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Spectral Distribution of Light in a Tobacco Canopy and Effects of End-of-Day Light Quality on Growth and Development[1]

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ABSTRACT

Shifts in spectral distribution of light were determined within and below a canopy of field-grown burley tobacco (*Nicotiana tabacum* L. cv. Burley 21). The leaves transmitted much far red light relative to red and blue light. Thus, shaded leaves received more far red light, relative to red and blue, than was received by unshaded leaves. Under field conditions, tobacco plants within rows grew taller than did those at the west end of rows.

Developmental effects of end-of-day red and far red light were studied in the controlled environment laboratory. Plants that received far red light last, each day, resembled plants shaded by other plants. The far red-irradiated plants developed longer internodes, were lighter green in color, and had thinner leaves than the red-irradiated ones. Plants of both treatments had the same number of leaves on the main axis. However, the red-irradiated plants developed branches from axils of lower leaves, while no branching occurred on plants that received far red radiation last each day.

Plants grown in dense populations are often taller and lighter in color than those grown in sparse populations. One difference in growth environment between dense and sparse populations is light intensity, because of shading by other plants. Spectral distribution of light received by shaded leaves in high populations may also differ from that received by unshaded leaves. Light of certain qualities (particularly red and far red, acting through the phytochrome system) is known to function in regulation of plant growth and development (2, 5, 18, 20). This report is concerned with spectral distribution of light within a canopy of field-grown burley tobacco, and the relationship of a shift in relative amounts of red and far red light on growth and development responses of tobacco plants under controlled environments.

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[2] Mention of a specific commercial product does not constitute endorsement by the United States Department of Agriculture or by the Kentucky Agricultural Experiment Station.

MATERIALS AND METHODS

FIELD STUDY

Plant Materials. Tobacco (*Nicotiana tabacum* L. cv. Burley 21) plants were started in conventional starting beds and transplanted to field plots on the Kentucky Agricultural Experiment Station South Farm near Lexington (38°N latitude). The plants were placed 45 cm apart in rows that were 100 cm apart. Energy measurements were taken several times during the growing season. Those presented in this report were obtained in a field of newly "topped" tobacco (a standard cultural practice in production of burley tobacco, the tops—inflorescences and small upper leaves—are removed and discarded when about one-fourth of the plants in a field have one or more open flowers). Each plant had about 25 leaves. Some of the leaves overlapped within and between the rows.

Radiation Measurements. Spectral distribution of solar radiation above, within, and below the canopy of field-grown tobacco was measured with a Spectroradiometer, model 3051 (Agricultural Specialties Co., Beltsville, Md.).[2] Other intensity values were obtained with a Weston Illumination Meter, model 756. Radiation measurements presented in this report were taken at about 1300 hours on September 1, 1967, a cloudless day. Transmission of sunlight through individual fully expanded tobacco leaves was tested with the same instruments on the same day.

CONTROLLED ENVIRONMENT STUDY

Plant Materials. The tobacco (cv. Burley 21) seedlings were started and grown in vermiculite for about 8 weeks under 14-hr, 1600-ft-c photoperiods at 28 C. During the starting period all plants were subirrigated daily with Hoagland's nutrient solution 1 (9). Roots were washed and cut back to a 1 cm "brush," and all leaves longer than 5 cm were removed at the beginning of the experimental period. Plants were placed about 30 cm apart in plastic pans, and roots were suspended in aerated nutrient solution (9) during the treatment period.

