

Influence of Daylength on Yield-Determining Processes in Six Groundnut Cultivars (*Arachis hypogaea*)

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(Accepted 30 October 1987)

ABSTRACT

Witzenberger, A., Williams J.H. and Lenz, F., 1988. Influence of daylength on yield-determining processes in six groundnut cultivars (*Arachis hypogaea*). *Field Crops Res.*, 18: 89–100.

The vegetative and reproductive growth of six groundnut genotypes (*Arachis hypogaea* L.) in two photoperiods were studied in a field experiment. Normal daylength was 11–13 h and long-day conditions (15–16 h) were provided by extending the day with tungsten-filament bulbs.

Yield differences between the photoperiod treatments were largely explained by changes in crop growth rate, partitioning, and the length of the effective pod-filling period. Long days resulted in increased crop growth rates but generally decreased partitioning and the duration of the crops' effective pod-filling phase. However, it was dependent on the genotype which of the yield-determining processes had been more influenced by day-length conditions. In some cases, partitioning contributed most to yield differences; in others, the duration of the effective pod-filling phase contributed most.

INTRODUCTION

The cultivated groundnut (*Arachis hypogaea* L.) exhibits a quantitative response to photoperiod. Although the time to flowering is little influenced by photoperiod, the vegetative growth is stimulated by long days (LD) and pod yields are decreased (Wynne et al., 1973; Wynne and Emery, 1974; Ketring, 1979; Emery et al., 1981). However, Fortanier (1957) found that photoperiods in the range of 9–14 h had little effect on the pod yield of the cultivar Schwarz 21, and Witzenberger et al. (1985), while evaluating six groundnut genotypes for photoperiodic effects under field conditions, found that the yields of two were insensitive to the photoperiodic treatments applied, while the others had changes in yield in response to photoperiod.

Submitted as ICRISAT Journal Article No. 583.

The number of flowers produced by groundnuts is either not affected or is promoted by long photoperiods (Cheliadinova, 1941; Fortanier, 1957; Wynne et al., 1973), and photoperiod seems to influence yield at a later stage of the pod development sequence. Under unfavourable photoperiod conditions, grain legumes may shed a greater number of their buds, flowers, and immature pods. For example, an increased rate of flower abscission in LDs has been observed for the soybean (*Glycine max* (L.) Merrill), a short-day plant (Hammer, 1969; Evans and King, 1975).

Growth chamber studies by Wynne et al. (1973) and Wynne and Emery (1974) showed that in LDs, although sufficient flowers were produced, their further development either failed or was delayed. The latter hypothesis is supported by Emery et al. (1981) who compared the results of a field experiment conducted by Wynne et al. (1973) in 1970 with their phytotron results. In the field experiment, the pod yield of Spanish-type groundnuts grown over a 130-day season and a 14-h daylength during pegging was comparable to that achieved in the phytotron under short-day (SD) conditions (9 h of light) for 108 days.

Although photoperiod has been shown to affect reproductive development in controlled environments, little research has been done to examine photoperiod effects of the crop physiological processes determining yield in field conditions. Photoperiod research in field conditions presents technical difficulties in providing light over sufficient areas at sufficient intensities to invoke the photoperiod response. However, controlled-environment facilities generally cannot provide enough plant material for growth analysis. Research to investigate the significance of the reported responses under field conditions was initiated at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), near Hyderabad, India, in 1982. The effect of day length (DL) on the final yield and quality attributes of six groundnut genotypes was reported by Witzemberger et al. (1985). This showed that the genotypes varied in response to photoperiod, and that field experimentation was possible.

The objective of this paper is to examine the yield-determining physiological processes (growth rates, partitioning of assimilates to the vegetative and reproductive sinks of the plant, and the length of the pod-filling phase) which were associated with these yield changes.

