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Light Quantity and Quality Effects on Source–Sink Relationships During Plant Growth and Development

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I. INTRODUCTION

Growing plants sense various components of their constantly changing environment and adapt by regulating source–sink relationships to favor survival as they proceed through their life cycles from seed germination to production of the next generation of seed. In addition to seasonal responses, this adaptation includes elongation of stems and alteration of the photosynthetic system when other plants are near. Thus, genetically identical plants may grow quite differently in dense versus sparse populations, or in spring versus autumn. These responses to growth environment are influenced by both quantity and quality of light and there may be interaction with temperature. Also, plant responsiveness to a given set of environmental conditions may differ at different plant ages. For example, some plants need to attain a "critical" age or size before they can "recognize" the environmental signal and change from vegetative to reproductive growth (Lang, 1952).

Plant size, shape, and longevity vary widely among species. Some germinate, grow, and produce the next generation of seed in a single year (annuals). Others start growth one year, survive over winter, and produce seed in the second year (biennials). Still others live for many years and produce many crops of seed (perennials). Even though plants differ widely in growth habit and tolerance to temperature extremes, moisture stress, etc., they all depend on products of photosynthesis and partitioning of photoassimilate to the various developing parts of the plant. The dominant sink for photoassimilate varies within a plant as it proceeds through its life cycle. Light quantity, light quality (spectral distribution), and temperature are variables that follow reasonably predictable annual patterns which can provide "signals" to the growing plant to modify source–sink relationships. In nature, the quantity of light is affected by a combination of day length, solar angle, atmospheric cover, and competition from other plants; the spectral distribution of light received at a given point depends on solar angle, atmosphere, transmission through leaves of larger plants, and reflection from nearby plants and other objects, including the soil surface.

The primary products of photosynthesis in many higher plants are partitioned into two pools. One leads to synthesis of starch within the chloroplasts, while the other is used for synthesis of sucrose in

the cytoplasm. The sucrose is translocated to other sites in the plant and the starch serves as a temporary reserve form of reduced carbon. Thus, a significant proportion of photoassimilate can remain unavailable for plant growth and development during the light period when plants are grown in alternating light and dark periods. During the dark period, starch which had accumulated in chloroplasts can be used to synthesize sucrose, which is then translocated to various metabolic sinks. Allocation of sucrose, synthesized during the dark period, to different parts of the plant has been shown to be different from that of sucrose synthesized during the light period (Chatterton and Silvius 1979; Huber 1983).

Both quantity and quality of light influence partitioning of photosynthate into the starch and sucrose synthesis pathways. In their controlled environment studies of photosynthate partitioning in soybean leaves, Chatterton and Silvius (1979) found that starch accumulation rates were inversely related to the length of the photosynthetic period. Plants were grown under (a) high intensity photosynthetic light for 7 h every day or (b) photosynthetic light for 7 h, followed immediately by low intensity incandescent light for 7 h every day, or (c) photosynthetic light for 14 h every day. After about 3 weeks, leaves grown under the first two light regimens partitioned approximately 90% of the photosynthate for starch accumulation, whereas only 60% of the photosynthate was used for starch synthesis in plants grown under the third light regimen. They concluded that differences in accumulation of starch within the leaves were associated with whole-plant morphological characteristics and with changes in photosynthetic and translocation rates. A similar influence of photoperiod on photosynthate partitioning was demonstrated by Huber and Israel (1982). Chatterton and Silvius (1980) further found that increase in starch accumulation rates in response to shortening of the photosynthetic period occurred in plants having either a C_3 or a C_4 mode of carbon fixation. This effect was found to be common to annuals, biennials, and perennials. Studies by Britz and Saftner (1988) with a gibberellin-deficient dwarf mutant of *Zea mays* showed that the photoperiodic response of photosynthate partitioning was not influenced by endogenous levels of gibberellic acid. Other studies showed that the amount of blue light received during the photosynthetic period (Britz and Sager 1990) and the ratio of far-red (FR) relative to red light (R) received during and at the end of the photosynthetic period (Kasperbauer 1971; Kasperbauer and Karlen 1986) affected regulation of source–sink relationships involved in plant adaptation and survival.

II. LIGHT QUANTITY

A. Day Length

Adapted plants usually go through the various stages of their life cycles at about the same time each year at a given location. They respond to a seasonal "signal" and change from vegetative to reproductive growth. Introduced agricultural plants, however, have provided some interesting challenges in that varieties adapted to one area may grow and develop quite differently in another.

Field plant observations and the classic research by Garner and Allard (1920) with annual plants such as soybean and tobacco (*Nicotiana tabacum* L.) led to the discovery that plants respond to day length in a way that results in switching the dominant sink from vegetative to reproductive growth. Garner and Allard coined the word *photoperiod* for day length and *photoperiodism* for the response to photoperiod.

Biennial plants such as sweetclover (*Melilotus alba* L.) germinate in spring and initially allocate most of the new photoassimilate to growth of upright shoots. However, as the season progresses, the rate of shoot growth slows and taproots enlarge rapidly as they store reserves to be used for rapid shoot growth, flowering, and seed development in spring of the second year. Taproots collected at monthly intervals from plants growing in an Iowa field are shown in Fig. 1. During the 3-month period (mid-August to mid-November), shoot growth rate slowed while taproots enlarged rapidly and developed

Figure 1 First-year biennial sweetclover taproots sampled from field plots near Ames, Iowa, on (1) August 20, (2) September 20, (3) October 20, and (4) November 20. (From Kasperbauer et al. 1962.)

numerous vegetative crown buds (see Fig. 1). The change from shoot to root growth dominance occurred during a period of decreasing temperature and decreasing natural photoperiod. Our studies suggested that photoperiod was more influential than temperature as a signal to these biennial plants to develop crown buds and store resources in taproots for use the following spring (Kasperbauer et al. 1963b). Fig. 2 shows the effect of photoperiod on shoot and root growth of sweetclover grown under identical temperatures. Those that received the longest photoperiods flowered early and did not develop enlarged taproots. In contrast the plants grown on 9-h days developed only low-growing rosette shoots and large fleshy taproots.

Better understanding of the environmental regulation of source–sink relationships can be important in determining, for example, the best time to incorporate nitrogen-fixing legumes such as sweetclover into the soil to maximize their value in sustainable agriculture. This can be as important in agriculture as the more widely studied source–sink relationships in which the developing seed is the primary focus.

Like annuals and biennials, perennial plants sense and respond to seasonal environmental signals. For example, shoots of forage grasses such as orchard grass (*Dactylis glomerata* L.) or Kentucky bluegrass (*Poa pratensis* L.) grow rapidly during the long days of spring and early summer; shoot growth slows and tillers form during shortening days of autumn; floral induction occurs during cool, short days; and floral initiation and expression occur during the long, warm days of spring and early summer (Gardner and Loomis 1953; Peterson and Loomis 1949). After the seed ripens, the stems die and the roots and crowns continue life through more annual cycles of vegetative and reproductive growth.

