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9 Shoot/Root Relationships and Bioregulation

Plants and roots are of many sizes and shapes, and they develop within a wide range of environments. Regardless of their various sizes and shapes, roots generally serve to anchor plants and to absorb water and nutrients. Some store food reserves that survive the winter and support early spring shoot growth.

When considering shoot/root relationships, one should realize that plants have evolved over many years and that each plant is genetically programmed for a number of alternative developmental patterns. That is, various genes will be activated or repressed by environmental factors such as day length, nitrogen availability, and light spectral shifts associated with plant population density. Also, the strategy of the individual plant must be to survive long enough to reproduce the next generation. Therefore, the plant must be able to detect and adapt to various environmental situations and to partition enough photoassimilate to the roots to support shoot growth and development under those conditions.

It is apparent that plants have evolved to "invest" photoassimilate where it will best contribute to survival of the plant and its reproduction in a given environment. For example, it has been observed that genetically identical plants grow quite differently in dense populations than in sparse populations, in fertile soil than in infertile soil, or in spring than in autumn.

As a plant physiologist, I ask how much root is needed, and how does the plant sense environmental variables that regulate partitioning of photoassimilate between shoots and roots? Also, is a more extensive root system always better, and how can we use this information in field crop management?

As with most biological responses, it appears that a combination of genetic and environmental factors serve as natural regulators. The remainder of this chapter will be devoted to a discussion of the regulation of shoot/root relationships.

GENETIC CONTROL

There are many differences in root development among plant species. Some of the most obvious are, of course, the fibrous roots of forage grasses contrasted with the roots of plants such as soybean (*Glycine max*) and cotton (*Gossypium hirsutum*). Within a species, some characteristics may serve as survival mechanisms under specific conditions while going undetected under other conditions. For example, the sandy soils of the southeastern coastal plain of the United States often overlay a hardpan that blocks penetration of most roots and thereby limits the rooting zone. As part of our research toward improved crop efficiency on such soil, we identified some cotton genotypes that grew well, while others wilted severely when grown over a subsoil hardpan in field plots without irrigation during the drought of 1986. In subsequent controlled-environment studies, roots of a genotype that grew well in the field test penetrated an artificially compacted soil layer, while a genotype that wilted in the field test failed to penetrate the compacted soil layer. This is an example of a genotypic difference in rooting characteristics that can express under specific conditions (the compacted subsoil layer in this example) while no rooting differences are apparent between the two genotypes in the absence of the compacted layer. This type of information should be useful in developing varieties for cropping systems that are less dependent on irrigation.

In another example of genotypic differences in rooting within a species, we have tissue culture regenerated tall fescue (*Festuca arundinacea*) plants with root characteristics that range from very fine to very coarse, even though the shoot growth appears to be the same. Some of these genetic lines (somaclonal variants) may prove to be superior under specific soil and water conditions. Culture and identification of superior somaclonal variants for a specific purpose is a possible agricultural benefit of plant biotechnology.

ENVIRONMENTALLY INDUCED REGULATION

As plants evolved, they developed capability to detect various factors of the environment and to regulate growth processes to favor survival in that environment long enough to reproduce the next generation. Some of the dominant environmental factors that regulate morphological development include nutrient and water availability, day length, and the spectral distribution of light associated with, for example, competition from other growing plants.

Nitrogen Availability

The influence of adequate or inadequate nitrogen is shown in Figure 9.1. The two sunflower plants were started from seeds that germinated in nutrient-free sand on the same date. The seedlings were transferred to hydroponic nutrient cultures when cotyledons opened. The plant on the left grew in an aerated "complete" nutrient solution, while the one on the right grew under identical conditions except that the nitrogen was withheld from the nutrient solution. The plant on the left was obviously healthy even though it had a small root system. With no water or nutrient limitations (and the same light environment), the plant invested most of its new photosynthate in shoot growth. From a survival standpoint, this growth strategy did not "waste" excess photoassimilate on an unnecessarily large root system. Instead, investment of more of the photoassimilate in larger leaves and stem increased the photosynthetic area, which led to a larger plant that could produce more seed. The nitrogen deficiency affected partitioning toward roots. It appears to be a survival response triggered by a stress factor. This rather simple experiment demonstrates adaptation of a plant to favor survival under a specific set of conditions.