MATERIAL AND METHODS

In the winter/spring (post-rainy) season of 1982/83, six groundnut genotypes (Robut 33-1, S7-2-13, M 13, TMV 2, Krapovickas St. 16, and NC Ac 17090) were grown under irrigation in the field. The two photoperiod treatments were the normal daylength (ND) at Hyderabad (17°30'N, 78°16'E) and LD conditions created by extending each day to 22:00 h with 100-W incandescent light bulbs 1.5 m above the crop and spaced at 4-m × 4.5-m intervals. This arrangement provided illumination of approximately 100 lux under the lamps. Thus the plants in the LD treatment received 15–16 h of light compared to 11–13 h

in the ND treatment. Treatments were replicated three times, resulting in a total of 36 plots. The crop management and the complete set of meteorological data are described in detail by Witzemberger et al. (1985).

Weekly sampling for growth analysis started when flowering commenced 49 days after sowing (DAS), and ended 126 DAS. The final harvest was at 140 DAS. For each of the 12 weekly harvests, 20–25 plants from a 1-m² area per plot were sampled by hand. A strip of 0.5 m was left between areas marked for sampling to avoid border effects.

Since the roots recovered represent a small portion of the total root system of groundnuts (J.H. Williams, unpublished data, 1978) the root stumps were cut off at the hypocotyl and discarded. The total number of plants was noted before measurements began. The plants were then ranked according to their size, five average plants selected as a subsample and the remaining plants processed as a bulk sample.

Pods were removed from the bulked plants, dried at 105°C to constant weight in a forced-draft oven, shelled and divided into juvenile, filling, and mature pods. Dry weight and the numbers of pods and kernels in each category were recorded. Vegetative plant parts were dried in the same way, and the dry weights of stems and leaves noted.

For the five plants of the subsample, the numbers of aerial pegs, subterranean pegs, and pods were counted, the length of the main stem measured, and the respective dry weights for leaves and stems determined. The leaf area of one subsample plant from each plot was measured with a LiCor* area meter (Model 3100); these leaves were then dried and weighed separately, and these observations used to estimate the specific leaf weight. Leaf area index (LAI) was calculated as a product of specific leaf area and the leaf dry matter obtained from the 1-m² harvested area. At final harvest only total shoot, pod and kernel dry matter were recorded.

Growth rates and partitioning factors (PF) were calculated by the method of Duncan et al. (1978). The data for each treatment ($G \times DL$) were plotted against time in order to identify the periods when growth was linear. Shoot and pod growth rates (SGR, PGR, respectively) for these periods were calculated using linear regression, and a test of parallelism was applied to determine the statistical significance of the effects of DL and G on growth rates. The PF of each treatment was calculated by dividing PGR by SGR, after adjusting both parameters (by a factor of 1.65 (McGraw, 1977)) for the higher energy (lipid) content of the pods.

Curves were fitted using regression techniques between measured parameters and days after sowing (DAS); those regression equations which accounted for most of the variability of the growth analysis data were used for plotting

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Figs. 1-4. Whenever a parameter had been measured at final harvest these data were included in the regressions.

The onset and the end of the pod-growth were gradual. Therefore the effective pod-growth period (D) was standardized as the time between 0.05 and 0.95 of the crops' maximum pod weight, using the regression equations to estimate these values.

RESULTS

Leaf area index

LAI in both photoperiodic treatments was about 1.0 for all genotypes at 50 DAS. Under the LD treatments, full ground cover ($LAI > 3.0$) was established earlier (Fig. 1), in 70-77 DAS compared with 85-90 DAS in NDS. Robut 33-1 and Krapovickas St. 16 achieved full ground cover 70 DAS in both photoperiods.