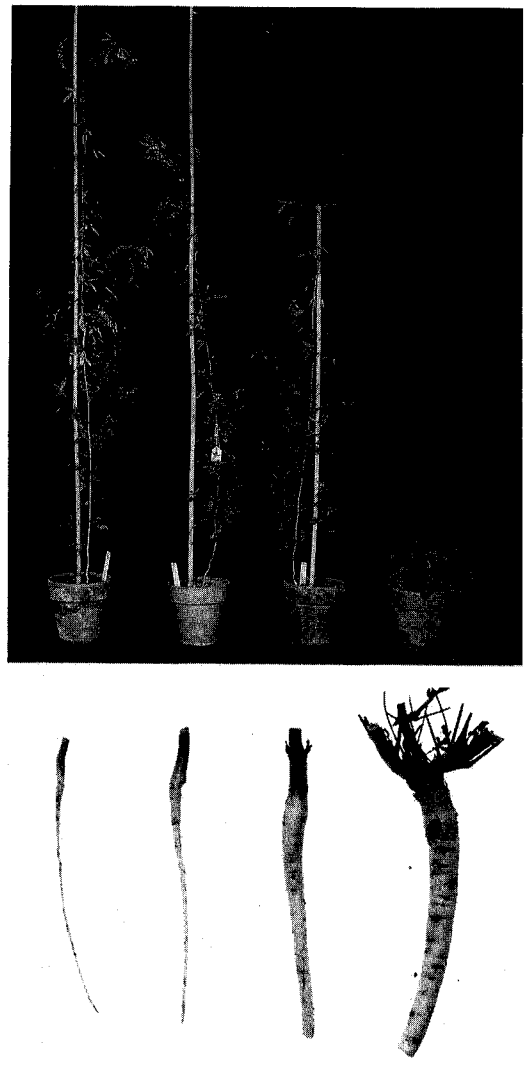

Figure 2 Flowering condition and shoot size (top) and taproot size (bottom) of biennial sweetclover plants after 100 days (from germination) under (left to right) 24-h, 20-h, 16-h, and 9-h photoperiods in a warm greenhouse. (From Kasperbauer et al. 1963b.)

Similarly, perennial trees and shrubs respond to seasonal signals that involve light quantity, light quality, and temperature as they proceed through the annual stages of vegetative and reproductive growth.

B. Full Versus Partial Sunlight

1. Overcast Weather

Overcast weather results in a decreased quantity of light and can influence plant development. A plant might respond to a period of overcast weather as it would to a shorter photoperiod. An agricultural

example involves the Burley type of tobacco (some other types respond differently to light and temperature signals). Because of the small size of tobacco seed (about 0.1 mg seed^{-1}), seedlings were traditionally started and grown to transplant size in cheesecloth-covered outdoor starting beds (Garner 1951). Ideally the seedlings would be about 5 cm apart in the starting bed, and after they grew to about 10 to 15 cm in height (and the danger of frost had passed) they would be transplanted to the field, where they would continue growth to nearly 2 m in height and produce numerous large leaves.

Some years there would be a period of overcast weather during the pretransplant period. That is, the plants would receive natural photoperiods at a decreased light quantity coupled with continuously cool temperatures. In years when such overcast conditions occurred during the last part of the pretransplant period, a large number of plants would become florally inducted before being transplanted and they would flower "prematurely" about a month after being transplanted to the field. This premature change from vegetative to reproductive growth resulted in fewer leaves per plant and was considered undesirable. This occurrence suggested that something associated with overcast weather (decreased light quantity and cool temperature) influenced early floral induction and the resultant change from vegetative to reproductive growth. The natural photoperiod averaged about 13.5 h during the usual pretransplant period in Kentucky where the experiments were conducted. Pretransplant experiments done in controlled environments followed by field growth are summarized in Table 1. Several key points were apparent. Some tobacco seedlings could not distinguish between 8-h full-intensity photoperiods and 13.5-h reduced-intensity photoperiods when temperatures were held near 18°C. Further, plants on 8-h full-intensity photoperiods at 18°C during the pretransplant period flowered early, whereas the same light conditions combined with 28°C temperature did not result in early flowering.

In a follow-up experiment on photoperiod–temperature interactions it was found that floral induction could be blocked in pretransplant seedlings on 8-h, full-intensity, 18°C photoperiods if either a brief exposure to red light or a 2-h period of elevated temperature (38°–40°C) was applied in the middle of the night (see Table 1). A short period of elevated temperature during the day was also effective. In addition to providing a basis for improved starting bed management, these experiments

Table 1 Posttransplant Response of Burley Tobacco to Photoperiod, Light Quantity and Temperature Applied During the Last 10 Days of the Pretransplant Period

Photoperiod[a]			Night interruption		Premature
(h)	μ mol m^{-1} s^{-1}	Temp., °C	Light[b]	Heat[c]	flowering, %
8	520	18	yes[b]	no	0[d]
8	520	18	no	no	100
8	520	28	no	no	0
8	520	18	no	yes[c]	0
13.5	100	18	yes[b]	no	0
13.5	100	18	no	no	33
13.5	520	28	no	no	0

[a]Photoperiods were from cool-white fluoresent lamps.
[b]Low-intensity red light was applied for 15 min in the middle of each night.
[c]Temperature elevated to 38°C to 40°C for 2 h in the middle of each night.
[d]Percentage of plants that flowered within 30 days after transplanting to the field in contrast to about 60 days for controls (prematurely flowered plants had fewer than 10 leaves versus about 28 for controls that were not inducted during the pretansplant period).
Source: Adapted from Kasperbauer 1969 and 1973.

with tobacco seedlings provided an insight into roles and interactions of light quantity, light quality, and temperature in regulation of source–sink relationships in a natural agricultural environment.

2. Sun Versus Shade

The shade of competing plants results in a decreased quantity of light. However, the decrease in quantity is not uniform for all wavelengths across the visible and far-red spectrum (Holmes and Smith 1977; Kasperbauer 1971). That is, shade from vegetation involves both decreased quantity and altered quality of light. Plant responses to shade from other plants include stem elongation, altered leaf shape, and altered cellular arrangement within the leaf. We examined tobacco leaves that developed in sun and in partial shade in a field near Lexington, Kentucky. Uniformly sized tobacco plants were grown during the 1968 season in a field away from other large plants or between rows of similar sized tobacco plants. Thus, the "shaded" plants were close to large plants but were shaded only at the beginning and end of each day. The "sun" leaves had greater specific leaf weight (16 versus 12 mg cm^{-2}), smaller area per leaf, and more stomates per area of leaf. In a more detailed study with beech (*Fagus sylvatica*) tree leaves that developed in full sun versus "shade" (leaves that developed within the canopy), Lichtenthaler (1981, 1984) similarly found sun leaves to have smaller area, greater specific leaf weight, and greater stomata density. They also found that the sun leaves had two layers of closely packed palisade parenchyma cells while the shade leaves (that developed within the canopy) were more likely to have a single layer of more loosely arranged palisade parenchyma cells. They noted that sun leaves had more chlorophyll per unit area, but shade leaves had a greater concentration on a dry weight basis. The sun and shade leaves in each of these examples developed in and adapted to differences in both light quality and light quantity.