From a practical standpoint, the plant grown on the complete nutrient solution demonstrates what could happen in a field situation when water and nutrients are metered into the root zone via a trickle irrigation system. This prioritization of photoassimilate partitioning to the shoots would appear to be desirable, unless (1) the top-heavy, poorly rooted plants were blown over by a high-velocity wind, or (2) the constant flow of water and nutrients was abruptly interrupted, which could cause severe damage before the plants could adjust to the stress condi-

Figure 9.1. Influence of nitrogen deficiency on seedling shoot/root relationships.

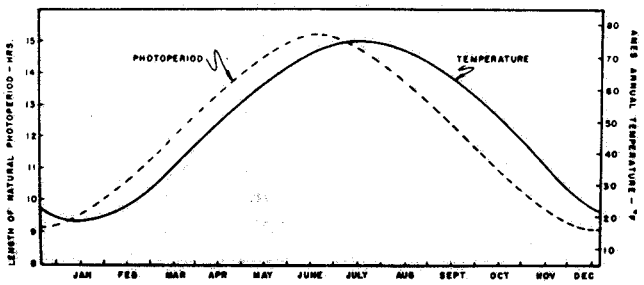
tions. On the other hand, a plant that began growth under somewhat stressed conditions could readily adapt to adequate, but not excessive, soil water and nutrients. This is basically what is involved in the practice of "hardening" seedlings before transplanting them from a protected

nursery to a field, where the plants adapt to the new set of environmental variables.

Photoperiod

Many plants are able to "measure" the day length (actually the period of uninterrupted darkness) to trigger the induction of flowering so that seeds can develop and ripen before freezing weather occurs. Many short-day annual plants such as cocklebur (*Xanthium pensylvanicum*) may germinate and start growth at various times during the season, and still flower at the same time. They are photoperiodically sensitive, and even though plants are of different ages and sizes when the "critical" photoperiod occurs, a sensing system within the plant causes the flowering process to begin. The plant that started growth in early spring would usually grow larger and be capable of supporting more flowers and seed. From a survival standpoint, however, both early and late plants would produce some seed for the next generation.

Biennial long-day plants such as sweetclover (*Melilotus alba*) also are able to measure photoperiod and regulate partitioning of photoassimilate to favor survival. During the seedling year, the seeds usually germinate in spring and develop shoots with relatively small tap roots while days are reasonably long. As days become shorter in late summer and early autumn, the shoots seem to stop growing while the tap roots enlarge rapidly and develop crown buds. The shoots may freeze in winter. New shoots develop rapidly from the crown buds during the following spring, at the expense of the stored reserves in the large tap roots. Figure 9.2 shows the rapid development of biennial sweetclover tap roots grown in a field at Ames, Iowa, and collected at monthly intervals beginning in mid-August. A rapid change in shoot/root ratio occurred during this period of naturally decreasing photoperiods and temperatures. In a parallel experiment to compare regulatory effects of naturally decreasing photoperiods under warm conditions, some sweetclover plants were moved intact (in blocks of soil) from the field to the soil bed of a greenhouse in mid-August. Both field and greenhouse received naturally decreasing photoperiods. However, the greenhouse minimum temperature was 22°C, while field temperature approached freezing in late October and November. As shown in Figure



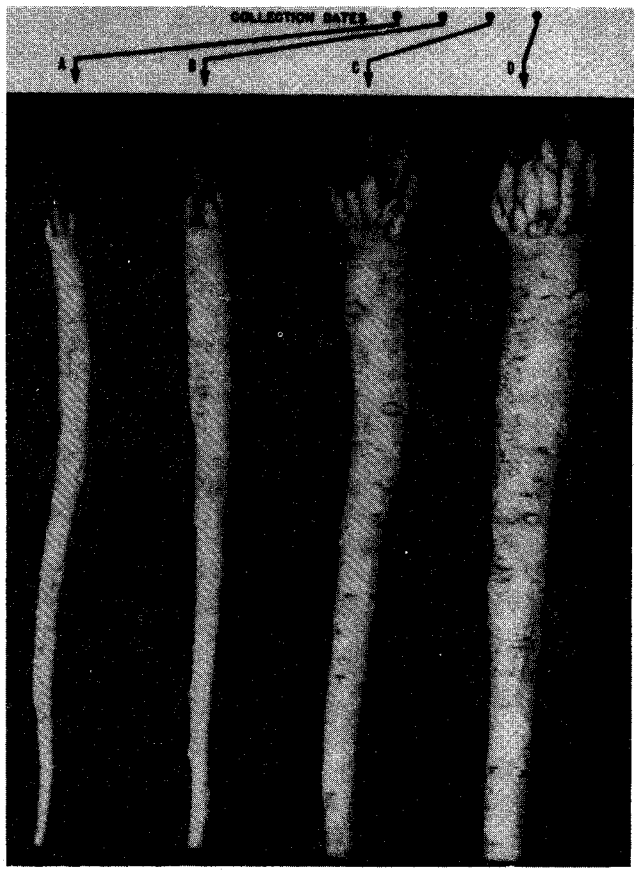


Figure 9.2. Field-grown biennial sweetclover tap roots dug August 20, September 20, October 20, and November 20.

