg pl^{-1} $°Cd^{-1}$) PDGR.

Genotypic differences for PDGR were pronounced at T_1 (Fig. 2). For example, VA 81B had a significantly greater PDGR (27–38 mg pl^{-1} $°Cd^{-1}$) than TMV 2 (14–16 mg pl^{-1} $°Cd^{-1}$), while NC Ac 17090 did not initiate any pod growth under T_1 regime. Interestingly, NC Ac 17090 had the highest PLGR at T_1 (Fig. 1).

Photoperiod effects on PDGR were relatively small for TMV 2 across all temperature regimes, whereas for Nc Ac 17090, PDGR was lower in LD at T_2 and T_3 regimes. However, none of these differences were significant (Fig. 2). On the other hand, VA 81B had greater PDGR in LD compared with SD at T_1 and T_2 regimes, with only the latter being significant.

Partitioning of dry matter to pods

The partitioning coefficient, Pf, was significantly ($P < 0.01$) influenced by photoperiod, temperature and genotype (Table 3). Temperature × photoperiod ($P < 0.05$), temperature × genotype ($P < 0.05$) and photoperiod × genotype ($P < 0.01$) interactions were also significant.

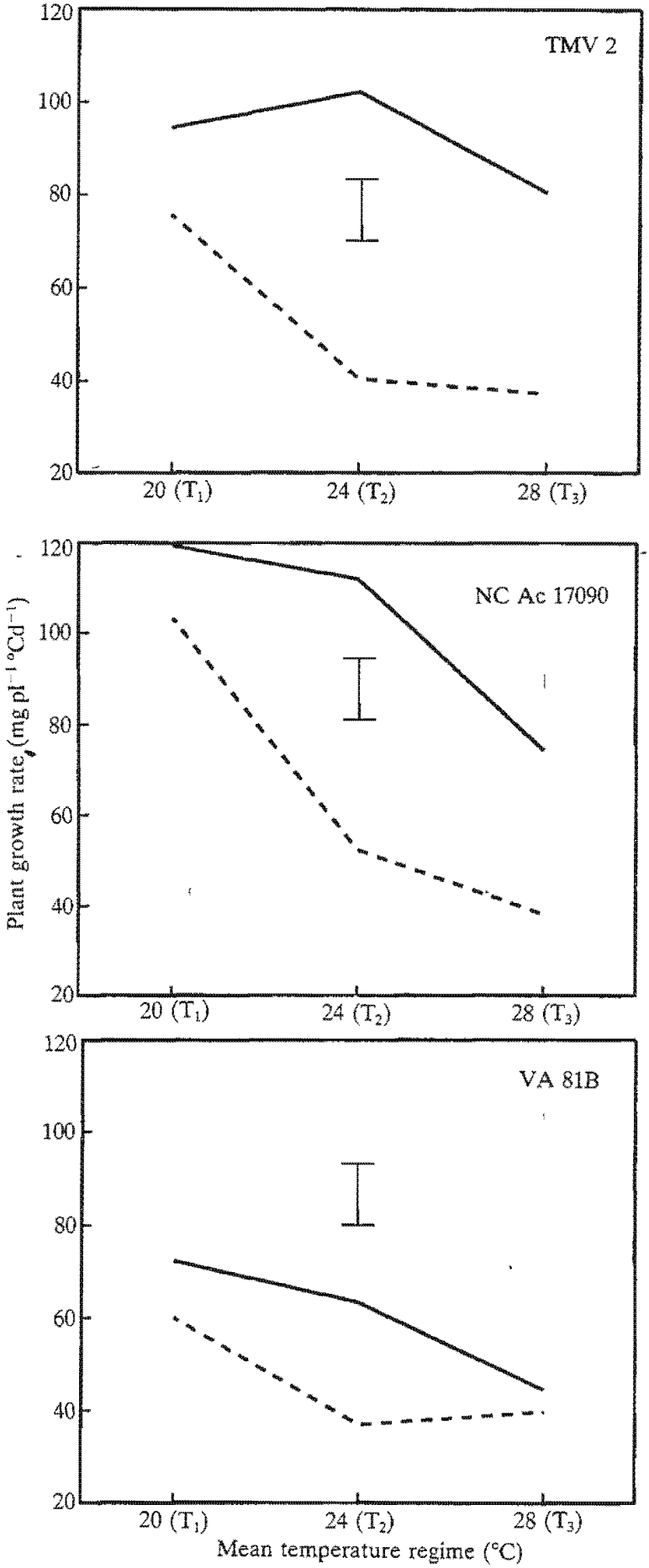

Fig. 1. Plant growth rates (mg pl^{-1} $°Cd^{-1}$) of TMV 2, NC Ac 17090, and VA 81B as influenced by two photoperiods (LD = solid line, SD = broken line) and three mean temperature regimes. Vertical bars represent SED.