Studies of spectral shifts in growing crop plant canopies were conducted in the late 1960s and 1970s (Holmes and Smith 1977; Kasperbauer 1971, 1973). Light spectral measurements were made in 1967 within and near growing tobacco canopies and these were compared with incoming sunlight at each measured waveband (Kasperbauer 1971). The percentages of light at each measured waveband within the 1.9 m tall canopy are shown in Table 2. Spectra (taken with a fixed-filter spectroradiometer) within the canopy, below a single leaf (transmission), in sunflecks on the soil near the tobacco, and in sunlight on a road away from any tall plants were compared. Most of the blue and red were absorbed by the leaves, but about 27% and 49% were transmitted at 725 and 791 nm, respectively. Unfortunately, the fixed-filter spectroradiometer used in that study could not measure at any points between 725 and 791 nm, which we now realize are very important in regulation of partitioning associated with field plant development (Kasperbauer and Karlen 1986, 1994). A comparison of values in the sunflecks near the tall plants with the values on the roadway showed that those at 791 nm were about 15% higher near the plants than on the roadway. Values at 725 nm were also higher in sunflecks near the tall plants than on the roadway, suggesting that reflected FR was involved. Similarity of upper leaf shape and stem elongation of close-spaced tobacco plants and leaf shape and stem elongation responses to extra FR in a controlled environment are discussed in Section III.

III. LIGHT QUALITY

In the mid-1930s, H. A. Borthwick and M. W. Parker of the U.S. Department of Agriculture initiated research at Beltsville, Maryland, to identify and characterize the mechanism involved in photoperiodic regulation of flowering and other developmental responses in plants. They used broad-band colored glass filters mounted below incandescent-filament lamps to provide light of different colors for different durations at different times during day and night in greenhouses and in growth rooms. They evaluated many plant species and found that red light was more effective than other colors when given near the middle of the night, indicating that a red-absorbing pigment was involved in photoperiodic control of

Table 2 Percentages of Incoming Sunlight Received at Indicated Wavebands Within and Below a Canopy of 190 cm Tall Tobacco at About 1 p.m. on September 1, 1967, Near Lexington, Kentucky

	Percentage of incoming sunlight[a] detected		
Approximate peak wavelength, nm	Below a single leaf	Within canopy	Below canopy
448	0.7	0.7	0.3
543	22.7	11.0	6.5
658	6.1	2.3	1.7
725	27.5	11.6	8.8
791	49.5	36.3	20.3

[a]The incoming sunlight was measured on a road, away from tall plants. Light at 791 nm was about 15% higher in sunflecks on the ground near tobacco plants than it was above the road, away from tall plants.
Source: Adapted from Kasperbauer 1971.

flowering. No detectable effect on flowering was noted when the brief treatment with colored light was given during the day. However, they noted that soybean plants developed differently when grown in a carbon-arc-lighted growth room with or without supplemental light from incandescent-filament lamps during the entire day (Parker and Borthwick 1949). The differences in growth and developmental responses were evidence of light quality involvement in regulation of photosynthate partitioning.

Research over the next 30 years led to development of action spectra for photoreversible control of seed germination, stem elongation, and flowering (Borthwick et al. 1948, 1954; Downs 1956; Downs et al. 1957; Hendricks 1958; Parker et al. 1945); and to extraction and characterization of phytochrome (Butler et al. 1959). The early assumption was that there was one phytochrome which existed in two photoreversible forms—an R-absorbing form (Pr) and an FR-absorbing form (Pfr)—and that Pfr was biologically active in regulating the numerous plant developmental processes (Hendricks 1964; Hendricks and Borthwick 1967). However, recent research has demonstrated the existence of a family of phytochromes (Abe et al. 1985; Pratt et al. 1991; Smith and Whitelam 1990), and there is evidence that one of the three phytochromes identified in *Avena* is more abundant in etiolated tissue (Wang et al. 1991).

Some early experiments with *Chenopodium rubrum* seedlings on the Beltsville spectrograph provided insight into adaptive growth responses to light quality. Although in vitro absorption peaks (Butler et al. 1964) and action peaks for "on–off" control of seed germination (Borthwick et al. 1954) are near 660 nm and 735 nm for the R- and FR-absorbing forms of phytochrome, different action peaks exist for adaptive developmental responses such as stem elongation and leaf shape in green plants. The red action peak in green plants is at about 645 nm because of competition from chlorophyll at 660 nm (Kasperbauer et al. 1963a, 1964). Application of R in the middle of the night is most effective for photoperiodic control of flowering, but FR during and at the end of the daily photosynthetic period is effective in regulating the developmental features associated with adaptation to the amount of shade from other nearby plants (Ballaré et al. 1987; Kasperbauer and Karlen 1986). Further, prolonged exposures to FR (as is received among close-spaced plants in nature) were more effective at about 750 to 770 nm than at 735 nm (the approximate in vitro absorption peak for the FR-absorbing form of phytochrome) for promotion of stem elongation and upright leaves (Kasperbauer 1992; Kasperbauer et al. 1963a).