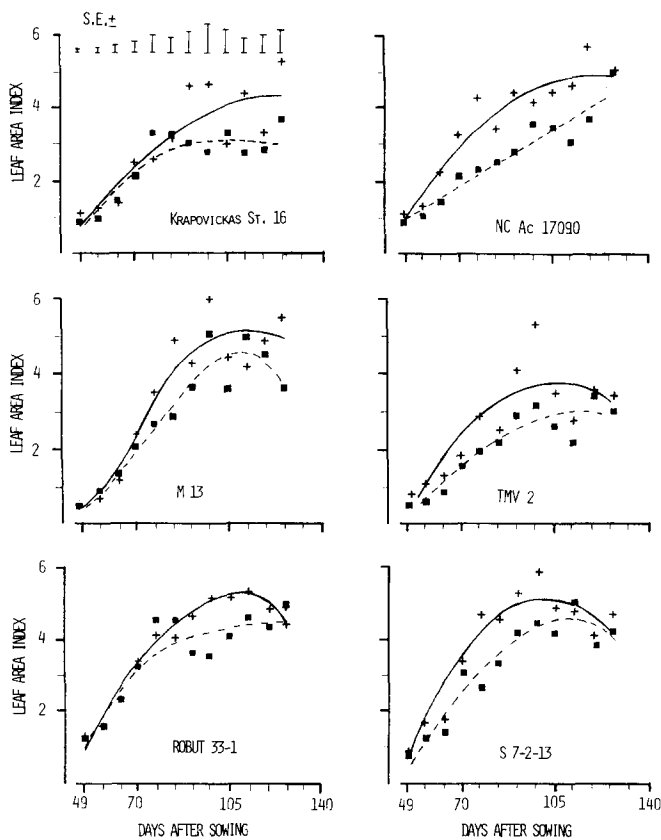


Fig. 1. Changes in leaf area index of six groundnut genotypes as influenced by the two photoperiodic treatments over the growing season. The standard errors (S.E.) are valid for all six cultivars.

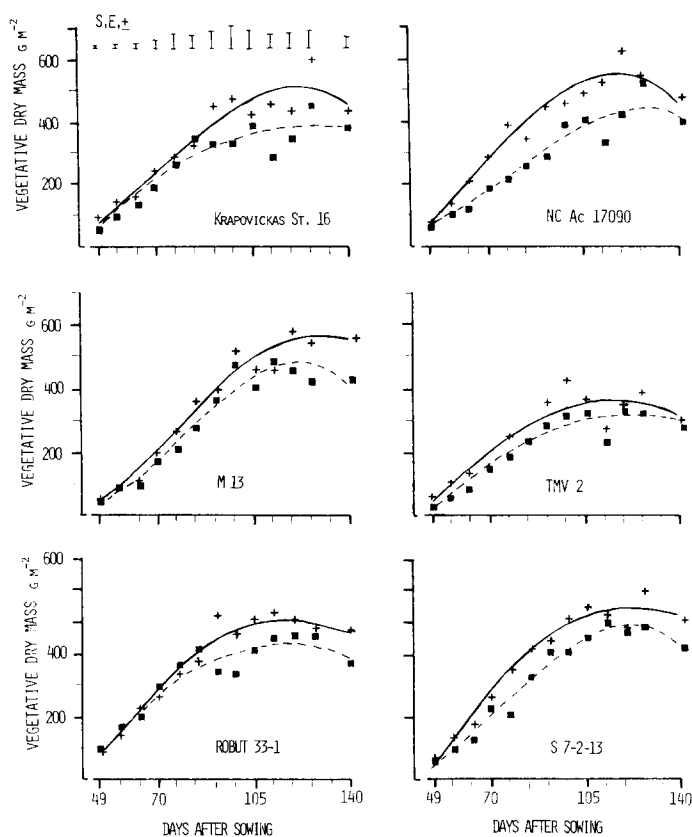


Fig. 2. Changes with time in the vegetative dry weights (g m^{-2}) of six groundnut genotypes as influenced by the two photoperiodic treatments. S.E.'s are valid for all six cultivars.

The development of LAI after full ground cover revealed greater differences between the DL treatments. All genotypes, except for TMV 2, achieved greater maximum LAIs under LD conditions than in ND. After reaching the peak value, differences in LAI between the two photoperiod treatments decreased progressively towards final harvest as more leaves were lost in the LD treatments. In M 13, these differences between LAI's in the two DLs were maintained for longer.

Vegetative dry matter

In general, vegetative dry weights were larger under LD conditions, as shown in Fig. 2. These differences developed slowly for Robut 33-1, M 13, and Krapovickas St. 16, but were apparent earlier for the other genotypes.