Source: Kasperbauer 1962.

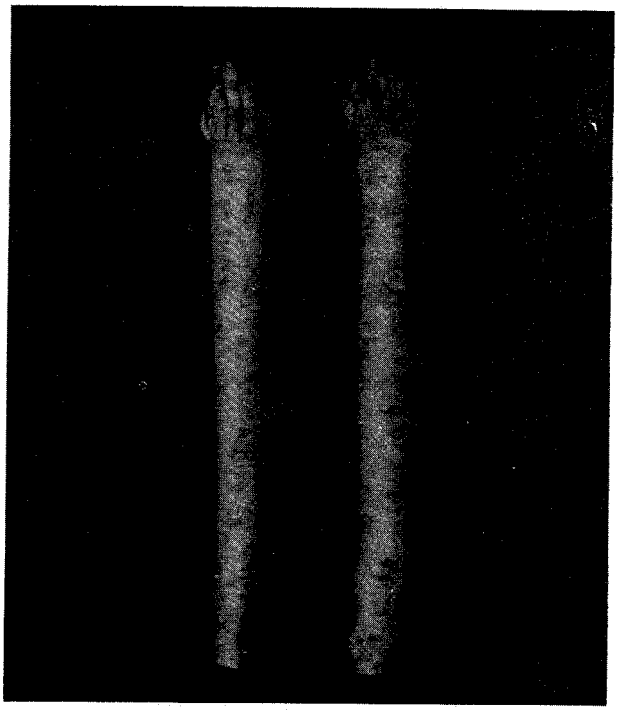


Figure 9.3. Tap roots from first year biennial sweetclover plants grown on natural photoperiods with natural (left) and 22°C minimum (right) temperatures until November.

Source: Kasperbauer 1963.

9.3, tap roots from both field and greenhouse sites were about the same size in mid-November. The tap root enlargement was dominated by photoperiodic control. The plants shown in Figure 9.4 were grown on four different photoperiods in a warm greenhouse. All were started from the same lot of biennial seed on the same day.

Those grown under the longest photoperiods flowered early and did not develop enlarged tap roots. In contrast, the plants grown on nine-hour photoperiods developed only low-growing shoots and large, fleshy tap roots. The appar-

