Short Communication

Light Effects on Development of an Indeterminate Plant

Received for publication August 28, 1978 and in revised form January 1, 1979

DAROLD L. KETRING
United States Department of Agriculture, Science and Education Administration, Agricultural Research and Department of Plant Sciences, Texas A&M University, College Station, Texas 77843

ABSTRACT

The peanut (Arachis hypogaea L.) plant is indeterminate in growth habit and day-neutral with respect to flower initiation. The Spanish-type cultivar used in this study begins flowering 3 to 4 weeks from planting under optimal environmental conditions. In this study, irradiance and photoperiod were used to alter the development of the peanut plant. Plants grown at low irradiance (300 microeinsteins per square meter per second) had the same number of leaves as the plants grown at high irradiance (500 microeinsteins per square meter per second), but they had a larger leaf surface area and were taller than plants grown at the high irradiance. However, flowering and other reproductive components (pegs, pods, and seeds) were reduced at low irradiance. Comparison of 8-, 12-, and 16-hour photoperiods at the high irradiance showed that the 16-hour photoperiod produced the largest amount of vegetative, but least amount of reproductive components. The plants grown at 8-hour photoperiod had one-third as much total leaf area as plants grown at 16 hours, but six times more weight of mature seeds. The larger amount of photosynthetic surface (leaf area) did not result in more reproductive growth. The results indicate that the peanut plant may readily redistribute its available assimilates between vegetative and reproductive growth in response to irradiance and photoperiod.

The peanut plant is indeterminate in growth habit and day-neutral with respect to flower initiation. Temperature (1, 2, 9, 10), and photoperiod (4, 5, 10) influence vegetative and reproductive development of this plant. Generally, peanut cultivars of different origin respond similarly to temperature, i.e. vegetative growth, flowering initiation, number of flowers per plant, and pod formation are retarded at temperature below about 25 to 27 C. Above 30 C vegetative growth may increase, but at higher temperatures the number of flowers per plant and pod production usually decrease (1, 2, 4, 9, 10). Quantitative differences between cultivars occur due to temperature treatment within the 25 to 30 C range and there is a photoperiod effect. At 30 C, Alegre (1) found that shortening the photoperiod to 9 h reduced the amount of flowering. Fortanier (4) found that with photoperiods of 12, 16, 20, or 24 h at constant irradiance (about 450 μE m⁻² s⁻¹) and temperature (32 C) differences in lengths of the main axes and number of leaves between 12- and 24-h photoperiods were small, but there was an increase in dry weight of the plants as the photoperiod was lengthened. The number of flowers increased as the photoperiod was lengthened from 12 to 24 h while the opposite occurred for fruit formation (4). A photoperiod of 9 to 14 h was suggested to be optimum for rapid fruit formation while longer photoperiods delayed fruiting. With a day/night temperature regime of 30/26 C, Wynn et al. (10) found that the three botanical types of peanuts (Spanish, Virginia, and Valencia) responded to different photoperiods by producing a higher fruit weight to plant weight ratio under short (9-h) photoperiods. Gautreau (5) concluded from tests with a Spanish-type cultivar that total radiation received by the plants was a predominant factor in the regulation of growth and fruiting. At a constant photoperiod of 15 h the early vegetative growth of a Virginia-type peanut cultivar increased as irradiance was increased (3).

Under favorable temperature flowering was initiated and fruiting occurred under both short- and long-day conditions, i.e. there were no inductive effect of photoperiod (1, 4, 10). Peanut plants responded to both photoperiod and irradiance, but the extent to which these change the proportion of vegetative to reproductive growth has not been well defined, particularly for mature peanut plants. My objective was to quantify the effect of light intensity and photoperiod on the relationship between fruiting and vegetative growth of the indeterminate, day-neutral peanut plant.