Treatments. Throughout the controlled environment experiment, all plants were kept in the same growth environment except during the daily irradiations with red or far red light. The chamber was kept at 25 C, and the plants received 8-hr, 2200-ft-c photoperiods from cool-white fluorescent lamps. Red light (360 μw/cm^2 over the wavelength band of 600–700 nm) was obtained by filtering radiation from cool-white fluorescent lamps through two layers of red cellophane. Far red (360 μw/cm^2 over the region of 700–770 nm) was obtained from internal reflector incandescent-filament flood lamps through two layers of red and two layers of dark blue cellophane. Red and far red irradiations were applied for 5 min each day, at

Table I. *Penetration (Energy Values Relative to Those Incident to Canopy Surface) of Visible and Near-Visible Radiation of Various Wavelengths*

Plants within the canopy were about 190 cm tall with an average of 25 leaves per plant. Individual leaves ranged in size from 75 cm long and 45 cm wide to 30 cm long and 10 cm wide.

Measured Peak Wavelength	Penetration		
	Below canopy	Within canopy	Below a single fully expanded green leaf
nm	%	%	%
391	0.5	0.9	1.7
432	0.3	0.7	0.5
448	0.3	0.7	0.7
483	0.4	0.6	0.9
511	0.6	0.8	3.3
543	6.5	11.0	22.7
576	3.4	5.0	14.7
601	2.1	2.6	10.8
629	1.4	1.7	7.9
658	1.7	2.3	6.1
686	1.9	2.2	6.6
725	8.8	11.6	27.5
791	20.3	36.3	49.5
I/I_0, ft-c	0.8	2.0	5.7

Table II. *Relative Shifts in Far Red to Red Light Ratio below Canopy (Ground Level), within Canopy (95 cm above Ground) and below a Single Leaf of Burley 21 Tobacco*

Values are relative to the ratio of FR/R in sunlight (which is arbitrarily set at 1.0) above the canopy. Values at 730 and 645 nm were used for far red and red light, respectively. The 645 nm value was used for red light because the *in vivo* action peak for Pfr in green plants is at about 645 nm, even though the action peak in nongreen material is about 660 nm (10).

Below Canopy	Within Canopy	Below Single Leaf
7.0	6.5	4.2

the end of the photoperiod, after which all plants were returned, in darkness, to their place in the controlled environment chamber.

Observations. Plants were measured and weighed after 18 consecutive days of treatment with end-of-day red or far red light. Physical data presented in this report reflect only the new growth that occurred during the treatment period. Only leaves longer than 5 cm, roots below the original cut, and new stem growth were included. Dry weights were obtained after the plant components were lyophilized to constant weight.

RESULTS AND DISCUSSION

Spectral Shifts within Tobacco Canopy. Energy distributions of visible and near-visible radiation above, within, and on the soil below a canopy of tobacco (cv. Burley 21) were measured in field plots several times during the growing season. Intensity and quality of light received at ground level changed rapidly during the season, as more leaves developed on the tobacco plants; however, spectral transmission through individual fully expanded leaves remained the same. The measurements shown in Table I were taken after the plants attained a height of about 190 cm.

Energy values for the various wavelengths within and below the canopy are expressed as percentages of solar radiation received, at each of the respective wavelengths, above the tobacco canopy. Transmission of various wavelengths through an individual fully expanded leaf is presented for comparison with canopy transmission. Although the pattern of spectral distribution within the canopy was similar to that transmitted through a single fully expanded leaf, some differences in magnitude occurred, owing to leaf movement and shading by stalks and midveins within the canopy. The leaves transmitted little blue and red light, but they were relatively transparent to far red light. Thus, tobacco leaves shaded by other leaves in the plant canopy received more far red light, relative to red, than was received by unshaded leaves. High absorptions of blue and red light, relative to far red light, also have been shown in green leaves of other plants (15).

Intensity values obtained with an illumination meter are shown at the bottom of Table I for further comparison. The spectroradiometer measurements clearly show that the decreased intensity of radiant energy below a single leaf, as well as within a tobacco canopy, is not uniform at all wavelengths. Therefore, plant responses attributed to reduced light intensity, as measured with an illumination meter, could be confused with responses to a shift in spectral composition of light received by the shaded leaves. This shift in light quality might not have an immediately detectable effect on photosynthesis in individual leaves, but it could be of biological significance if the shift in light quality resulted in differences in growth, development, and chemical composition patterns. Differences in chemical composition of field-grown tobacco have been associated with stalk position (1).

