THE EFFECTS OF RED AND FAR-RED IRRADIATION ON THE VEGETATIVE DEVELOPMENT OF PEA AND COCKLEBUR

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The vegetative growth of many plants is regulated significantly by light quality and intensity. Several responses are controlled by light quality; these include seed germination, pigment formation, unfolding of the plumular hook, elongation of stems, and leaf expansion. Recent studies have shown that the basic underlying photoreaction involved in each case is the same (Borthwick and Hendricks, 1960; Butler and Downs, 1960; Downs, 1959; Hendricks, 1959; Meijer, 1959). Light is absorbed by a blue-green pigment, phytochrome, which appears to exist in two forms. The photochemical reaction may be written as given below.

$$\text{Pigment } RH_2 + A \underset{\text{7200-7400 Å max}}{\overset{\text{6500-6600 Å max}}{\rightleftharpoons}} \text{Pigment FR} + AH_2$$

In this formula, *R* and *FR* refer to the red and far-red absorbing pigment forms, respectively (Hendricks, 1959). It has been shown that the effects of red radiation can be markedly reduced or even entirely eliminated in some cases by a subsequent exposure to wavelengths in the far-red portion of the spectrum (Hendricks, 1959; Meijer, 1959; Van der Veen and Meijer, 1959).

The present investigation was undertaken to examine the effects of red and far-red light on certain aspects of the vegetative development of garden pea and cocklebur.

Materials and Methods

Cultural procedure. Seeds of garden pea (*Pisum sativum L.*), variety Thomas Laxton, were soaked for 19 hours in flowing tap water at 8-10°C and then sown approximately 4 cm apart in unglazed clay pots or plastic flats containing vermiculite, thoroughly wetted with tap water. At the end of a germination period of 72 hours in a dark controlled-environment room at 21°C, approximately 50% of the seedlings had emerged. At this time the containers were divided into groups, each containing a minimum of twenty uniform tagged seedlings, and subjected to the various light treatments. The remaining plants in the containers were permitted to grow with the tagged seedlings but were not used in the experiment.

Achenes of cocklebur (*Xanthium pensylvanicum* Wallr.) were germinated by the procedure described by Vergara and McIlrath (1960) and planted approximately 8 cm apart in quartz sand in plastic flats. The seedlings were grown under non-inductive conditions of 20 hours of light per day in a controlled-environ-

ment room at 70±2°F and received approximately 2000 ft-c. of light from General Electric Power Groove fluorescent lamps supplemented with 60-watt incandescent bulbs (approximately 12% of the total wattage). When two nodes became visible, the plants were subjected to the various light treatments. Six plants constituted a series in each treatment.

Both cocklebur and pea plants were watered three times per week during the course of the experiment, the former with a complete nutrient solution (Hoagland and Arnon, 1950) and the latter with distilled water.

Irradiation procedure. All seedlings were exposed to an 11-hour photoperiod between 9 a.m. and 8 p.m. daily. In the six treatment series plants were exposed to various light qualities for the following number of hours: Group A—11 incandescent (I); Group B—9I and 2 far-red (FR); Group C—9I and 2 red (R); Group D—11 fluorescent (F); Group E—9F and 2FR; Group F—9F and 2R. A temperature of 21±2°C and a relative humidity of 60-75% were maintained. When red or far-red light constituted a portion of the treatment, it was always given during the final 2 hours of the light period.

The lamps and filters utilized to produce each type of light regime are indicated in Table 1. The filters were similar to those described by other workers (Liverman, 1959; Na-

TABLE 1.—Light Sources and Energies Utilized in the Various Experiments.

Irradiation	Lamp	Filters	Light Energies, μW/cm²	
			Experiment	
			I	II-III
Incandescent	1000-watt incandescent, General Electric, RB 52 (I)*	None	1565	3700
Fluorescent	40-watt warm white fluorescent, General Electric (F)*	None	1132	3700
Red	40-watt warm white fluorescent, General Electric	Two layers of red cellophane	1827	3700
Far-red	1000-watt incandescent, General Electric RB 52	Two layers of red and two layers of blue cellophane	1152	3700

* Percentage spectral energy distribution: 4000-5000 Å — I 10.1, F 19.2; 5000-6000 Å — I 24.1, F 48.8; 6000-7600 Å — I 65.7, F 32.0.

kayama, *et al.*, 1960). The radiant energies for the various types of light were determined with a Weston Illumination Meter (type 756) which had been previously calibrated with a thermopile for each type of irradiation (Van der Veen and Meijer, 1959). The Weston meter readings were taken at the level of the plants. The spectral energy distribution of the visible light from the incandescent and fluorescent lamps (Table 1) was taken from the tables presented by Weitz (1956).