Reproductive dry matter

Four genotypes produced larger final pod dry weights in the normal photoperiod (Fig. 3, and Witzemberger et al., 1985). However, this significant treat-

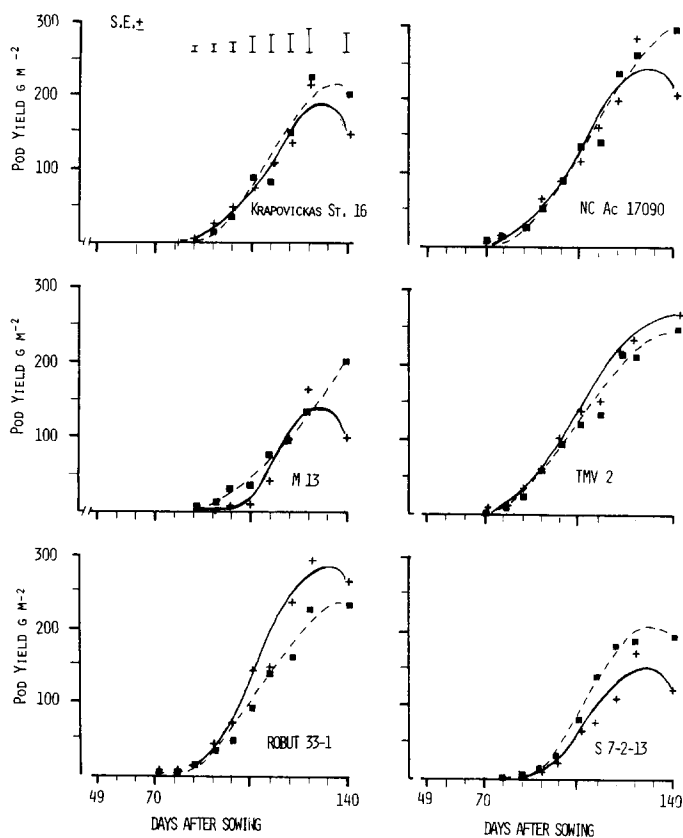


Fig. 3. Changes with time in the pod dry weights (g m^{-2}) of six groundnut genotypes as influenced by the two photoperiodic treatments. S.E.'s are valid for all six cultivars.

ment effect was established only in the last 2 weeks of the growth period for M 13, Krapovickas St. 16, and NC Ac 17090, while it developed progressively from about 80 DAS for S7-2-13. In M 13, although the first pods were present in both DL treatments after 84 DAS, pod growth was very limited until 105 DAS in the LD, whereas growth in NDs was greater during this period.

Total dry matter (TDM)

At final harvest, the TDM (after energy adjustment) was only slightly influenced by photoperiod (significantly so only for Robut 33-1) but differences between genotypes existed (Witzenberger et al., 1985). However, growth analysis showed that photoperiod affected the way this final biomass was produced (Fig. 4). Generally, curvilinear responses were observed; however with Krapovickas St. 16 and Robut 33-1 in ND, the accumulation of TDM was linear with time.