Shifts in amounts of far red light relative to red light received below a single leaf and in the tobacco canopy are shown in Table II. The ratio of red to far red light is important because it functions, through the phytochrome system, in controlling morphological development (2). The absorption peaks of phytochrome, *in vitro*, are near 660 nm and 730 nm (3). However, the red action peak in green plants is near 645 nm because of competitive absorption at 660 nm by chlorophyll (10).

The reversible photochemical change from the red-absorbing form to the far red-absorbing form of phytochrome, and vice versa, depends upon the intensity and energy distribution of the light received, as well as the absorption coefficients and quantum efficiencies of the two forms of phytochrome (7). In a given waveband the reaction is driven toward photochemical equilibrium in about a minute at intensities of less than 1% of sunlight (7). Thus, the intensities within the tobacco canopy (Table I) were sufficient to establish photoequilibrium quickly between Pr[3] and Pfr.

Small changes in amounts of red relative to far red light have been shown to alter the Pr/Pfr equilibrium appreciably (10, 11), and the equilibrium level at the beginning of the night plays a major role in plant development. Therefore, a shift in ratio of red to far red light in a plant canopy may affect the equilibrium between the two forms of phytochrome sufficiently to influence development of the plants growing within the canopy.

Stalk Length of End-of-Day "Sun" and "Shade" Field Tobacco. In order to test some effects of shading within a tobacco canopy, growth of plants at the west end of rows was compared with growth of others within east-west rows. Developing leaves on plants at the west end received sunlight until sunset while those in mid-row were partly shaded. Plants from within rows

[3] Abbreviations: Pr and Pfr: red- and far red-absorbing forms of phytochrome, respectively.

were taller; however, the number of leaves per plant did not differ with plant position in the row (Table III).

Similarly, Shaw and Gossett (17) showed that stem elongation of tobacco seedlings grown in sunlight was positively correlated with the number of plants per unit area. Others (21) found that tobacco plant population significantly affected leaf area and leaf geometry, such that individual leaves were slightly shorter and much narrower at high populations as compared with the low. These morphological differences may have been caused by a shift in spectral composition of light received during plant development; however, the response to light quality may have been confused with response to light intensity and other factors in the field.

Developmental Responses to End-of-Day Red and Far Red Light in Controlled Environments. Since the ratio of red to far red radiation differed widely in light received by the uppermost leaves and that received by shaded leaves (Table II), developmental responses of tobacco to end-of-day red and far red light were compared. In preliminary tests of multiple reversibility of the effects of red and far red light (unpublished), tobacco plants always responded to the quality of light received last prior to darkness; therefore, single 5 min end-of-day exposures to red or far red light were used in this work to maintain equal total energies received by both treatment groups. In this manner, it was possible to test one factor of shading (light quality) on plants that, except for the brief red and far red irradiations, received the same environments. The number of leaves developed per plant during an 18-day treatment period did not differ between end-of-day treatments; however, leaves on plants that received far red light last, each day, were relatively narrow, light green in color, and had less dense laminae than did leaves from plants that received red light at the end of their daily illumination periods (Table IV). Red-irradiated plants had shorter stems and heavier roots. Branching (suckering) occurred from the axils of lower leaves on red-irradiated plants, but no branches developed on plants that received far red light last each day.

Photoreversibility of the action of red by far red light, and vice versa, is evidence of phytochrome involvement; however, little is known about the events following the photochemical reaction (6). Phytochrome may be involved in cell membrane permeability (8) and in some manner influence effective levels of natural growth substances. It seems likely that control of stem lengthening and lateral branching ultimately resides in a change in the balance of natural growth substances within the plant. Antagonisms and synergisms exist between groups of growth regulators, and changes in their relative concentrations influence growth expression (13).