A. Controlled Environments and Plant Spacing

It was well known by tobacco farmers that closeness of seedlings in conventional outdoor starting beds could influence stem length and root size (Garner 1951). Experiments were initiated in 1964 to determine relationships among plant spacing, FR, and allocation of photoassimilate among developing leaves, stems, and roots, and whether light environment during the pretransplant period would affect growth after the seedlings were transplanted to the field. The objective was to learn enough about the effects of quantity and quality of light during seedling growth to develop "tailor-made" transplants suited to mechanical transplanters. The spectroradiometer available in 1964 was not sufficiently compact to measure light spectra among seedlings within the starting bed. However, the stem elongation and leaf angle responses of close-spaced tobacco seedlings were very similar to those that had been observed in *C. rubrum* seedlings that were exposed to FR wavelengths on the Beltsville spectrograph (Kasperbauer 1992; Kasperbauer et al. 1963a, 1964) (i.e., the closest spaced plants in the starting bed and those that received extra FR at about 755 nm on the spectrograph for a "prolonged" period had the longest stems and leaves that were lighter green and more upright). The close-spaced seedlings also had smaller root systems, suggesting that the stem growth of close-spaced seedlings was at the expense of new root growth (and that the relative amount of FR could act through phytochrome and alter source–sink relationships in growing plants). Experiments were then conducted with tobacco seedlings in controlled environments to test effects of supplemental R and FR. The approach was to keep all environmental variables constant except for 5 min d^{-1}, when plants received R or broad-band FR. The 5-min exposures to R, FR, or FR followed immediately by 5 min of R were applied after either 0, 4, or 8 h of darkness had elapsed following 8-h photosynthetic periods. The treatments started soon after germination and were repeated each day for about 6 weeks. Representative plants are shown in Fig. 3. As had been observed earlier with *C. rubrum* on the spectrograph (Kasperbauer 1992; Kasperbauer et al. 1963a), the stem elongation and leaf angle responses were greatest when the FR was applied at the beginning of the uninterrupted night. Although less pronounced, the response to FR was still evident if applied after 8 h. Seedlings that received 5 min of R had horizontal, dark-green leaves and short stems regardless of whether 0, 4, or 8 h of darkness elapsed before the treatment. Results of this controlled environment experiment coupled with observations of responses to closeness of other seedlings in the starting bed suggested that the response to nearness was due to more FR and that the FR/R photon ratio was the important variable in field plant recognition of potential competition from other plants (Kasperbauer 1971).

Other experiments were done to determine morphological responses to the FR/R ratio received at the end of the photosynthetic period in controlled environments. Responses to FR (a high FR/R ratio) in the controlled environment were also consistent with response to close spacing in the field after transplanting. Plants that received extra FR in the controlled environments developed longer internodes, heavier stems, less massive roots, longer leaf midveins, and less biomass per area of leaf lamina (Table 3). They fixed more CO_2 per mass of leaf and had higher concentrations of sugars in stems, midveins, and leaf lamina. Cellular arrangement in the FR-treated relative to the R-treated leaves was similar to that in shade-grown relative to sun-grown leaves, respectively.

Representative chloroplasts from leaves that received FR (high FR/R ratio) or R (low FR/R ratio) at the end of each day during development are shown in Fig. 4. As summarized in Table 4, chloroplasts from leaves that developed with the higher FR/R ratio were smaller and they had more grana with fewer thylakoid layers per granum. They also had fewer and smaller starch grains but more sugar when sampled 2 h after the final FR treatment. Sugar concentrations decreased in both FR- and R-treated leaves during the dark period, but sugar concentrations were still higher in FR-treated leaves at the end of the 16-h dark period (see Table 4B). In addition to the obvious morphological effects (see Table 3), these results (Table 4) suggested phytochrome involvement in development of the photosynthetic

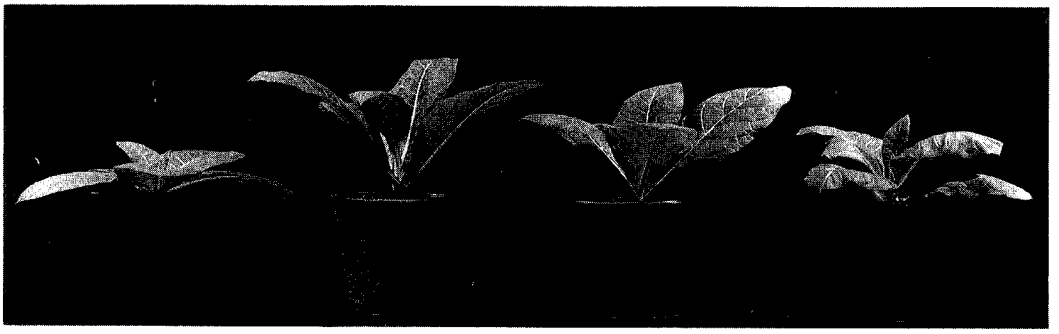

Figure 3 *Nicotiana tabacum* seedlings that received (left to right): 5 min R at the end of day, 5 min FR at the end of day, 5 min FR after 4 h of darkness, or 5 min FR after 8 h of darkness (middle of night) following 8 h photosynthetic periods in a controlled environment. Plants were photographed after about 6 weeks of daily treatment. (From Kasperbauer 1992.)

apparatus and in carbon partitioning at the cellular level as well as at the organ level (Huber et al. 1990; Kasperbauer 1988; Kasperbauer and Hamilton 1984).

Photoreversible control of these morphogenic and chemical responses suggested that a low level of Pfr at the beginning of the night was involved in metabolic events that led to prioritization of photoassimilate partitioning which resulted in growth of longer stems, leaving less of the photoassimilate available for new root growth (Kasperbauer 1971). However, the results did not indicate whether the low level of Pfr initiated a chain of events leading to "competition-adapted" development or whether the events occurred because the level of Pfr was too low to signal a chain of events leading to "sun-adapted" plant characteristics (Kasperbauer and Peaslee 1973). The authors suggested the possibility that some unrecognized factor other than Pfr level associated with FR/R photon ratio might be the initiator of events that affect morphogenesis in growing plants. Nevertheless, it was apparent that FR was a dominant factor in initiation of morphological responses that might have survival value among close-spaced plants (Kasperbauer 1971; Kasperbauer and Hamilton 1984; Kasperbauer and Peaslee 1973).

The working hypothesis that evolved from the controlled-environment experiments was that the amount of FR relative to R could act through the phytochrome system to prioritize allocation of photoassimilates to growing plant parts resulting in morphological features that might favor survival of a plant among other close-spaced plants under field conditions. That is, partitioning of more photoassimilate to development of a longer stem would increase the probability that a plant could keep some leaves in sunlight above competing plants. Also, leaves that were photosynthetically more efficient might favor survival when the amount of photosynthetic light received in the plant canopy was

Table 3 Physical and Chemical Responses of *Nicotiana tabacum* Seedlings to 5 min FR (high FR/R ratio) or 5 min R (low FR/R ratio) at the End of Each 8-h Photosynthetic Period in a Controlled Environment for 3 Weeks

	End-of-day light and FR/R ratio		
Characteristic	FR (High)	R (Low)	Sig[a]
Physical			
Stem length, mm	126	37	*
Leaves/plant, no.	8.0	8.2	NS
Leaf length/width, ratio	2.13	1.83	*
Leaf thickness, mg cm^{-2}	18.9	24.7	*
Shoot fresh wt., g			
Stem	8.1	2.8	*
Leaf midvein	13.9	11.6	*
Leaf lamina	20.8	32.6	*
Root fresh wt., g	6.1	10.6	*
Shoot/root, ratio	7.02	4.43	*
Chemical			
Chlorophyll *a/b*, ratio	1.97	1.87	*
CO_2 uptake, mg g^{-1} fresh wt h^{-1}	8.3	6.9	*
Free sugars, mg g^{-1} dry wt.			
Stems	97.5	37.6	*
Leaf midveins	37.8	11.5	*
Leaf lamina	13.3	9.8	*

[a]Statistical significance: *, values in the same row differ at the 5% level; NS, values are not significantly different at the 5% level.
Source: Adapted from Kasperbauer 1971, Kasperbauer and Peaslee 1973, and Kasperbauer et al. 1970.

decreased by shade from competing plants. Many field-plant-spacing and controlled-environment studies were done to explore the concept further.