MATERIALS AND METHODS

Plant Culture. Arachis hypogaea L. cv. Starr, Spanish-type peanut plants were used in these experiments. The plants were grown in 20-cm-diameter plastic pots that contained a mixture of Vermiculite/agricultural Vermiculite/acid-washed sand 1:1:1 (v/v/v). Modified Hoagland nutrient solution containing additional Ca²⁺ (10 mm) and NO₃⁻ (25 mm) was applied (200 ml) every 3 days. Also, the plants were watered with distilled H₂O as needed. The plants were grown in Sherer model Cel 25-7 HL growth chambers equipped with 10 F48T12/CW/VHO 110-w fluorescent lamps supplemented by 12 25-w incandescent lamps. All new lamps were installed in the chambers at the start of each experiment. Irradiance at that time ranged from about 530 to 600 μE m⁻² s⁻¹ measured 41 cm from the fluorescent lamps (about the top of the plant canopy for mature plants). Irradiances were measured with a Lambda LI-185 light meter using the LI-190S quantum sensor. Treatments were imposed by changing the irradiance at initiation of flowering (26 days from planting) or by changing the photoperiod at 21 days from planting (flowering was initiated at 23 to 26 days in these experiments). This allowed all plants to develop uniform vegetative growth for at least 21 days. The light treatments were continued for the duration of the experiment. Temperatures were maintained on 12 h/12 h cycles

1 Cooperative Investigations of USDA-SEA, Agricultural Research and the Texas Agricultural Experiment Station, Texas A&M University.
2 Present address: Agronomy Department, Oklahoma State University, Stillwater, Oklahoma 74074.

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at 30/25 ± 1 C. RH was not controlled, but it usually exceeded 60%. All plants were harvested at 91 to 95 days from planting, which is about the minimum irradiance time for these plants grown under cultivated conditions. Number of leaves, leaflet area, and lengths of the main stem axis and both cotyledonal laterals were determined from four plants in each experiment at harvest.

Statistical Analyses. Paired treatments (500 versus 300 μE m⁻² s⁻¹ or 16- versus 8-h photoperiods) with 16 plants (maximum for each chamber) per treatment were run simultaneously in separate chambers and the experiment was repeated with the treatments reversed in the same chambers. Data were calculated on a per-plant basis. Student's t test was used to determine whether the differences between mean values of the treatments were significant.

RESULTS AND DISCUSSION

Irradiance. Plants at the low irradiance had the same number of leaves, but greater total leaf surface area, longer main stem axes, and longer cotyledonal laterals than plants grown at the high irradiance (Table I).

Cumulative numbers of flowers per plant were reduced at the low irradiance (Fig. 1A) and each sequential reproductive component (pegs, mature pods, and seeds) was also less than at the high irradiance (Table II). There was no significant difference in immature reproductive components between the two irradiances. The low irradiance did not delay fruit formation, but the amount of fruit sustained by the plants to maturity was reduced. Concurrently, vegetative growth, particularly leaf area, increased under the low irradiance treatment. Although the number of flowers per plant was reduced, three times more flowers than mature pods were produced at the low irradiance. Thus, initiation of reproductive growth was not the limiting factor under low irradiance. Since vegetative growth increased under low irradiance while the remaining reproductive components (pegs, mature pods, and seeds) decreased, the plants quantitatively changed the proportion of vegetative to reproductive growth in response to irradiance.

Photoperiod. The irradiance experiments were conducted with 12-h photoperiods and the high irradiance was the same as that used for a shorter (8-h) and a longer (16-h) photoperiod. These data are compared with those from the longer and shorter photoperiods. Plants that received 8 h of light per day had fewer leaves and reduced total leaflet area while the main stem axes and cotyledonal lateral lengths were the same as for plants that received 12 h of light (Table III). The plants that received 8 h of light were somewhat chlorotic and it was clear that these plants did not receive a sufficient daily period of light. In contrast, the most extensive vegetative growth occurred for plants grown with 16 h of light per day (Table III). The determinations for number of leaves and total leaflet area were somewhat conservative since

Table I. Effect of Irradiance on Vegetative Development of cv. Starr Spanish-type Peanut Plants

<table>
<thead>
<tr>
<th>Irradiance</th>
<th>Leaves</th>
<th>Total Leaflet Area</th>
<th>Main Axis Length</th>
<th>Cotyledonal Lateral Length</th>
</tr>
</thead>
<tbody>
<tr>
<td>μE m⁻² s⁻¹</td>
<td>No. cm²</td>
<td>cm</td>
<td>cm</td>
<td>cm</td>
</tr>
<tr>
<td>500</td>
<td>66.9 1583.6**</td>
<td>25.3**</td>
<td>32.2*</td>
<td>31.5**</td>
</tr>
<tr>
<td>300</td>
<td>69.1 1875.7</td>
<td>47.2</td>
<td>50.6</td>
<td>51.0</td>
</tr>
</tbody>
</table>

