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Light signals perceived by crop and weed plants

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Abstract

Light signals perceived by specific plant photoreceptors such as phytochromes, cryptochromes and phototropin play a central role controlling the physiology and development of weed and crop plants. Knowledge about these controls has been gained in the last decade thanks to the combination of eco-physiological experiments under conditions of natural radiation with classical photobiological techniques and genetic and biotechnological tools. This progress has important ramifications for our understanding of the physiology of crop growth and development, as well as the mechanisms of crop–weed competition. In this paper we discuss some of the recent advances in the field of environmental photomorphogenesis and highlight their agricultural implications. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Biotechnology; Cryptochrome; Photomorphogenesis; Phytochrome; Plant density; Shade avoidance; Yield

1. Introduction

Solar radiation is an essential determinant of crop yield in many ways — via photosynthesis, sunlight fuels crop growth and development. Solar radiation is also a major determinant of the energy balance of the soil and the plants, and drives water and nutrient transport. In addition, light perceived by specific photoreceptors (non-photosynthetic pigments) including phytochromes, cryptochromes and phototropin, induces photomorphogenic responses, influencing both the pattern of investment of captured resources and the ability of the plant to capture further resources. The effects of light signals perceived by these photoreceptors can be different for the crop and the accompanying weeds. Consequently, photomorphogenic responses of crop and weed plants are predicted to alter the interactions between these two components of the system.

In this paper we outline the current state of knowledge about photomorphogenic controls of plant development in crop canopies, and highlight areas in which the manipulation of photomorphogenesis could be used to alter crop–weed interactions and crop yield. For more comprehensive discussions of the agricultural implications of photomorphogenic signaling, the reader is referred to previous reviews by Smith (1992), Ballaré et al. (1992b, 1995a, 1997), Sánchez et al. (1993), and Holt (1995).

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2. Processes controlled by photomorphogenic mechanisms

2.1. Seed germination

The seeds of a large number of weed species require light for germination (Baskin and Baskin, 1998; Casal and Sánchez, 1998). Weed seeds are frequently dispersed during crop harvest and buried during soil preparation for fallow. These seeds experience prolonged periods of darkness in the soil, until some of them become briefly exposed to light during subsequent tillage operations. This brief exposure to light is enough to induce germination of significant quantities of weed seeds (Scopel et al., 1991; Botto et al., 1998b).

The ability of weed seeds to germinate in response to very brief exposures to light can be acquired during burial (Taylorson, 1972; Scopel et al., 1991). This sensitization has been interpreted as a transition from the low-fluence to the very-low-fluence response modes of phytochrome action (Scopel et al., 1991). For some species, this sensitization process is believed to be dependent on exposure to low temperatures during winter; however, this is not always the case. In *Datura ferox*, sensitization occurs at relatively warm temperatures (Scopel et al., 1991), and the process is influenced by depth of burial, showing an optimum around 5 cm, and it is impaired by the presence of plant cover (Botto et al., 1998a). Phytochrome A, a specialized member of the phytochrome family, operates like an antenna in the perception of these very-low-fluences of light (Botto et al., 1996; Shinomura et al., 1996). Very often, weed seeds that require brief exposures to light to induce germination will not germinate when exposed to prolonged periods of intense sunlight on the surface of the soil (Botto et al., 1998a).

The seeds of most crops do not require light to germinate and are normally buried in complete darkness. Very likely, this sowing practice has been a pressure for selection against a light requirement for germination in the case of crop seeds.

Genetic differences in seed photoresponses are not only observed between crops and weeds but also among different weed species. Seeds of many weeds only germinate when present very close to or on the surface of the soil and in the absence of vegetation cover. In this case, the stimulus is not a brief pulse of light but the high red to far-red photon ratio (R:FR) of sunlight (Deregibus et al., 1994; Insausti et al., 1995). The R:FR of sunlight reaching bare soil is approximately 1.1 during most part of the day (Smith and Holmes, 1977); when light reaches green plant organs, the R:FR decreases due to selective light absorption (strong for R, weak for FR), transmission and reflection (both weak for R and strong for FR); see Holmes and Smith (1977). Small reductions of the R:FR (for instance from 1.1 to 0.8 or 0.9) are enough to inhibit or reduce germination in several species, including *Lolium multiflorum*, *Silene gallica*, and *Brassica campestris* (Deregibus et al., 1994; Batlla et al., 2000). These slightly reduced R:FR ratios are typical of sparse canopies, with leaf area indexes below one. Changes in R:FR that regulate seed germination are perceived by other members of the phytochrome family (phytochrome B is quantitatively the most important); see Botto et al. (1995). These examples illustrate how versatile phytochrome-mediated light perception can be. Whereas some seeds are able to distinguish between full darkness and milliseconds of light, others are able to distinguish between full sunlight and light with slightly decreased R:FR. The perception of these signals allows weed seeds to germinate simultaneously with (or slightly earlier than) the crop, when photosynthetic light and other resources are abundant.