When uniform-sized seedlings were transplanted to the field in different spacing arrangements, close-spaced plants began developing longer internodes and narrower leaves even before mutual shading occurred. Characteristics of leaves and stems from representative plants grown for 6 weeks in close, normal, or wide spacings are summarized in Table 5. Note that the longest stems and the greatest leaf length to width ratios were evident on close-spaced field plants and FR-treated chamber plants (Tables 3 and 5). It was suggested that the growing part of the plant responded morphologically to the FR/R photon ratio that existed during the development of that part. For example, different spacings in the starting bed or different quantity and quality of light in the controlled environment resulted in morphological differences. However, after transplanting, they responded to conditions that existed in the field. The one exception to the preceding statement concerned the seedlings that became florally inducted during the pretransplant period. They flowered within 4 to 5 weeks after transplanting regardless of the nearness of other plants in the field. To test the hypothesis that internode elongation was a "local" response, Burley tobacco seedlings were started in 5-cm (diameter) peat pellets that were packed against each other in the starting trays. After 4 weeks the seedlings were transplanted to large pots of soil and grown in a controlled environment in which half of the plants received 5-min FR and the

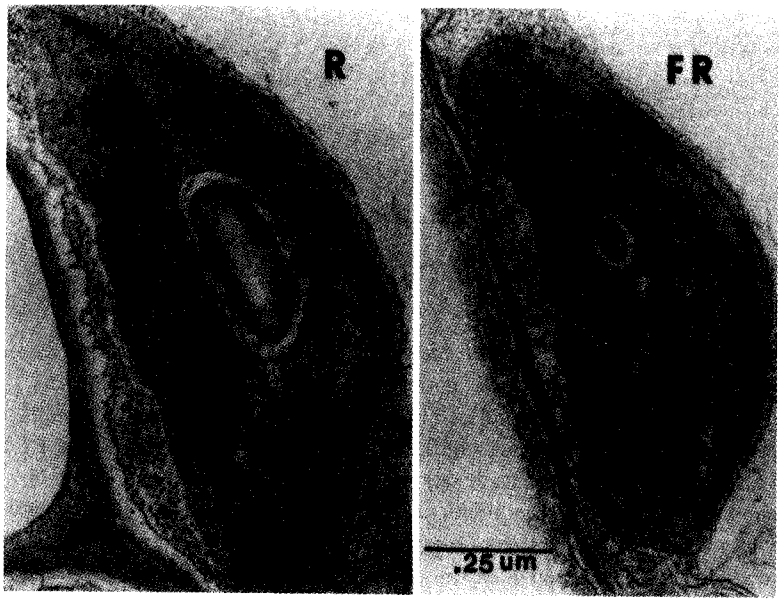

Figure 4 Chloroplasts from tobacco leaves that received brief exposures to R or FR light at the end of the photosynthetic period each day during development in a controlled environment. Leaves were sampled 2 h after the final R or FR treatment. (From Kasperbauer and Hamilton 1984.)

Table 4 Chloroplast Characteristics and Sugar Concentrations in Tobacco Leaves That Received Brief Exposures to FR or R (High and Low FR/R Ratio, Respectively) at the End of the Photosynthetic Period Each Day During Development in a Controlled Environment with 8-h Days Alternated with 16-h Dark Periods

	End-of-day light and FR/R ratio		
Characteristics	FR (High)	R (Low)	Sig. (P = 0.05)
A. Chloroplast characteristics 2 h after last treatment			
Chloroplast length, μm	1.24	1.41	*
Grana/chloroplast, no.	20	17	*
Thylakoid layers/granum	11	18	*
Starch grains/chloroplast, no.	0.14	0.82	*
Starch grain size			
Length, μm	0.13	0.25	*
Diam., μm	0.06	0.12	*
B. Sugar concentration in leaves 2 and 16 h after last treatment			
	mg g^{-1} dry wt.		
2 h	32.2	21.2	*
16 h	20.2	15.3	*

Source: Adapted from Kasperbauer and Hamilton 1984.

Table 5 Field Plant Spacing Effects on Leaf Shape and Stem Length of Tobacco 6 Weeks After Being Transplanted to Field Plots

	Plant spacing, cm		
Characteristic	30 × 30	45 × 100	120 × 120
Leaf length/width, ratio	2.23	1.86	1.65
Stem length, mm	773	674	560

other half received 5-min R at the end of each day. After 2 weeks, each group was split into two subgroups. One continued on its original end-of-day treatment for 2 more weeks while the other subgroup was transferred to the other end-of-day light. All seedlings developed elongated internodes while they were crowded during the first month. After they were transplanted to the large pots, those that received FR or R at the end of each day for the entire 4 weeks developed only long or short internodes, respectively. However, the plants that received R for 2 weeks followed by FR for 2 weeks developed the following internode pattern: long (when crowded), short (while they received R), and long again (while receiving FR). Internodes on the other subset were long, long, and short in response to crowding, FR, and R, respectively. Other interesting observations were that lateral branches began to develop from axillary buds that developed during the 2 (or 4) week periods with end-of-day R (a low FR/R ratio), and that development of the branches was suppressed when the plants were switched to the other treatment (a high FR/R ratio). The message from this experiment is that the quality of light that exists during development of a plant part regulates the source–sink relationships during development of that part. Another agricultural example involves "compensation" for missing plants. For example, soybean and other plants capable of branching can respond to nearness of other plants on one side by inhibiting lateral branch growth while growing into the "vacant" space on the other side. The branching response (or inhibition of it) has been attributed to the ratio of FR relative to R received at the various regions that are still capable of growing.