** Significantly different at 0.01 level of confidence.
* Significantly different at 0.05 level of confidence.

Table II. Effect of Irradiance on Reproductive Development of cv. Starr Spanish-type Peanut Plants

<table>
<thead>
<tr>
<th>Irradiance</th>
<th>Total Pegs</th>
<th>Subterminal Pegs</th>
<th>Mature Pods</th>
<th>Immature Pods</th>
<th>Mature Seeds</th>
<th>Immature Seeds</th>
</tr>
</thead>
<tbody>
<tr>
<td>μE m⁻² s⁻¹</td>
<td>No.</td>
<td>No.</td>
<td>No.</td>
<td>No.</td>
<td>No.</td>
<td>No.</td>
</tr>
<tr>
<td>500</td>
<td>18.2</td>
<td>16.8**</td>
<td>10.8*</td>
<td>2.8</td>
<td>21.1**</td>
<td>7.08**</td>
</tr>
<tr>
<td>300</td>
<td>14.3</td>
<td>13.5</td>
<td>7.8</td>
<td>2.2</td>
<td>15.2</td>
<td>4.97</td>
</tr>
</tbody>
</table>

** Significantly different at 0.01 level of confidence.
* Significantly different at 0.05 level of confidence.

Table III. Effect of Photoperiod on Vegetative Development of cv. Starr Spanish-type Peanut Plants

<table>
<thead>
<tr>
<th>Photoperiod</th>
<th>Leaves</th>
<th>Total Leaflet Area</th>
<th>Main Axis Length</th>
<th>Cotyledonal Lateral Length</th>
</tr>
</thead>
<tbody>
<tr>
<td>h</td>
<td>No. cm²</td>
<td>cm</td>
<td>cm</td>
<td>cm</td>
</tr>
<tr>
<td>16</td>
<td>87.1 3283.2a</td>
<td>59.8a</td>
<td>63.1a</td>
<td>64.1a</td>
</tr>
<tr>
<td>12</td>
<td>66.9b 1583.6b 25.3b 32.2b</td>
<td>31.5b</td>
<td></td>
<td></td>
</tr>
<tr>
<td>8</td>
<td>47.6c 1020.8c</td>
<td>27.4b</td>
<td>29.3b</td>
<td>31.3b</td>
</tr>
</tbody>
</table>

1 Data from Table I for comparison.

FIG. 1. Effect of irradiance (A) and photoperiod (B) on cumulative flowering of cv. Starr Spanish-type peanut plants. Irradiances were 500 μE m⁻² s⁻¹ (a) and 300 μE m⁻² s⁻¹ (b). Photoperiods were as shown. Day 1 of flowering was 23 to 26 days after planting.

Some leaves abscised from the lower nodes as canopy density increased and light penetration decreased. The vegetative growth of this cultivar in response to photoperiod differs from that of the Schwartz 21 cultivar used by Fortanier (4). He did not find a large change in stem length or in number of leaves as the light period was increased from 12 to 24 h. This suggests that there may be genetic diversity among peanut cultivars in their response to photoperiod.

There was a prolonged duration of flowering by plants that received 16 h of light (Fig. 1B), which agreed with the data of
Table IV. Effect of Photoperiod on Reproductive Development of cv. Starr Spanish-type Peanut Plants

<table>
<thead>
<tr>
<th>Photoperiod</th>
<th>Total Pegs</th>
<th>Subterranean Pegs</th>
<th>Mature Pods</th>
<th>Immature Pods</th>
<th>Mature Seeds</th>
<th>Immature Seeds</th>
</tr>
</thead>
<tbody>
<tr>
<td>h</td>
<td>N0</td>
<td>N0</td>
<td>N0</td>
<td>N0</td>
<td>N0</td>
<td>g</td>
</tr>
<tr>
<td>16</td>
<td>21.0a</td>
<td>10.2c</td>
<td>1.8c</td>
<td>2.2a</td>
<td>2.8c</td>
<td>0.60c</td>
</tr>
<tr>
<td>12</td>
<td>18.2a</td>
<td>16.8a</td>
<td>10.8a</td>
<td>2.8a</td>
<td>21.1a</td>
<td>7.08a</td>
</tr>
<tr>
<td>8</td>
<td>15.0b</td>
<td>13.8b</td>
<td>6.3b</td>
<td>2.2a</td>
<td>10.8b</td>
<td>3.81b</td>
</tr>
</tbody>
</table>