2.2. Shoot elongation and branching

After seedling emergence, mutual plant shading and competition for photosynthetic light becomes intense when the canopy begins to close. However, interference between crop and weed seedlings can be established much earlier. The reflection of FR by green plant parts lowers the R:FR of horizontally propagated light before there is a significant degree of mutual plant shading (Ballaré et al., 1987). In turn, this modifies the light environment in the stem tissue, and elicits changes in stem elongation rate (Ballaré et al., 1990); see Fig. 1. Phytochrome B appears to play an important role perceiving this early signal of competition (Whitelam and Smith, 1991; Ballaré et al., 1991a; Yanovsky et al., 1995a). The pattern of distribution of the products of photosynthesis is altered in this way before photosynthesis is reduced by mutual shading.

The most characteristic effects of reduced R:FR are enhanced axis elongation and reduced branching.

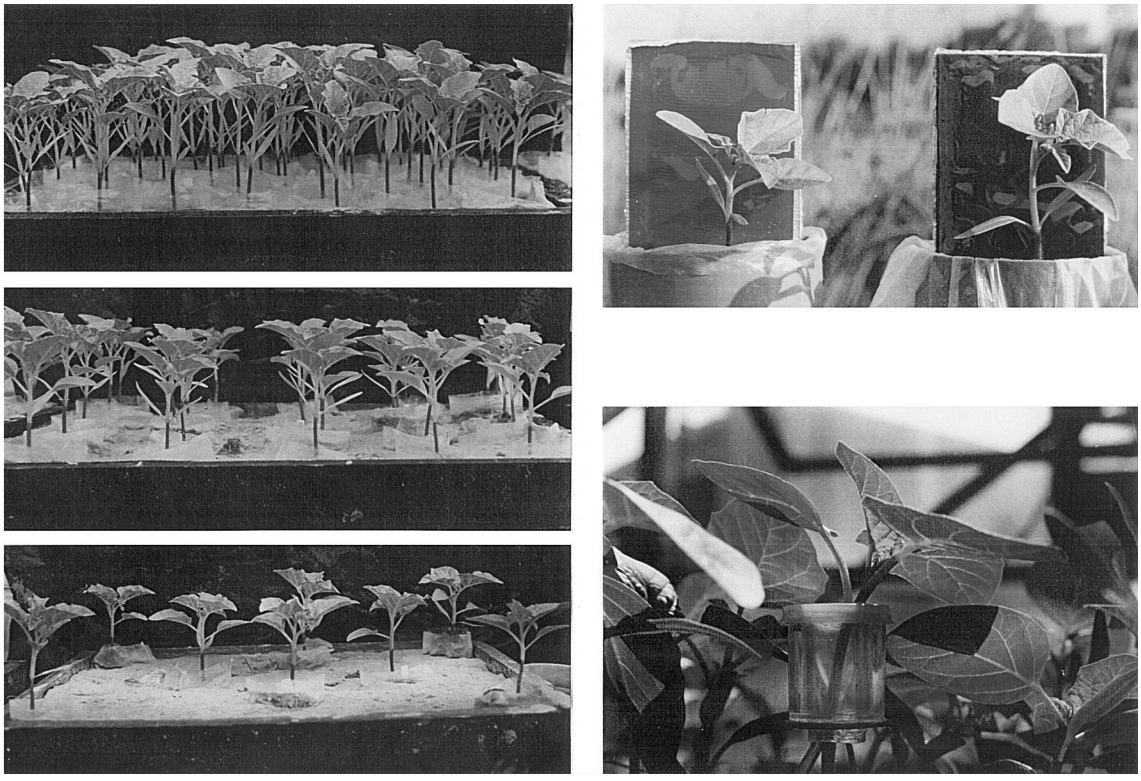

Fig. 1. Photomorphogenic responses of *Datura ferox* to the proximity of neighbors. *Left panels*: Effects of increasing plant density on plant morphology and stand architecture. Notice the increase in plant height with density, particularly in the plants located at the center of the high density stand. *Top right*: Selective mirrors used to mimic the proximity of neighbors; the mirror on the right-hand side reflects FR with high efficiency, which promotes shoot elongation in plants grown under full sunlight. *Bottom right*: Collar filters used to alter the light environment of individual internodes in plants grown in real canopies. When the filters were filled with copper sulfate, which absorbs FR, the elongation response at low densities was abolished. For details, see Ballaré et al. (1987, 1990).