B. FR Reflected from Plants

Observation of unexpected results in a multifactor field experiment with soybean in South Carolina led to major advancement in confirmation of reflected FR effects on field plant growth and development. In the late 1970s and early 1980s, Hunt et al. (1985) grew soybean plants in different row spacings and row orientations with and without irrigation. They observed that soybean plants grown in loamy sand (low water-holding capacity) had higher seed yields in north–south (N–S) rows when irrigated, but yields were higher in east–west (E–W) rows in the nonirrigated plots (occasional water stress). We hypothesized that such a response could occur if an environmental variable associated with N–S row orientation of soybean plants could cause them to partition more biomass to shoot growth and less to root growth. Because extra FR (a higher FR/R photon ratio) in earlier controlled-environment experiments had caused seedlings to develop larger shoots and higher shoot/root biomass ratios (Kasperbauer 1971) (see Table 3), we measured the FR/R ratio near the upper leaves of growing soybean plants at various times of day in N–S versus E–W rows (Kasperbauer 1987; Kasperbauer et al. 1984). Measurements were made near the top of plants because Parker et al. (1945) had found the most recently expanded leaves to be most responsive to light quality. The field measurements were made with a portable spectroradiometer equipped with the light collector (about 1 cm by 1 cm) mounted on a 1.5-m fiber optic probe and capable of rapidly measuring at 2-nm intervals from 300 to 1100 nm. Spectroradiometric measurements in field plots during the summer of 1983 quickly confirmed FR reflection from growing plants and effects on FR/R photon ratios received by nearby soybean plants. When spectra were

measured in N–S versus E–W rows at different times of day, the highest FR/R ratios were received by plants in N–S rows, especially near the beginning and end of day (Kasperbauer et al. 1984). This light quality pattern was attributed to directional FR reflection from the heliotropic soybean leaves. In the controlled environment part of that study it was noted that shoot/root biomass allocation in response to FR/R ratio in soybean seedlings was essentially the same as previously found for tobacco (see Table 3). In addition, soybean (legume) seedlings growing in low-nitrogen soil developed more nitrogen-fixing nodules on the more massive root systems that developed in response to R (the lowest FR/R ratio) received by the growing shoots (Kasperbauer et al. 1984).

Since FR/R ratio was altered by FR reflection from nearby plants (Ballaré et al. 1987, 1990; Kasperbauer 1987; Kasperbauer et al. 1984; Kasperbauer and Karlen 1986) as well as within growing canopies (see Table 2), the reflection, transmission, and absorption spectra were determined for three ages of soybean leaves using an integrating sphere attached to the portable spectroradiometer. The spectra of light reflected from, transmitted through, and absorbed by the three different ages of leaves are shown in Fig. 5. The curves show percentages at each measured wavelength (at 5 nm intervals from 400 to 800 nm) relative to the incoming light at the same wavelengths. Note that the FR reflection plateau for all of the leaf ages begins at about 750 nm, well beyond the Pfr absorption peak of about 735 nm. It should be noted that the earlier spectrographic studies with intact green plants showed FR responsiveness to prolonged irradiations at 755 to 795 nm (Kasperbauer et al. 1963a), and Vogelmann and Björn (1984) found that the measurable amount of FR at 750 nm could be enhanced through photon scattering within fleshy leaves. Thus, the effective FR/R ratio that reaches phytochrome within a leaf can be much greater than the ratio received at its exterior surface because the effective amount of R is decreased through competitive absorption by chlorophyll (Kasperbauer et al. 1963a), while the effective amount of FR may be enhanced within the tissue (Seyfried and Fukshansky 1983; Vogelmann 1986, 1993; Vogelmann and Björn 1984). Other studies have shown that epicuticular materials on the leaf surface can differ with quantity and quality of light during leaf development (Wilkinson and Kasperbauer 1972), and that leaf surface materials can influence the entry and focus of light within the leaf (Poulson and Vogelmann 1990; Vogelmann 1986).

When 24 different spectra for each row direction (N–S versus E–W) were averaged, bush bean plants (growing in fertile soil with no water stress at the Kentucky State University Research Farm) in both N–S and E–W row orientations received about the same quantity of photosynthetically active light. However, those in N–S rows received higher FR/R ratios than those in E–W rows (Table 6). Like those of the soybean plants grown in South Carolina (Kasperbauer 1987; Kasperbauer et al. 1984), leaves of bush bean in Kentucky functioned as directional FR reflectors and the plants in N–S rows grew taller and produced heavier shoots with greater fruit biomass per plant.

Southern pea (*Vigna unguiculata* L.) seedlings were used in a test of row orientation effects on shoot/root biomass ratios associated with FR reflection patterns (Kasperbauer and Hunt 1994). Some seedlings in each row orientation were grown in tubes of irrigated soil that were imbedded within the rows. Seedlings in N–S rows received higher FR/R ratios near the end of each day. The shoot/root dry matter ratios were 3.06 and 2.60 for N–S and E–W rows, respectively, after 3 weeks of growth. It should be noted that the row orientation effects on soybean, bush bean, and southern pea (all legumes) included directional FR reflection from heliotropic leaves, and higher FR/R ratios resulted in greater allocation to shoots when the seedlings were grown in fertile soil without any water stress. The importance of early shoot/root photoassimilate allocation and the development of nitrogen-fixing nodules on legume seedling roots may differ according to soil nitrogen availability and soil moisture content. We hypothesize that E–W row orientation of legume seedlings growing on low-nitrogen, droughty soils might have the advantage of more massive early roots, less moisture stress, more early symbiotic fixation of nitrogen, and greater productivity, whereas, N–S rows could favor greater shoot growth and increased productivity on soils with high available nitrogen and no water stress.

Spacing of wheat (*Triticum aestivum* L.) seedlings also influenced the amount of reflected FR and