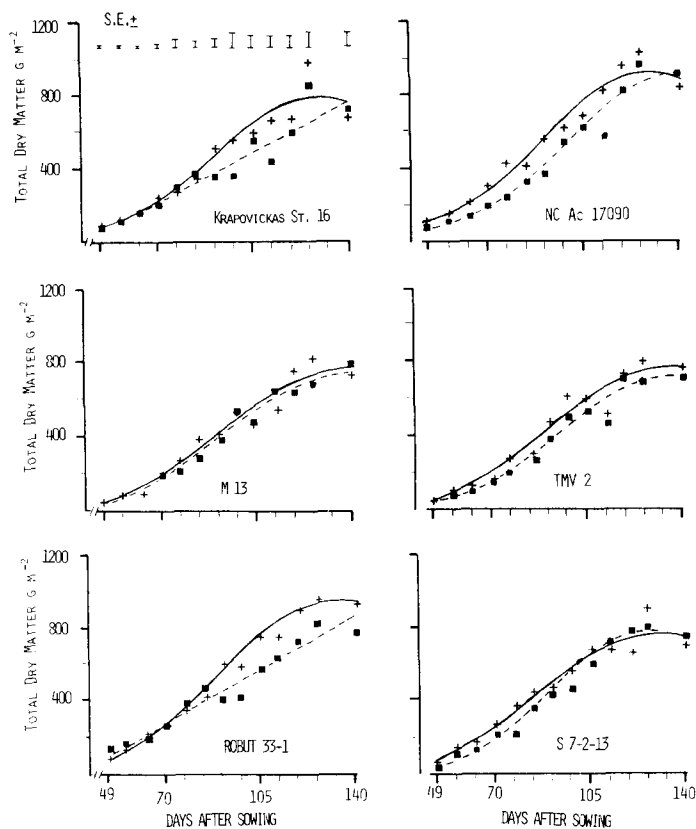


Fig. 4. Changes with time in the energy-adjusted total biomass (g m^{-2}) of six groundnut genotypes as influenced by the two photoperiodic treatments. S.E.'s are valid for all six cultivars.

Shoot and pod growth rates (SGR and PGR)

All genotypes responded to the LD treatment with an increase in SGR (Table 1), but only the 25.2% increase of M13 proved to be statistically significant in the test for parallelism. The influence of DL on PGR (Table 1) was not statistically significant and was not uniform across genotypes. Three genotypes (Robut 33-1, M 13, TMV 2) had higher PGRs under LD conditions, two (Krapovickas St. 16, NC Ac 17090) had similar PGRs in the two photoperiods, while the PGR of S7-2-13 was increased by ND.

Partitioning and pod growth periods (PF and D)

The partitioning to reproductive sinks of all genotypes was greater under ND conditions, but markedly so only for S7-2-13 and Krapovickas St. 16. For the genotypes Robut 33-1, M 13, TMV 2 and NC Ac 17090 the differences between the PF in ND and LD were less than 10%. However, substantially different PFs

TABLE 1

Effect of day length (LD: long day, ND: normal day) on shoot growth rate (SGR) and pod growth rate (PGR) of six groundnut cultivars, ICRISAT Center, India, post-rainy season 1982/83

Cultivars	DL	SGR \pm S.E.	R^2 and (n)	PGR \pm S.E.	R^2 and (n)
		(g m ⁻² day ⁻¹)		(g m ⁻² day ⁻¹)	
Robut 33-1	LD	12.62 \pm 1.29	0.94 (7)	7.17 \pm 0.85	0.93 (6)
	ND	8.90 \pm 1.03	0.90 (9)	5.40 \pm 0.50	0.96 (6)
s7-2-13	LD	11.08 \pm 0.54	0.97 (7)	4.41 \pm 0.50	0.94 (6)
	ND	10.36 \pm 0.88	0.96 (7)	5.59 \pm 0.64	0.94 (6)
M 13	LD	11.73 \pm 0.65	0.98 (6)	5.63 \pm 1.06	0.87 (5)
	ND	9.37 \pm 0.77	0.97 (5)	4.56 \pm 0.54	0.96 (4)
TMV 2	LD	13.40 \pm 2.01	0.90 (6)	5.19 \pm 0.36	0.97 (97)
	ND	11.24 \pm 0.93	0.97 (6)	4.67 \pm 0.50	0.93 (7)
Krapovickas St. 16	LD	10.40 \pm 0.82	0.96 (8)	4.96 \pm 0.68	0.91 (6)
	ND	8.80 \pm 1.23	0.85 (10)	4.95 \pm 0.72	0.88 (97)
NC Ac 17090	LD	11.22 \pm 1.40	0.93 (6)	5.66 \pm 0.49	0.96 (7)
	ND	10.40 \pm 1.10	0.93 (8)	5.77 \pm 0.50	0.97 (7)

TABLE 2

Partitioning factors (PF) and effective pod-filling periods (D) and average and final pod weights of six groundnut cultivars as influenced by the two day-length treatments (LD: long day, ND: normal day), ICRISAT Center, India, post-rainy season 1982/83