The Pf was highest (0.59) under the T_2 regime and declined under both T_1 (0.24) and T_3 (0.38) regimes. The Pf under SD (0.5) was significantly greater than that under LD (0.3). Genotypes differed significantly for Pf with VA 81B having the greatest Pf (0.6) and NC Ac 17090 having the least (0.24). As for PDGR, the Pf was highest at T_2 for all genotypes but declined at both T_1 and T_3 regimes (Fig. 3). The genotypic differences in Pf were more pronounced, particularly in T_1, where NC Ac 17090 did not partition dry matter to pods, while VA 81B had the greatest Pf (0.5).

The photoperiod effects on Pf were not apparent under the T_1 regime in all genotypes. However, as the temperature increased, the photoperiod effects became significant in TMV 2 and NC Ac 17090 with Pf being significantly lower in LD than in SD in the T_2 and T_3 regimes (Fig. 3). With VA 81B, the effect of LD in reducing Pf was only marginal under the higher temperature regimes.

Discussion

The present study confirms the presence of temperature × genotype (Bagnall & King, 1991*a*,*b*) and photoperiod × genotype (Anon., 1989; Bell, Shorter & Mayer, 1991*b*; Bell *et al.*, 1991*a*) interactions for reproductive growth in groundnut.

First flower appearance, depending on the genotype, was advanced by 4–8 days in LD, but only at the low temperature regime (Table 4). This observation is in contrast with the earlier work which suggested that groundnut is a day-neutral plant as far as time to flowering is concerned (Summerfield & Wien, 1980; Leong & Ong, 1983; Anon., 1989; Bagnall & King, 1991*a*). However, both short days (Tetenyi, 1957; Sengupta, Sirohi, Pokhriyal & Kaim, 1977) and long days (Wynne & Emery, 1974) have been reported to hasten the appearance of first flower. Wynne *et al.* (1973) observed genotypic differences in temperature × day length interaction for time to flowering. These inconsistencies in the phenological responses to photoperiod might be due to variation in experimental environment and/or genotypes used in various experiments.

Temperature had a significant effect on phenology. Number of days to emergence and flowering progressively reduced with a rise in temperature as observed in earlier studies (Leong & Ong, 1983; Bagnall & King, 1991*a*; Bell *et al.*, 1991*a*,*b*). The influence of temperature at the plant level (Fortanier, 1957) and variation in genotypic sensitivity to temperature at the crop level (Williams *et al.*, 1975; Bell *et al.*, 1991*a*,*b*) are well documented.

In the present study, PLGR was appreciably higher in LD than in SD in TMV 2 and NC Ac 17090 (Fig. 1). The positive response on plant growth under LD was also observed by Ketring (1979) and Witzenberger *et al.* (1985, 1988). Sensitivity of PLGR to photoperiod was apparent in photoperiod × genotype interactions at the three temperature regimes. For example, in VA 81B, the effect of photoperiod on PLGR was relatively small at the three temperature regimes compared with the other two genotypes suggesting relative insensitivity of this genotype to photoperiod. In all genotypes, the photoperiod effect on PLGR was more pronounced at T_2 regime. Present results confirm variation in genotypic sensitivity to photoperiod in differing temperature regimes in groundnut as observed by Bell *et al.* (1991*a*,*b*). However, in the case of isolated plants, the radiation interception is determined by the leaf area rather than energy flux, so the effects observed in the present study on PLGR are largely attributable to variations in leaf area (S N Nigam *et al.*, unpublished). Even small differences in temperature and irradiance arising from a particular photoperiod treatment in growth chambers were shown to alter leaf area and plant size (Wynne & Emery, 1974; Bagnall & King, 1991*b*). Thus, NC Ac 17090, which had the highest PLGR in the present study was not found to have significantly superior crop growth rate in field