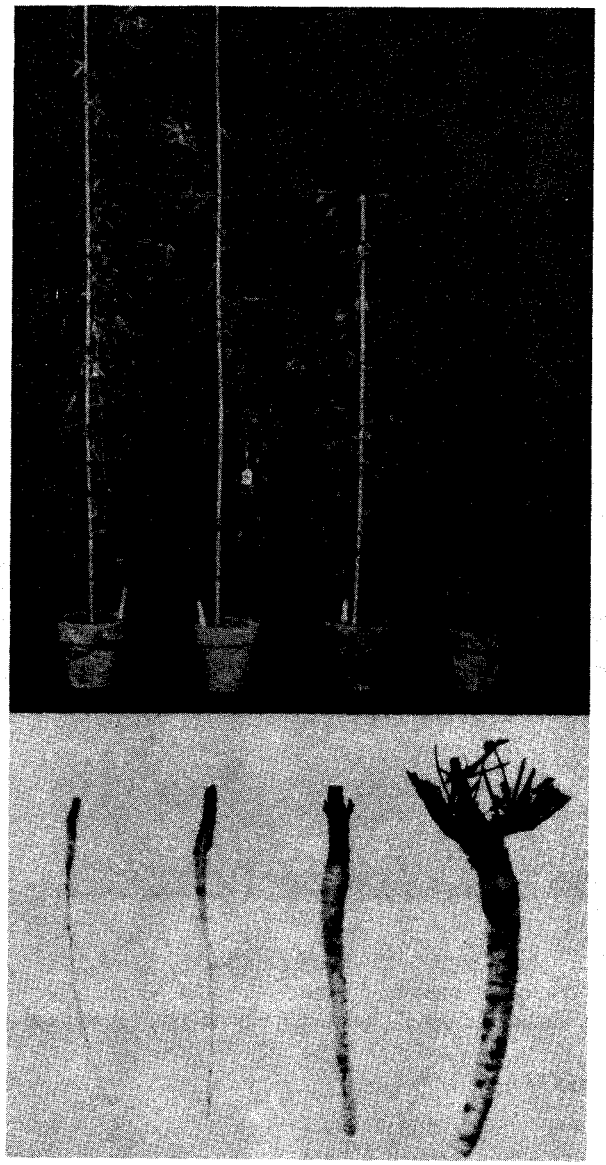


Figure 9.4. Plant size and flowering condition (top) and root size (bottom) of biennial sweetclover plants after 100 days (from germination) of exposure to photoperiod treatment. Left to right: 24-hour, 20-hour, 16-hour, and 9-hour photoperiods in a warm greenhouse, grown in 10-cm clay pots.

Source: Kasperbauer 1963.

ent "signal" from the short photoperiod was that winter was coming and there would not be enough growing days to allow the plants to flower and develop ripe seed before a killing frost. In contrast, those on the longest days received a photoperiodic "signal" that there was plenty of time to flower and develop ripe seed before winter. Consequently, they did not form storage roots because the life cycle (from seed to the next generation of seed) was completed.

Knowledge of photoperiodic regulation of shoot/root relationships is important in management of root crops. It is especially relevant in the use of biennial legumes as "green manure" crops to incorporate organic matter for soil improvement. An important point is that even though the shoots of biennial legume plants seem to stop growth late in the season, root enlargement continues with the decreasing day lengths, until the shoots freeze.

Light Spectral Distribution

Spectral composition of light can alter the shoot/root ratios of developing plants. The regulatory mechanism and plant responses have been studied in detail under controlled environments. Recent research has shown that the same light-sensing mechanism also responds to naturally occurring spectral differences associated with plant population density (nearness of competing plants), row orientation (especially in broadleaf plants), and soil or mulch color under field conditions. It is now apparent that plants are capable of sensing competition from nearby plants and to modify developmental patterns according to the amount of competition (Kasperbauer 1987, 1988).

Controlled-environment studies have shown that the ratio of light received at 735 nm (called far-red and usually designated FR) relative to that received at 645 nm (called red and designated R) is measured by a photoreversible pigment (phytochrome) within the growing plant. Phytochrome is present in minute quantities relative to chlorophyll and the carotenoids, and the greatest concentrations of phytochrome are present in regions of actively dividing or recently divided cells. While light from 400 to 700 nm is absorbed by photosynthetic pigments and results in production of photosynthate, the photoequilibrium level of phytochrome (as regulated by the FR/R ratio) appears to play a major role in partitioning and use of photosynthate within the plant, as an adaptation to environmental conditions.

In a controlled-environment experiment summarized in Table 9.1, a high FR/R ratio caused soybean seedlings to develop longer stems and smaller root systems. Parallel experiments with wheat (Triticum aestivum) and tobacco (Nicotiana tabacum) resulted in the same trends. That is, a higher FR/R ratio resulted in longer stems, fewer lateral branches or tillers, a smaller root system, and a higher shoot/root dry matter ratio. If such a system could function under field conditions to sense competition from other plants and regulate partitioning of photoassimilate among plant components, it might serve as a regulator of plant adaptation to competition and favor survival.

Under field conditions, we measured the spectral distribution of incoming sunlight and compared it with spectral distribution of light received at various points in plant canopies grown in different population densities and row orientations. As expected, the various wavelengths of light were not absorbed equally by growing plants. Examination of a typical soybean leaf showed that the leaf absorbed most of the visible light and reflected or transmitted most of the FR (Figure 9.5). The same patterns were found for tobacco, tomato (Licopersicon esculentum), corn (Zea mays), and wheat, supporting the concept that a common regulatory mechanism might exist among these species. Since each green leaf reflected FR, it was reasonable to

TABLE 9.1. Influence of FR/R ratio on soybean shoot/root relationships.