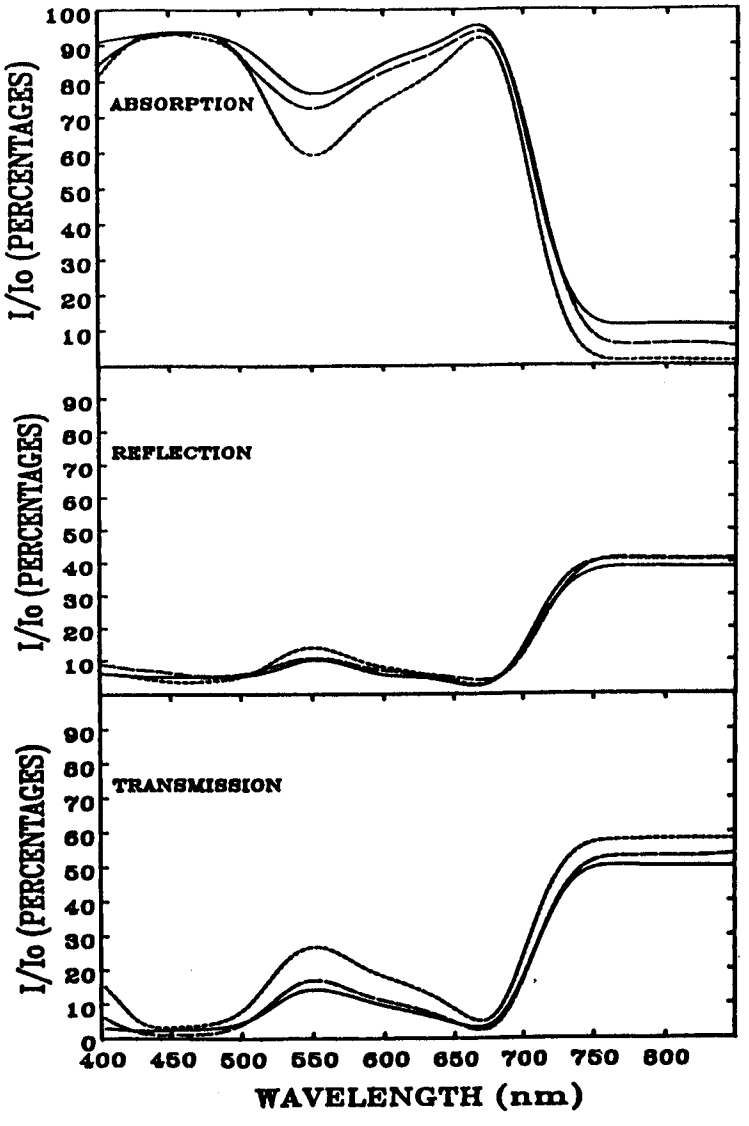

Figure 5 Light absorption, reflection, and transmission from expanding (dots), just expanded (dashes), and fully expanded (solid lines) soybean leaves. Absorption percentages were calculated by subtracting values for transmission and reflection from 100 at each measured wavelength. (From Kasperbauer 1988.)

FR/R ratio received by nearby seedlings (Kasperbauer and Karlen 1986). Effects of the higher FR/R ratio received by close-spaced plants resulted in development of longer leaves and fewer tillers per plant. The suppressed tiller formation on wheat seedlings that received the higher FR/R ratios (the closest spaced ones) was consistent with formation of fewer basal branches on tobacco (Kasperbauer 1971) and soybean (Kasperbauer et al. 1984) seedlings in response to an increased FR/R ratio. Thus, leaf elongation and branching (tillering) responses of grass and broadleaf plants to FR/R levels associated with nearness of other growing plants are essentially the same. However, stem internode elongation responses that are so widely studied in dicotyledonous plants (Ballaré et al. 1987, 1990;

Table 6 Row Orientation Effects on Light Received Near the Shoot Apex of Bush Bean Plants During Field Growth and on Plant Productivity

Characteristic	Row orientation	
	N–S	E–W
Light[a]		
Photosynthetic, μmol m^{-2} s^{-1}	389 ± 62	393 ± 59
Photomorphogenic, FR/R photon ratio	1.85 ± 0.23	1.48 ± 0.13
Plant productivity		
Green beans, g fresh wt $plant^{-1}$	59 ± 8.3	43.0 ± 4.1

[a]Light coming to the shoot tips of two representative plants in each row orientation was measured from the N, S, E, and W at 1100, 1330, and 1530 h on a cloudless day near Frankfort, Kentucky. Each light value in the table is the mean ±S.E. for the two plants, four directions, and three times during the day (i.e., means are for 24 separate readings). Rows were 1 m apart and plants within rows were 10 cm apart. *Source*: Adapted from Kaul and Kasperbauer 1988.

Downs et al. 1957; Kasperbauer 1971; Kasperbauer et al. 1984; Nakata and Lockhart 1966) are less obvious in wheat (Kasperbauer and Karlen 1986) and other grass seedlings in which the stem is at or near the soil surface and covered by several layers of leaves.

Corn seedlings were started and grown for several weeks in plant spacing and row orientation studies in which light spectra were recorded and plants were measured for leaf length and width, leaf area, stem length, and biomass allocated to leaves, stems, and roots (Kasperbauer and Karlen 1994). The spectral pattern of reflection from individual corn leaves was very similar to reflection from individual soybean leaves (see Fig. 5). Closeness of other plants greatly influenced the FR/R ratio and the allocation of resources within the seedlings (Table 7). This included early elongation of internodes even though the stems were at or near the soil surface and covered with several layers of leaves when the stem elongation response to FR/R ratio began. However, the corn leaves were not heliotropic and differences in FR/R ratio and seedling morphological features between N–S and E–W rows were not statistically significant (Kasperbauer and Karlen 1994).

C. Reflection from Soil Surface

After it was apparent that field-grown plants responded morphologically to the amount of FR and FR/R ratio reflected from other green plants (Kasperbauer et al. 1984; Kasperbauer and Karlen 1986), we tested whether plants would also respond to spectral differences in light reflected from different colored soils or from plant residues left on the soil surface from a previous crop. This is relevant to field crop production because natural soil colors vary widely, as do plant residues that are left on the soil surface in some conservation tillage procedures. Studies that were started at the Coastal Plains Soil, Water and Plant Research Center near Florence, South Carolina, in 1984 and 1985 revealed differences in spectra of upwardly reflected light over different colored soils with and without a partial (about 80%) cover of dead plant residue (Kasperbauer and Hunt 1987). A 10-cm height above the soil was selected for measurements because it is in the establishment zone for most seedlings, and seedlings are highly responsive to spectral composition of light whether given in a controlled environment (Downs et al. 1957; Kasperbauer et al. 1963a), or reflected from nearby plants or other objects outdoors (Ballaré et al. 1987, 1990; Kasperbauer 1987; Kasperbauer et al. 1984; Kasperbauer and Karlen 1986, 1994). Reflection from brick-red soil was similar to that over black from 400 to 500 nm, and similar to that over

Table 7 Field Plant Spacing Effects on FR/R Ratio and Growth Characteristics of 4-Wk-Old Corn Seedlings Before Mutual Shading

	Plant spacing, cm		
Characteristic	30 × 30	60 × 60	120 × 120
Photon ratio[a]			
FR/R	1.93	1.29	1.17
FR′/R	2.18	1.37	1.22
Largest leaf			
Length, mm	804 ± 16[b]	772 ± 6	735 ± 12
Width, mm	98 ± 1	103 ± 1	106 ± 2
L/W, ratio	8.31 ± .11	7.50 ± .07	6.93 ± .10
Stem			
Length, mm	387 ± 9	285 ± 11	211 ± 12
Diam., mm	24 ± 1	28 ± 1	28 ± 1
Fresh wt., g	105 ± 5	102 ± 6	70 ± 7
Leaf[c]/stem, wt. ratio	1.82 ± .06	2.22 ± .21	2.83 ± .22

[a]R, red light at 645 nm; FR, far-red light at 735 nm; FR′, at 755 nm. Values in the table are means for eight scans (two each from N, S, E, and W) at 0830 h ± 30 min 5 June 1985 near Florence, South Carolina. FR/R photon ratios are relative to ratio in incoming sunlight at time of measurement.