Cultivars	DL	PF (%)	D (days)	Pod weight	
				Avg. (g)	Final (g m ⁻²)
Robut 33-1	LD	93.7	41	0.78	264.2
	ND	100.1	47	0.81	230.3
s7-2-13	LD	65.6	32	0.91	118.4
	ND	90.0	35	0.76	190.6
M 13	LD	79.2	24	0.76	98.4
	ND	80.4	48	1.21	202.7
TMV 2	LD	64.0	53	0.71	269.8
	ND	68.6	52	0.68	245.4
Krapovickas St. 16	LD	78.7	36	1.24	148.5
	ND	92.8	38	1.26	204.4
NC Ac 17090	LD	83.2	43	0.99	207.2
	ND	91.5	53	0.93	297.7
S.E.				\pm 0.101	\pm 27.72

(< 70% for TMV 2 and > 90% for Robut 33-1) existed between genotypes. The duration of the pod growth was generally longer in ND treatments, but usually the extension was 1 week or less, only exceeding this for NC Ac 17090 (10 days) and M 13 (24 days). Duration also varied substantially from 32 to 53 days between the cultivars (Table 2).

TABLE 3

Changes in yield-determining factors (SGR: shoot growth rate, PF: partitioning factor, *D*: effective pod filling period), actual final yield (*Y*) and predicted final yields (PY), here presented in form of ND/LD ratios, to describe the differences in yield between ND and LD treatments, ICRISAT Center, India, post-rainy season 1982/83

Cultivars	<i>Y</i>	SGR	PF	<i>D</i>	PY
Robut 33-1	0.87	0.71	1.07	1.15	0.87
s7-2-13	1.61	0.94	1.37	1.09	1.40
M 13	2.06	0.80	1.02	2.00	1.63
TMV 2	0.91	0.84	1.07	0.98	0.88
Krapovickas St. 16	1.38	0.85	1.18	1.06	1.06
NC Ac 17090	1.44	0.93	1.10	1.23	1.26

DISCUSSION

While the photoperiodic response to light of various wavelengths in groundnuts and the qualities of this radiation provided by our array of lamps are not known, the photoperiod responses reported here show that groundnuts are influenced by this treatment. Earlier research at ICRISAT (M. Pal, unpublished data, 1982) had indicated that the threshold for photoperiod effects was about 50 lux, but it is to be noted that in this experiment the variances found in the photoperiod treatments were greater than in the control, suggesting that distribution of the light could have been improved.

Pod yield (*Y*) can be considered in terms of the equation:

$$Y = \text{SGR} \times \text{PF} \times D \quad (1)$$

Since it was our intention to compare the yield-determining processes between the two treatments, we calculated separately for each genotype ND/LD ratios for the actual final yields and for each of these yield-determining factors. The calculated ratios (Table 3) were substituted in the equation, modifying it as below:

$$Y_{\text{ND/LD}} = \text{SGR}_{\text{ND/LD}} \times \text{PF}_{\text{ND/LD}} \times D_{\text{ND/LD}} = \text{PY}_{\text{ND/LD}} \quad (2)$$

Equation (2) allowed us to identify those yield-determining factors which were most sensitive to photoperiod. For this purpose the actual ND/LD yield ratio of each genotype was also compared with the product (PY) of the component factor ND/LD ratios (the predicted relative change in yield due to photoperiod).

The ratios of the final yield between DL treatments were accurately predicted for Robut 33-1 and TMV 2. Although LD increased SGR by 42% and 19% respectively, the decrease in PF for both genotypes and the moderate shortening

of *D* for Robot 33-1 countered the LD effects on SGR resulting in yields from the photoperiod treatments being not significantly different.

For those genotypes with greater final yields in the ND treatment, decrease in SGR under ND conditions ranged from 6% to 20% below those observed in LDs; however, the ratios showed that PF and *D* responses were specific for genotypes. The 37% greater partitioning in ND was largely responsible for the higher final yield of S7-2-13. In contrast, the PF of M 13 was not modified by DL and the greater final pod yield could be attributed to the doubling of *D* in the ND treatment. In both Valencia genotypes (Krapovickas St. 16 and NC Ac 17090), higher final yields in ND were associated with moderate increases in both PF and *D*.