Several investigators (4, 14) found that red irradiation resulted in decreased assayable auxin, and in a depressed rate of stem elongation. However, applied gibberellin, rather than auxin, counteracted the stem growth inhibition triggered by red light (14). Also, lateral buds have been released from auxin-induced apical dominance by application of cytokinins to aerial parts of intact plants (16). It is possible that stem inhibition and lateral branch formation on the red-radiated tobacco plants (Table IV) were controlled by a shift in the auxin-gibberellin-cytokinin balance as a consequence of the end-of-day radiation. The ecological implication is apparent. Isolated plants of many species branch profusely and develop more flowers and seed per plant than do plants of the same species grown in more dense populations.

Dry matter accumulations in various plant components during the 18-day treatment period are shown as average weight per component and as percentages of the total dry matter that accumulated in each of the various plant components within each radiation group (Table V). Lower total photosynthate accumulation (*i.e.*, dry weight per plant) in the far red-irradiated tobacco plants may have been due to a lower photosynthetic capacity of the relatively thin leaves that developed as a consequence of the end-of-day radiation (Table IV). In addition to the pronounced differences in developmental morphology (Tables IV and V), end-of-day manipula-

Table III. *Stalk Length, Leaf Number, and Leaf Weight of Burley 21 Plants Grown in Various Row Positions*

Plant Position within Row	Plant Characteristic		
	Stalk length	Leaves/plant	
	cm	*no.*	*g fresh wt*
West end	140	27	1502
Fourth plant	150	27	1496
Mid-row	163	28	1485
LSD 0.05	13	NS	NS
LSD 0.10	10	NS	NS

Table IV. *Characteristics of Tobacco Plants That Received 5 min Red or 5 min Far Red Radiation at End of Each Day for 18 Consecutive Days*

All plants were kept in the same growth chamber, except during daily red and far red irradiations.

End-of-Day Radiation	Average Growth per Plant[1]						
	Stem		Leaf				Root weight
	Length	Weight	No. per plant	Midrib	Lamina		
	cm	*g*		*g*	*g*	*mg/cm²*	*g*
Red	3.7	2.8	8.2	11.6	32.6	24.7	10.6
Far red	12.6	8.1	8.0	13.9	20.8	18.9	6.1
Significance of difference[2]	*	*	NS	NS	*	*	*

[1] Averages for 10 plants per treatment. Data represent new growth during the 18-day treatment period. Weights are expressed on fresh basis.

[2] Not significant (NS), or significant at $P = 0.05$ (*).

Table V. *Dry Matter Distribution in Tobacco Plants That Received 5 min Red or 5 min Far Red Light at End of Each Day for 18 Consecutive Days*

All plants were kept in the same controlled environment chamber, except during daily red and far red irradiations.

End-of-Day Radiation (5 min)	Weight of Dry Matter[1] per Component				
	Stem	Leaf		Root	Total
		Midrib	Lamina		
			g		
Red	0.187 (05%)	0.515 (15%)	2.291 (64%)	0.572 (16%)	3.565
Far red	0.403 (14%)	0.573 (21%)	1.497 (53%)	0.329 (12%)	2.802
Significance[2] of difference	*	NS	*	*	*

[1] Averages for 10 plants per treatment. Data represents increase in dry matter during the 18-day treatment period.

[2] Not significant (NS), or significant at $P = 0.05$ (*).

tion of phytochrome with red and far red light have influenced the content and distribution of several chemical constituents. Tobacco plants that received end-of-day red light had higher concentrations of alkaloids and free amino acids and lower concentrations of soluble phenolics, free sugars, and organic acids than did plants that received end-of-day far red light (12, 19).

Although the foregoing work was done with one species (*N. tabacum*), the evidence shows that light quality (spectral composition), as well as light intensity, should be considered when evaluating influence of shade from competing vegetation within a plant canopy. The shift in red relative to far red light, operating through the phytochrome system, within a canopy of growing plants appears to play a major role in the mechanism controlling adaptive morphological development.

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