Harvest procedure. The pea seedlings were permitted to grow under the light conditions described for 14 days, at which time the morphological age of the plants in tenths of nodes was determined using a modification of the method of Higgins (1952). This technique is based on scoring the plant's morphological age in terms of number of nodes produced and it permits stages beyond the last discernible node to be designated in tenths of nodes (Figs. 1 and 2).

After the morphological ages of the plants in each group had been determined, the shoots were cut at the level of the cotyledons, and the lengths were recorded to the nearest millimeter of the third internode. The widths of the stipules and leaflets at node five were also determined. The total surface area of the leaflets and stipules at node five was measured with an Aminco leaf area meter.

The length of the second internode of cocklebur was measured to the nearest millimeter. These plants were irradiated simultaneously with the pea seedlings.

Statistical analyses were carried out according to established procedures (Snedecor, 1946).

Results and Discussion

Influence of Quantity and Quality of Light on Internodal Lengths of Pea and Cocklebur. Internodal lengths were greatest when irradiation with either incandescent or fluorescent lamps was followed by far-red radiation (Table 2).

With respect to pea, it is of interest that the multifold increase in light energy during Experiment II, compared with that in Experiment I, had a pronounced effect in the fluorescent series, groups D-F, and a slight but statistically insignificant effect in the incandescent series, groups A-C, (Table 2).

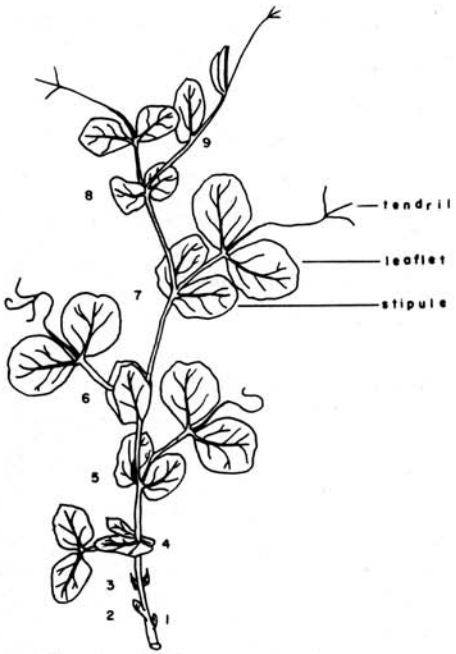

Fig. 1.—Garden pea, variety Thomas Laxton. Nodes are numbered; terminal growing point located between stipules at node 9.