Variations in shoot growth rate may arise for any of a number of reasons, these being: variations in the amount of energy intercepted; the distribution of the assimilate between the roots and shoots; or variations in the photosynthetic efficiency of the intercepted radiation. Although total light interception should have been comparable between DL treatments after LAI exceeded 3–3.5 in both DL treatments, the crops exposed to LDs all had greater SGRs. Therefore, the reasons for this greater shoot growth rate are not clear from the data collected. Although it is possible that shoot growth could increase at the expense of root growth, it also is possible that canopy arrangement differed to allow more efficient use of the intercepted light. Photoperiod has been observed significantly to change the angles of the side branches (A. Witzemberger, unpublished data, 1984). Differences in SGR between DL treatments could have been also associated with photosynthetic and respiratory changes since photoperiod has been reported to influence the photosynthetic process (Sestak, 1971). A greater net assimilation, as a result of photosynthesis due to the additional light provided by the DL extension, can be excluded as a factor contributing to the greater vegetative mass in LD, since Bhagsari (1974) found that groundnuts have a photosynthetic compensation point of about 2.7 klx and the lamps used for extending the day provided an illumination not exceeding 100 lx at the crop surface.

Since the final pod yields either were similar in both DL treatments, or were decreased by LD, the increase mainly contributed to the greater accumulation of vegetative dry matter. Clearly, part of the additional assimilate contributed to the larger leaf area under LD conditions. This result is in agreement with Ketring (1979) who observed both more and larger individual leaves. In contrast, Fortanier (1957) found (for a different cultivar) that extended day length using different periods of low or high illumination invoked only relatively small changes in these parameters.

Under ND conditions, these genotypes produced final pod yields similar to, or higher than, those under LD, despite the lower SGRs because of either an increase in partitioning to pods, a longer pod-growth phase, or both. Partitioning of assimilates was increased for all genotypes by ND, revealing that even

those with lower absolute PGRs in ND had a proportionally greater distribution of assimilates to their reproductive sinks. These changes in partitioning were consistent with the effects of photoperiod observed in controlled environments (Wynne et al., 1973).

The final yield-determining factor (the duration of the pod-filling phase) was lengthened in the normal photoperiod for all the genotypes, particularly so for M 13, where it was doubled. The longer *D* in NDS was associated with a slower decline in vegetative structures at the end of the growing period, by which time substantial decreases in vegetative dry mass had started in the LD treatment. The reasons for, and implications of, this effect are not clear.

Another limitation to *D* is the deterioration of pegs, which may start soon after the earliest pods reach their maximum dry weight. For most of the genotypes, a loss of pod mass towards final harvest was observed, particularly so in the long photoperiod. This phenomenon is an indication that these treatments had achieved maturity and that the estimates of duration are not limited by the times allowed for growth.

The results of this field study differed from earlier research in phytotrons (Wynne et al., 1973; Wynne and Emery, 1974; Emery et al., 1981), in that the effect of photoperiod on pod yield in phytotrons was much greater at comparable stages of growth. Differences in either the genotypes or DL treatments investigated could be responsible for these differences in results. In the growth-chamber studies, the illumination to create LD treatments was much greater than in this experiment (± 100 lx vs. ± 3200 lx). Additionally, the plants in pots were given interrupted dark periods, while this crop was exposed to an extended day. Other agronomic research at ICRISAT (A. Witzemberger, unpublished data, 1985) has shown that interrupting the dark period may reduce groundnut yield more than an extension of the day; therefore, careful consideration of the management of photoperiod treatments is necessary for experiments investigating the influence of photoperiod on groundnuts in both field and phytotron. Attention should also be paid to the strength of illumination for the LD treatment. However, since the duration of pod growth was varied by photoperiod, it will be very important in experiments involving photoperiod to monitor plant maturity closely and consider harvest dates carefully.

ACKNOWLEDGEMENTS

This work was supported by the International Agricultural Research Funds of GTZ (Deutsche Gesellschaft fuer Technische Zusammenarbeit). Additional financial support was given by the Heinrich Hertz Stiftung (Foundation), Duesseldorf, and the Fritz ter Mer Stiftung, Leverkusen. We gratefully acknowledge the support and facilities provided by ICRISAT, particularly the as-

sistance of P. Arjuno Rao in growth analysis work, and C.K. Ong and J.A. Wightman for comments and suggestions on earlier drafts of this paper.

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