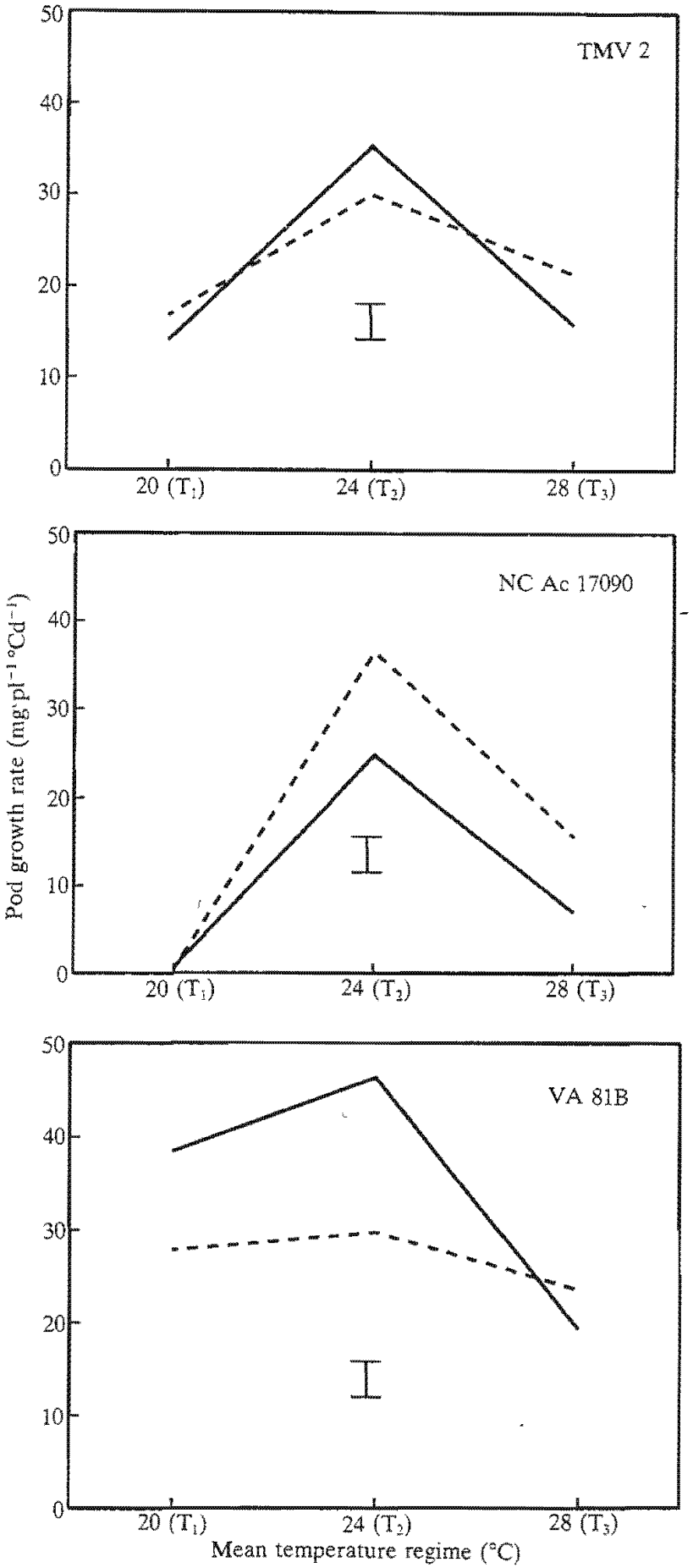

Fig. 2. Pod growth rates (mg pl^{-1} $°Cd^{-1}$) of TMV 2, NC Ac 17090, and VA 81B as influenced by two photoperiods (LD = solid line, SD = broken line) and three mean temperature regimes. Vertical bars represent SED.