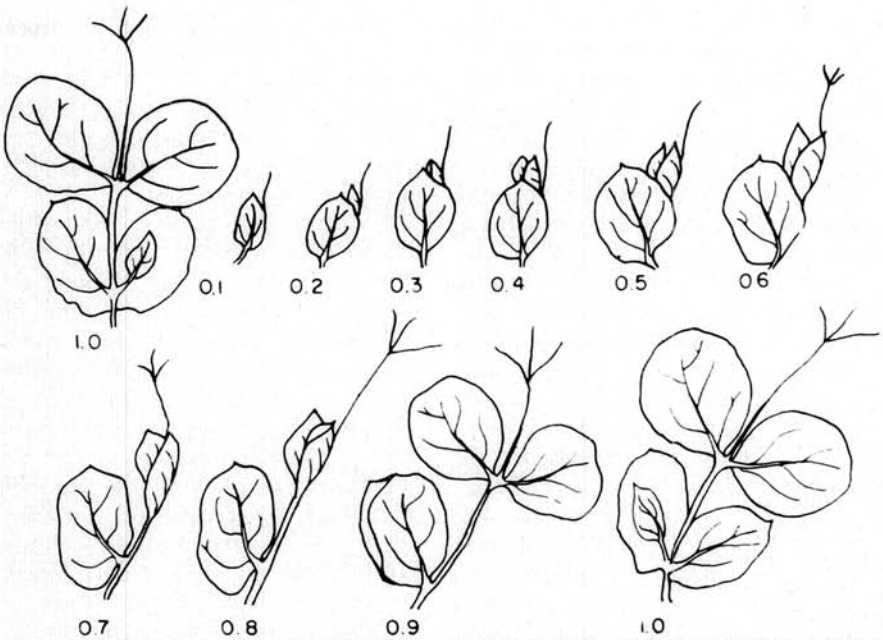

Fig. 2.—Stages in leaf development of garden pea, variety Thomas Laxton. (1.0) illustrates a completed node at the tip of the plant at which point occurs a mature leaf composed of two leaflets, two stipules, and a tendril. Between the pair of stipules is an immature stem which supports a small, tightly closed leaf bud; (0.1) bud develops, increases in size, and the tendril unfolds from between the pair of stipules; (0.2) leaflets, closely held together, begin to show between the stipules; (0.3) leaflets and tendril elongate; (0.4) leaflets separate, both leaflets and tendril elongate; (0.5) separated leaflets and tendril continue to elongate; (0.6) leaflets begin to separate from the stipule; (0.7) leaflets become completely separated from the stipules; (0.8) leaflets begin to unfold, become separated further from the tightly closed stipules; (0.9) leaflets unfold completely, stipule begins to unfold; and (1.0) leaflets and stipules have attained maximum expansion and between the stipules is a tightly closed leaf bud.

The greater energy from the fluorescent light source in Experiment II, as compared with Experiment I, resulted in internode lengths which where 51, 27, and 34 per cent less for plant groups D, E, and F, respectively. The difference in internodal growth of peas at the different light energies under fluorescent and incandescent lamps can probably be explained on the basis of the wavelengths of light emitted by these sources. Fluorescent lamps, with high red and almost no far-red emission, would be expected to maintain the phytochrome system predominantly in the far-red absorbing form and hence less elongation should result (Downs, 1959). In Experiment I, however, internodes were as long or longer in plants grown under fluorescent lamps as in those grown under an incandescent source (Table 2). Apparently the quantity of red light for groups D-F in Experiment I was not sufficient to maintain enough of the pigment in the far-red form to limit elongation. In

Experiment II, however, in groups D-F the increased energy from the fluorescent lamps increased the relative amount of red (and also blue) light received by the plants without any appreciable increment in the far-red, thus maintaining enough pigment in the far-red absorbing form to cause less growth of the internodes. The increased energy in the blue wavelengths may have also been important since Wassink and Stolwijk (1956) have demonstrated that at high energies, in the order of 3700 $\mu W/cm^2$, blue light is very active in inhibiting elongation. In Experiment I, plants subjected only to light from a fluorescent source (group D) were appreciably shorter than those (group F) given such light plus a supplementary treatment of red (Table 2). Incandescent lamps produce considerable red as well as far-red light, and the increased energy from this source in Experiment II for groups A-C did not change the ratio of these two light qualities. Thus one would not expect to get appreciably greater internodal elongation with increased energy from this source, assuming that the initial light energy was not seriously limiting other processes required to sustain growth, such as photosynthesis.

That the pea plants received an appreciable quantity of red light from the incandescent source was apparent from the fact that no significant difference was found in the internodal lengths of plants grown under incandescent lamps with or without supplementary treatment with red light (groups A and C, Experiments I and II); plants receiving supplementary treatment of far-red (group B) were, however, significantly different from those (group A) exposed only to light from incandescent lamps (Table 2).

Although no significant differences were found among the internodal lengths of the cocklebur plants exposed to the various incandescent light treatments (groups A-C, Experiment III), the values are in the

TABLE 2.—Effect of Light Treatment on the Length of Internodes of Pea and Cocklebur Plants.