FR/R ratio* at end of photosynthetic period	Dry matter distribution			
	Shoots		Roots	
	Leaf blades	Stems + petioles	Roots	Nodules
	(%)			
Low	43.9	23.6	30.1	2.4
High	43.6	33.2	21.3	1.9

*All seedlings were grown in the same controlled-environment chamber. The only treatment difference was that half of the plants received a high and the other half received a low FR/R light ratio for five minutes at the end of the daily photosynthetic period for twenty consecutive days.

Source: Kasperbauer 1987

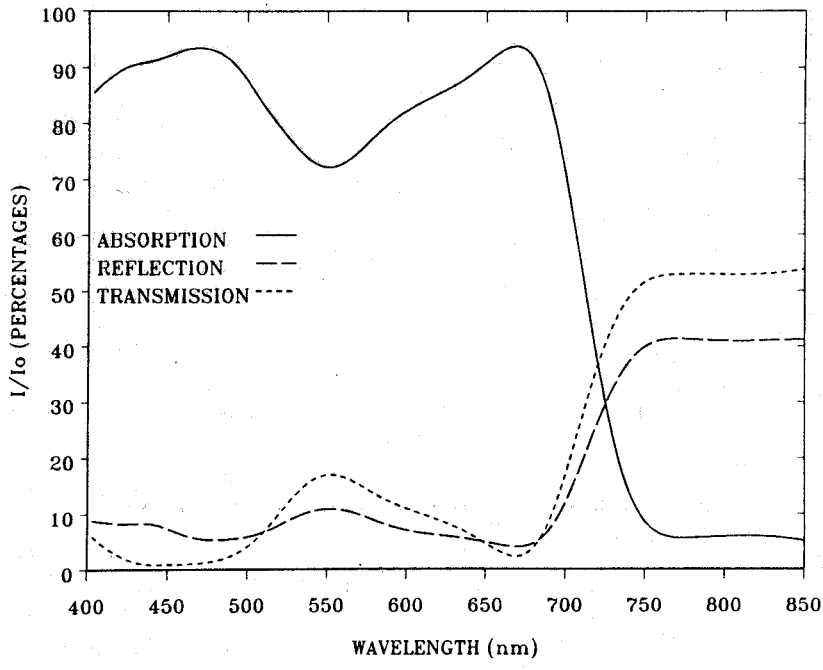


Figure 9.5. Absorption, transmission, and reflection of light from a typical soybean leaf. I/Io refers to radiation absorbed, transmitted, and reflected at five-nanometer intervals relative to incident radiation at the same wavelengths.

Source: Kasperbauer 1987

expect that a plant surrounded by many other plants (FR reflectors) would receive a higher FR/R ratio than an isolated plant or one in a low population density.

Subsequent light measurements in plant population density, row-orientation, crop species, and plant age studies clearly showed that a plant growing in a high plant population density received a higher FR/R ratio than one growing in a low population density. Also, broadleaf plants, such

as soybean and bush bean (Phaseolus vulgaris), growing in north-south as compared with east-west rows received slightly higher FR/R ratios because of heliotropic movement of the leaves (that is, individual leaves became directional FR reflectors). The row-orientation effects on FR/R ratio in corn plots were less pronounced. As predicted from the controlled-environment studies, plants that received higher FR/R ratios in the field developed longer stems, fewer lateral branches or tillers, longer and narrower leaves, and smaller root systems. That is, the FR/R and shoot/root ratios were highly influenced by the nearness of competing plants. This pattern occurred even when the roots developed in root-tight containers (embedded in the soil) such that plants in all field plant spacings and row orientations had the same volume of rooting medium. The indicated pattern of morphological development in the field was already evident in seedlings soon after emergence, long before mutual shading and reduced photosynthetically active light became a factor. Very young seedlings are highly sensitive to the FR/R ratio, and they are dramatically influenced by even subtle changes in the ratio. The sensing of competition from other plants and the partitioning of photoassimilate to the stem (at the expense of lateral branches or roots) in a high plant population density would allow a plant to increase its probability of keeping some leaves in sunlight above competing plants and of surviving and producing some seed. On the other hand, a low FR/R ratio (as would occur in a low population density) would favor increased partitioning to branches and roots. This adaptation to low population density should allow the individual plant to support development of more seed.

In the foregoing examples, growing plants responded to the FR/R ratio supplied by lamps and filters in controlled environments and to amounts of reflected FR associated with the nearness and number of competing plants in field studies. It is apparent that plants have evolved to respond differently to various wavelength combinations, and it is also apparent that the plants cannot discern the source of the spectral alterations. This line of reasoning led us to consider developmental effects of the spectral distribution of upwardly reflected light from variously colored soils and mulches. We found that plants developed different shoot/root ratios when grown over different soil surface colors, even when the root temperatures were kept constant by use of insulation panels below the various soil surface colors (Hunt et al. 1989). It is evident that the spectral distribution of reflected light can influence photoassimi-

late partitioning within a plant and affect its shoot/root relationships.