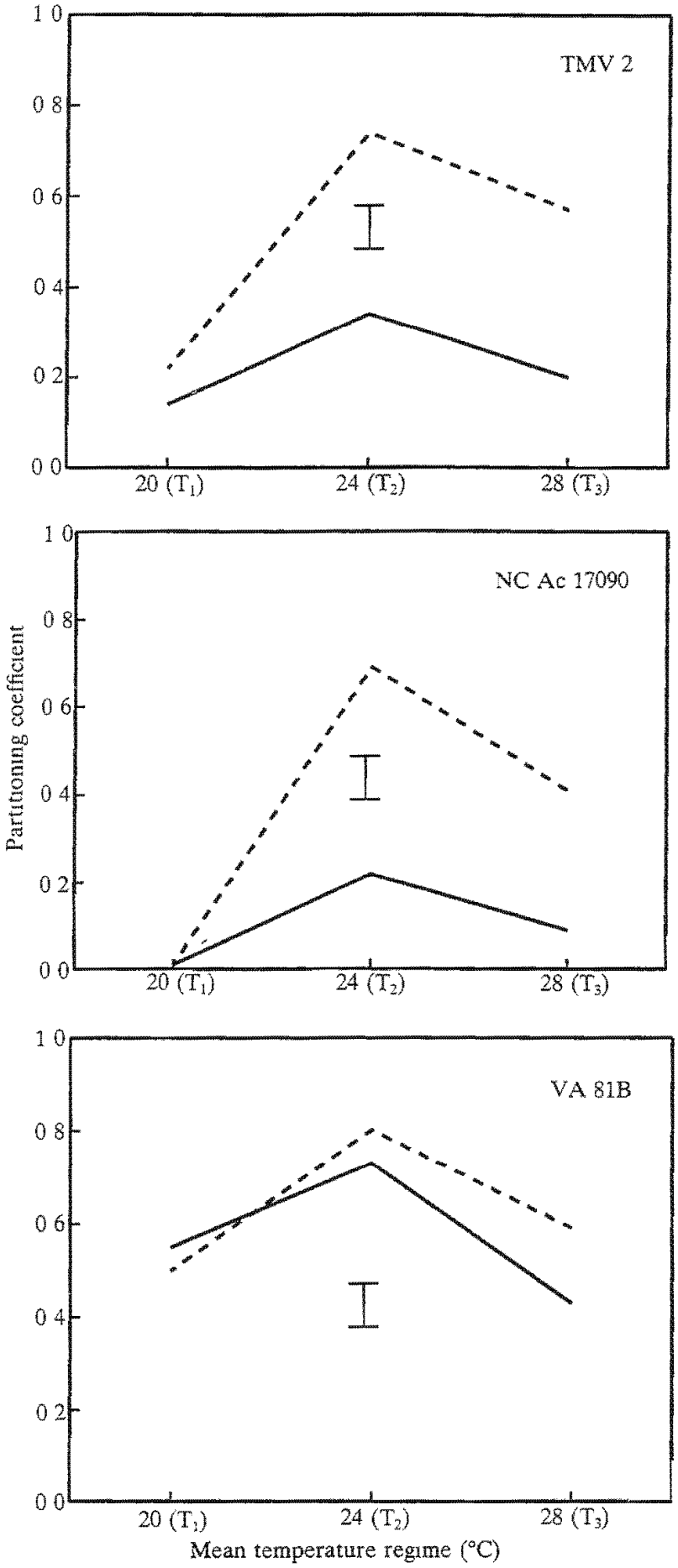

Fig 3 Partitioning coefficient, Pf, of TMV 2, NC Ac 17090, and VA 81B as influenced by two photoperiods (LD = solid line, SD = broken line) and three mean temperature regimes Vertical bars represent SED

studies where crop management ensured complete radiation interception by the canopy (Witzenberger *et al.*, 1988). It was interesting to note that TMV 2, which showed photoperiod insensitivity of Pf in field studies at the ICRISAT Center (Witzenberger *et al.*, 1985, 1988), showed significant photoperiod effects for partitioning to pods in the present phytotron study. The reasons for this discrepancy are not clear and will be the subject of future research. Bell & Harch (1991) also highlighted the apparent differences in relative photoperiod sensitivity of groundnut genotypes observed in the glasshouse and field studies.

It was apparent that Pf, in general, was affected by photoperiod at T_2 but not at T_1 (Fig. 3) indicating that the critical temperature for photoperiod action lies between T_1 (22/18°C) and T_2 (26/22°C) regimes. Further research on this aspect is of considerable significance not only in crop modelling, but also in developing methodologies for selecting genotypes for adaptation in environments with variable temperature and photoperiod regimes.

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