Plant Group	Treatment	Pea Internode 3, mm		Cocklebur Internode 2, mm
		Expt. I	Expt. II	Expt. III
A	I	49.2 ± 1.3	53.3 ± 1.6	111.7 ± 1.7
B	I + FR	57.5 ± 1.7	58.5 ± 1.9	112.5 ± 2.9
C	I + R	52.1 ± 1.8	53.6 ± 1.7	100.2 ± 5.4
D	F	59.1 ± 1.9	29.1 ± 1.2	26.0 ± 1.2
E	F + FR	65.7 ± 2.1	48.2 ± 1.0	87.3 ± 1.8
F	F + R	62.8 ± 1.9	41.5 ± 1.4	24.3 ± 0.4

sequence of magnitude to be predicted if internodal elongation in this species were a red - far-red controlled response (Table 2). The failure of cocklebur plants to show significant differences among the various incandescent treatments, as contrasted with pea, is indicative of the variability among species in responding to a given light treatment.

The difference in internodal lengths of cocklebur plants (Experiment III) grown under fluorescent (group D) and incandescent (group A) lamps was found to be highly significant (Table 2); internodal elongation was drastically curtailed by fluorescent illumination. This inhibition by light from fluorescent lamps, however, was partially overcome by exposure to far-red light; a highly significant difference was evident between group D or F and group E. A supplementary treatment of red light caused a slight but insignificantly greater inhibition of internodal elongation than light from fluorescent lamps alone (Table 2).

Downs (1959), working with loblolly pine, soybean, and tomato, found that longer internodes were produced when the plants entered the dark period with the pigment system predominantly in the red absorbing form which would occur under incandescent supplemental light. Additional work with several varieties of beans further supported the general statement that a brief exposure to far-red radiation before the beginning of the dark period promoted internodal elongation. Meijer (1959) observed that far-red (near infrared) stimulated elongation in Petunia, Calendula, Perilla, Helianthus, bean, and tomato plants. The results with pea and cocklebur plants were consistent with the observations of these workers.

Influence of Quantity and Quality of Light Upon the Morphological Age of Pea Plants. An acceleration of the morphological aging of pea plants resulted from the greater light energy used in Experiment II (Table 3). In the incandescent series, groups A-C, the morphological age was 3.6, 12.0, and 1.8 per cent greater, respectively, in Experiment II than in Experiment I. Greater maturity in the fluorescent groups, D-F, was even more pronounced, the values showing a 10.5, 18.0, and 8.6 per cent increase over those of Experiment I.

Supplemental far-red irradiation not only resulted in longer internodes in pea plants but also depressed the rate of node initiation. This was true whether this light quality followed illumination from incandescent or fluorescent lamps (Table 3). It was slightly more effective, however, when given after light treatment from a fluorescent source. Although supplemental treatment with red light appeared to have a slight influence on the rate of node initiation, statistically it proved to be insignificant.

In the discussion of the influence of fluorescent illumination on internodal length it was pointed out that perhaps the blue light from this source was of importance, for plants grown under fluorescent light only were significantly shorter than plants receiving fluorescent plus a supplemental red-light treatment. With respect to morphological age, however, no significant difference existed between these two treatments, indi-

TABLE 3.—Morphological Age of Pea Plants Expressed as Mean Node Number.

Plant Group	Treatment	Average number of nodes	
		Experiment I	Experiment II
A	I	5.5 ± 0.07	5.7 ± 0.03
B	I + FR	5.0 ± 0.07	5.5 ± 0.03
C	I + R	5.6 ± 0.09	5.7 ± 0.03
D	F	5.7 ± 0.06	6.3 ± 0.10
E	F + FR	5.0 ± 0.08	5.9 ± 0.06
F	F + R	5.8 ± 0.11	6.3 ± 0.10

TABLE 4.—Average Widths of Leaflets and Stipules and Average Area of Leaflets and Stipules at Node Five.

Plant Group	Treatment*	Stipule Width, mm	Leaflet Width, mm	Area of leaflets and stipules, cm²
A	I	10.4 ± 0.4	16.4 ± 0.5	10.4
B	I + FR	9.5 ± 0.2	13.6 ± 0.7	8.4
C	I + R	11.4 ± 0.3	16.9 ± 0.7	10.8
D	F	13.6 ± 0.4	17.2 ± 0.6	12.0
E	F + FR	12.3 ± 0.4	16.9 ± 0.8	11.7
F	F + R	15.1 ± 0.5	19.6 ± 0.5	12.4

* Plants received light energies of 3700 μW/cm².

cating that blue light was not a determining factor in the rate of node production.