The use of variously colored mulches and plant residue covers to modify the reflected light spectrum and the partitioning of photoassimilate among plant components (without interfering with incoming sunlight) appears to offer opportunity for increasing the quantity and quality of crop productivity. One mulch color may favor leaf crops, another may favor fruit, and another may favor root crops. Further knowledge of the bioregulatory role of light and its manipulation under field conditions appears to have great potential for future crop production systems.

In summary, the growth and development of a plant is the result of its genetics and the environment within which it is grown. Plants have evolved the capability to sense various environmental factors and to activate or repress genes to regulate developmental patterns that favor survival of the plant long enough to produce the next generation. The relationship between the quantity of visible light and the amount of photosynthesis has been widely studied. However, awareness of the role of light reflected from competing plants or from different colors of soil or mulch to regulate partitioning of photoassimilate is just now being realized. My question concerning the best root size for a plant is still unanswered. Certainly, the largest root system is not always on the largest plant. Better understanding of the natural bioregulation of shoot/root relationships under field conditions will be highly useful in future plant-soil-water-light management systems.

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REFERENCES

Decoteau, D. R., M. J. Kasperbauer, and P. G. Hunt. 1989. Mulch surface color effects on yield of fresh-market tomatoes. Journal American Society of Horticultural Science 114:216-219.

Hunt, P. G., M. J. Kasperbauer, and T. A. Matheny. 1987. Nodule development in a split-root system in response to red and far-red light treatment of soybean shoots. Crop Science 27:973-976.

Hunt, P. G., M. J. Kasperbauer, and T. A. Matheny. 1989. Soybean seedling growth responses to light reflected from different colored soils. Crop Science 29:130-133.

Kasperbauer, M. J. 1986. Tall fescue plant modification through tissue culture, haploids and doubled haploids. In Proceedings of sixth international congress of plant tissue and cell culture, ed. D. A. Somers, B. G. Gengenbach, D. D. Beisboer, W. P. Hackett, and C. E. Green, 124. Minneapolis: University of Minnesota Press.

Kasperbauer, M. J. 1987. Far-red reflection from green leaves and effects on phytochrome-mediated assimilate partitioning under field conditions. Plant Physiology 85:350-354.

Kasperbauer, M. J. 1988. Phytochrome involvement in regulation of photosynthetic apparatus and plant adaptation. Plant Physiology Biochemistry 26(4):519-524.

Kasperbauer, M. J., H. A. Borthwick, and S. B. Hendricks. 1964. Reversion of phytochrome 730 (Pfr) to P660 (Pr) in Chenopodium rubrum L. Botanical Gazette 125(2):75-80.

Kasperbauer, M. J., R. C. Buckner, and W. D. Springer. 1980. Haploid plants by anther-panicle culture of tall fescue. Crop Science 20:103-106.

Kasperbauer, M. J., and G. C. Eizenga. 1985. Tall fescue doubled haploids via tissue culture and plant regeneration. Crop Science 25:1091-1095.

Kasperbauer, M. J., and F. P. Gardner. 1962. Day length controls root size and flowering in sweetclover plants. Crops and Soils June 62:21.

Kasperbauer, M. J., F. P. Gardner, and I. J. Johnson. 1963. Taproot growth and crown bud development in biennial sweetclover as related to photoperiod and temperature. Crop Science 3:4-7.

Kasperbauer, M. J., F. P. Gardner, and W. E. Loomis. 1962. Interaction of photoperiod and vernalization in flower-

ing of sweetclover (Melilotus). Plant Physiology 37:165-170.

Kasperbauer, M. J., and P. G. Hunt. 1987. Soil color and surface residue effects on seedling light environment. Plant and Soil 97:295-298.

Kasperbauer, M. J., and D. L. Karlen. 1986. Light-mediated bioregulation of tillering and photosynthate partitioning in wheat. Physiologia Plantarum 66:159-163.

Kaul, K., and M. J. Kasperbauer. 1988. Row orientation effects on FR/R light ratio, growth and development of field-grown bush bean. Physiologia Plantarum 74:415-417.