[b]Values are means for 10 plants ± S.E.

[c]Leaf weight includes blades plus sheaths.

Source: Adapted from Kasperbauer and Karlen 1994.

white from 600 to 700 nm. Further, the brick-red soil and the straw residue reflected higher FR/R ratios than the other soil colors (Kasperbauer and Hunt 1987).

The next step was to determine whether plant residue or soil surface color could influence reflected light sufficiently to modify seedling growth. Soybean seedlings grown over brick-red soil and straw residue received higher reflected FR/R light ratios than those grown over white soil; they grew taller, had less root growth, and developed higher shoot/root biomass ratios (Hunt et al. 1989). The same pattern of results was obtained with cotton and southern pea seedlings (Kasperbauer and Hunt 1992, 1994). When the insulation panel surfaces were painted instead of being covered with different colored soils or plant residues, growing plants responded the same to either soil-covered or painted surfaces if they reflected the same spectrum of light. That is, plants grown over the red surfaces received higher reflected FR/R ratios and less blue than plants grown over white, and those over red surfaces grew taller and had lower leaf/stem and higher shoot/root biomass ratios.

Painted surfaces were used for outdoor experiments because plant residues and soils were removed from the insulation panels by rain and wind. This approach allowed growth of the plants outdoors in full summer sunlight for photosynthesis, and reflection of a FR/R ratio that acted through photomorphogenic pigments within the plants to regulate partitioning of the photoassimilate to developing roots, shoots, and fruits. The working hypothesis (based on previous experiments that involved controlled environments, reflection from other plants, and upward reflection from colored soils and painted panels) for the use of colored mulches in the field was that an upwardly reflected FR/R ratio higher than the ratio in incoming sunlight would signal the growing plant to partition more of its new photosynthate to shoot (and fruit) growth, while a FR/R ratio lower than that in incoming sunlight would favor partitioning to roots.

The research was extended to vegetable crops. Irrigated tomatoes grown in summer sunlight over mulches with red surfaces produced significantly greater fruit yield than those grown with conventional black or white mulches (Decoteau et al. 1989). Similarly, field grown early-crop bell peppers produced more fruit when grown over red than over black or blue mulches (Kaul and Kasperbauer 1992).

The work with quantity and quality of upwardly reflected light was extended to other crop plants and mulch colors to provide a range of reflected FR/R ratios and a range of quantities of blue and photosynthetically active light. Cotton seedlings developed longer stems over green and red surfaces, which reflected low amounts of blue and higher FR/R ratios than were present in incoming sunlight (Kasperbauer 1994). In addition to the longer stems, cotton seedlings that received the highest FR/R ratios in upwardly reflected light had the thinnest leaves and the highest concentrations of chlorophyll and light harvesting chlorophyll protein (LHC-II) (Bradburne et al. 1989). At maturity, irrigated cotton had more bolls, fiber, and seed per plant when grown over colors that reflected less blue and higher FR/R ratios (Kasperbauer 1994). Closer examination of the cotton fibers that developed in bolls over the different colored mulches revealed that the soil surface colors that reflected the highest FR/R ratios and resulted in the longest stem internodes also resulted in the longest fibers (Kasperbauer 1994). These responses indicate that the quality of light reflected from a mulch surface can affect the partitioning of photoassimilate and the quality as well as quantity of plant products.

Characteristics of upwardly reflected light and some field-grown shoot and root crop plant responses are summarized in Table 8. The largest roots and the smallest shoot/root biomass ratio for a root crop (radish) developed over the orange mulch, which reflected a FR/R ratio lower than the ratio in incoming

Table 8 Characteristics of Upwardly Reflected Light, Shoot Size, and Biomass Distribution in Plants Grown in Field Plots over Colored Mulches in Sunlight

Characteristic	Mulch surface color		
	Green	White	Orange
A. Upwardly reflected light[a] (relative to incoming sunlight)			
PPF (400–700 nm), %	11	44	21
Blue (400–500 nm), %	8	39	7
R (645 nm), %	8	46	36
FR (735 nm), %	10	46	35
FR' (755 nm), %	15	46	34
B. Shoot crop[b] (soybean, seeded 24 June, measured 25 July)			
Stem length, mm	226a	193b	199b
C. Root crop[b] (radish, in field 18 April to 12 May)			
Leaf wt., g	18.6a	14.3b	19.0a
Root wt., g	65.9b	54.6c	79.6a
Shoot/root, ratio	.282a	.262b	.239c

[a]PPF, photosynthetic photon flux.

[b]Values for both soybean and radish are means for three replicates of 20 plants each for each color of mulch. Radish seedlings were started in 5 cm (diam.) pots of potting soil, selected for uniformity, and transplanted to field plots at the two-leaf stage. Plants were spaced at least 30 cm apart. Trickle irrigation tubes were placed below the mulches to prevent water stress. Values in the same row followed by different letters differ at the 5% level of significance.

Source: Adapted from Kasperbauer 1992.

sunlight. All of these responses were as could be predicted from the controlled environment experiments summarized in Table 3.

Seedlings grown over white surfaces received higher quantities of reflected photosynthetic light (Table 8), but they accumulated least biomass. This response was observed repeatedly with a number of shoot and root crops when grown outdoors in summer sunlight (Bradburne et al. 1989; Kasperbauer 1992, 1994; Kasperbauer and Hunt 1992). Clearly, the greatest quantity of photosynthetic light did not result in the greatest accumulation of biomass. One possible explanation is that the greater quantity of blue light reflected from the white surfaces might affect the photosynthetic system. For example, cotton seedlings grown over the white surfaces had lower concentrations of chlorophyll and light-harvesting chlorophyll protein (Bradburne et al. 1989). Perhaps the greater quantity of photosynthetic and blue light (incoming plus reflected) over the white surfaces outdoors in summer can affect chloroplast position within the cell, as has been demonstrated in the laboratory with high versus low intensity light (Haupt 1982; Seitz 1979ab; Seitz 1987; Wada et al. 1993). We have initiated study of chloroplast movement in cells of leaves grown outdoors in summer sunlight over different colored mulches.

IV. SUMMARY

Plants are able to sense their total environment, integrate the information, and adapt to constantly changing environmental conditions as they proceed through the life cycle from seed germination to the next generation of seed. Light quantity and light quality play a very important role in regulating source–sink relationships involved in allocation of photoassimilate within the growing plant. Seasonal change in day length (and temperature) as well as competition from nearby plants are major contributors to change in quantity and quality of light. The phytochrome system within the plant functions as a constant sensor of photoperiod and the FR/R ratio indicative of competition from other plants. It then functions in regulation of metabolic events that result in adaptive responses such as stem length, leaf shape and thickness, amount of branching (or tillering), relative root size, and flowering.

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