Influence of Light Quality on the Growth of Leaflets and Stipules of Pea. Although in general the widths of the stipules on plants of the fluorescent series tended to be greater than those on plants in the incandescent group, the stipules of plants of group D were not significantly wider than those of group C (Fig. 3; Table 4). Stipule enlargement as a consequence of supplementary irradiation with red light was quite apparent. It was likewise obvious that supplementary irradiation with far-red light inhibited stipule expansion (Table 4).

Red light given subsequent to incandescent illumination appeared to be of little consequence in leaflet expansion, since such supplementary treatment did not result in a signifi-

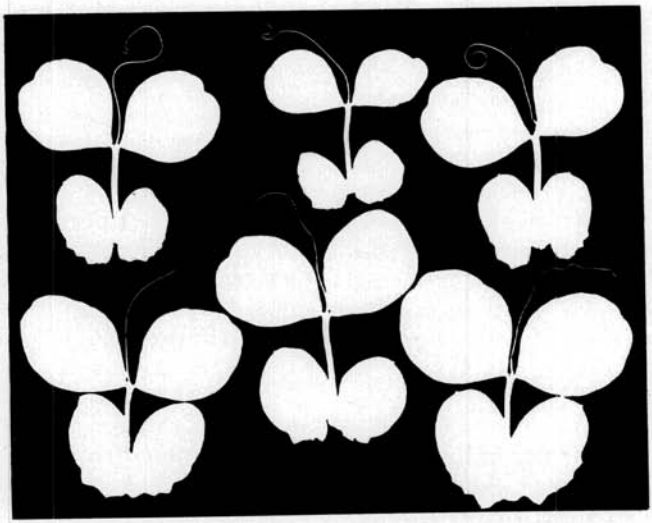

Fig. 3.—Leaf and stipule size at node five. From left to right: top row, groups A through C; bottom row, groups D through F.

cantly greater leaflet width than that which occurred under incandescent lamps (Table 4). A significantly increased leaflet width did result from red light treatment in the fluorescent series, however. With far-red supplementary illumination, on the other hand, significantly narrower leaflets were produced in the incandescent series while no significant effect could be found in the fluorescent group. The reasons are obscure for this apparent red-light effect in the fluorescent group but not in the incandescent series, and also for the far-red effect in the incandescent group but not in the fluorescent series. It is interesting that the stipules responded differently than did the leaflets to the various light treatments.

The area of the stipules and leaflets combined did not show the clear cut relationships exhibited when these organs were considered individually (Fig. 3). This is to be expected in view of the differential responses of these organs to the various light treatments. The general tendency was apparent, however, for the stipules and leaflets to have a greater area when produced under fluorescent rather than under incandescent lamps; under each of these types of illumination these organs exhibited a greater area with red light treatment and a smaller area with far-red illumination.

These results appear to be consistent with the observations of other workers (Liverman, 1959; Parker *et al.*, 1949; Went, 1941).

Summary

Common garden pea (*Pisum sativum* L.), var. Thomas Laxton, and cocklebur (*Xanthium pensylvanicum* Wallr.) plants were grown under various light treatments in 11-hour photoperiods. These included 11 hours of incandescent or warm white

fluorescent, and 9 hours of incandescent or fluorescent followed by a supplementary illumination of 2 hours of red or far-red irradiation. The plants were harvested after a 2-week exposure to the various light treatments. The criteria selected as indices of vegetative growth in pea were internodal elongation, morphological age of plants measured in tenths of nodes, width of stipules and leaflets, and total area of leaflets and stipules. Only internodal elongation was measured in cocklebur.

Internodes were generally shorter on pea and cocklebur plants illuminated with fluorescent lamps only. Exposure to red light following incandescent or fluorescent illumination did not result in significantly shorter internodes, but far-red light following such illumination resulted in significantly longer internodes.

The morphological age of pea plants was greatest for plants grown under fluorescent illumination. Exposure to supplemental red light did not result in a significant increase in morphological age following either fluorescent or incandescent illumination. Far-red light, however, depressed the rate of node initiation significantly under both conditions.

The widths of stipules on plants illuminated with incandescent or fluorescent light alone were significantly different from those given subsequent treatment with either red or far-red light.

The widths of leaflets on plants under incandescent illumination were significantly different from those receiving supplemental treatment with far-red light but not from those receiving red light. For plants receiving fluorescent illumination, the reverse was true.

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