1 Data from Table II for comparison.

Fortanier (4). But there was no significant difference in cumulative number of flowers per plant between 8 and 12 h of light for the duration of these experiments (Fig. 1B). Total pegs were the same for 12- and 16-h photoperiods, but the number of pegs reaching the soil (subterranean pegs) and values for all other reproductive components (mature pods and seeds) of plants grown in 16 h of light were reduced even below those of plants grown in 8 h of light (Table IV). Immature pods and seeds were the same for plants in all photoperiods (Table IV). Thus, there was no apparent delay in maturation but an over-all reduction in mature fruit formation when vegetative growth was increased. This was also true for plants grown at different irradiances (Tables I and II). Under long photoperiods and with increased photosynthetic surface, it might be expected that more reproductive growth would occur; however, a 12-h photoperiod was optimum for reproductive growth in relation to total leaflet area (photosynthetic surface) produced (Tables III and IV). This 12-h photoperiod was in the range of the 9 to 14 h suggested by Fortanier (4) for optimum fruit formation by the Schwarz 21 cultivar. The extensive vegetative growth under long photoperiods and more reproductive growth under short photoperiods agreed with the data of Wynne et al. (10); but the data in Tables III and IV indicate that there was an optimum photoperiod at a given irradiance.

How can these data be interpreted in view of present concepts of the photoperiodic responses of plants? Since there was no inductive effect of light with respect to flower initiation or fruiting, these responses cannot be interpreted as photoperiodic in the strictest sense. The data suggest that pod and seed formation might be interpreted as a quantitative short-day response. This does not take into account the facts that vegetative growth (plant height and particularly leaf area) increased at low irradiance (300 μE m⁻² s⁻¹) with a 12-h photoperiod (Table I) and also increased at high irradiance (500 μE m⁻² s⁻¹) with a 16-h photoperiod (Table III) while in both instances reproductive growth (mature pods and seeds) decreased (Tables II and IV).

Leaf area was the primary measurement of vegetative growth in this study because in other work (6) no relationship between shoot dry weight and seed formation was found. Regression analysis between leaf area produced under the different light treatments and each reproductive component gave negative correlation coefficients of −0.76, −0.72, −0.66, and −0.71 for subterranean pegs, number of mature pods, seed number, and seed weight, respectively. The negative correlation between leaf area and reproductive components was significant at the 0.05 level except for seed number. However, the association between these growth phases may not be direct.

Compared to the 12-h photoperiod, both leaf area and reproductive growth were reduced under the 8-h photoperiod (Tables III and IV). Perhaps due to an insufficient daily photoperiod, photosynthetic was limiting both growth phases. However, these plants had one-third as much leaf area and produced six times more weight of mature seeds than plants grown with a 16-h photoperiod (Table III and IV). Extending the photoperiod beyond 12 to 16 h apparently enhanced vegetative growth at the expense of reproductive growth. Shading in the lower canopy due to extensive vegetative growth, as indicated by leaf abscission from the lower nodes, could have reduced the effective photosynthetic contribution of lower leaves to fruit formation which contributed to reduced reproductive growth. Steward (8) found that photoperiod caused changes in plant metabolism. Alterations in plant metabolism due to photoperiod might also explain the observed changes in vegetative and reproductive growth of these plants.

At low irradiance (300 μE m⁻² s⁻¹) compared to high irradiance (500 μE m⁻² s⁻¹) with an equal 12-h photoperiod, available photosynthetic may have limited reproductive growth (Table II); but the increased leaf area and plant height indicate there was sufficient photosynthetic for growth (Table I). Nelson (7) has shown that translocation of assimilates from shoots to roots is affected by irradiance. Reduced translocation of photosynthate to developing pods and seeds could also account for the observed change in proportion of vegetative to reproductive growth under low irradiance.

Further research is necessary to elucidate the mechanism, but these Spanish-type peanut plants readily changed the proportion of vegetative to reproductive growth in response to light conditions. Perhaps other indeterminate, day-neutral plants respond to light conditions in a similar manner.

LITERATURE CITED

4. Fortanier EJ 1957 Control of flowering in Arachis hypogaea L. Dois Theis Agr. Univ Wageningen

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