Increased stem growth has been observed in many cultivated and weedy dicots (e.g., Morgan and Smith, 1979). In grasses, low R:FR can reduce tillering and enhance leaf sheath growth (Casal et al., 1985). These processes are so sensitive to R:FR that stem growth of *Sinapis alba* seedlings can be increased by more than 50% in response to FR back reflected by green fences placed to the South (Southern hemisphere) to avoid shading the target plant (Ballaré et al., 1987); see Fig. 2. Similarly, plants of *Paspalum dilatatum* grown in pots placed at low densities (<7 plants m^{-2}) do not shade each other but show a reduction of tillering of 40% compared to isolated controls (Casal et al., 1986). Qualitatively similar results were obtained by Davis and Simmons (1994) working with barley. In *P. dilatatum*, the reduction in tillering was fully reversible by the addition of small (photosynthetically negligible) amounts of R to the base of the plants (Casal et al., 1986). In *L. multiflorum* micro swards, reductions in plant tillering in response to plant density precede changes in dry matter gain. Low R:FR reduce the rate of site filling, i.e., the ratio between number of tillers and tiller bud positions (leaves); see Casal et al. (1987). At least in *L. multiflorum*, small to moderate reductions in R:FR (e.g., to 0.5) have strong effects on tillering and there is no obvious indication of further inhibition by more intense reductions of the R:FR (Casal et al., 1987).

With continued canopy growth, mutual shading becomes more intense. R:FR is further reduced and can go down to approximately 0.1 at the base of dense stands. The low R:FR signal, which immediately after emergence is detectable only on vertically oriented organs, becomes also intense at the level of the leaves.

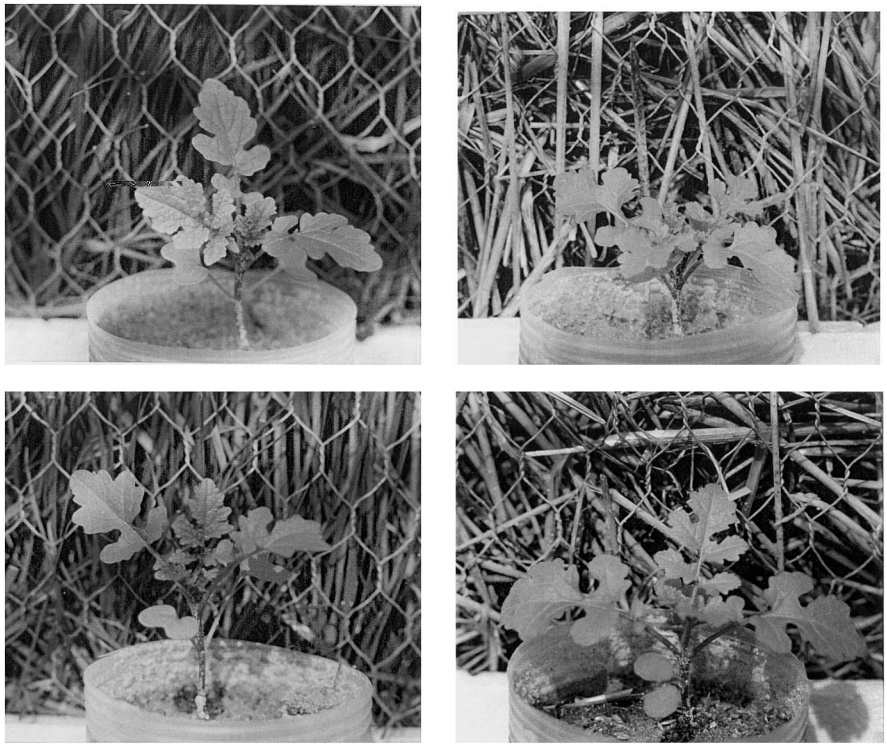

Fig. 2. Remote detection of plant neighbors. Mustard plants placed in front of green grass fences (left panels), which reflect FR and lower the R:FR of the side light, grow taller than the counterparts placed in front of similar fences that were bleached by the application of a herbicide (right panels). For details, see Ballaré et al. (1987).

At least in *S. alba*, treatment of the leaves with low R:FR induces a promotion of stem growth that persists for many hours, even after the low R:FR signal is eliminated (Casal and Smith, 1988). In addition, mutual shading reduces the photon flux density at all wavelengths, first in the stem and later in the leaves, particularly those leaves placed in lower strata. The reduction in the blue waveband is perceived by cryptochromes (in particular cryptochrome 1) and the reduction of FR is perceived by phytochrome A (Yanovsky et al., 1995a, 1998). These changes in the light environment also trigger morphological responses, such as increased stem elongation (Ballaré et al., 1991b).

Photomorphogenic responses may involve changes in the partitioning of photoassimilates. The *lh* mutant of cucumber is deficient in phytochrome B and exhibits constitutively exaggerated stem growth, characteristic of plants grown in dense stands (López Juez et al., 1992). This mutant has heavier stems than the wild type, but the difference in dry weight is not as large as the difference in length; the *lh* mutant has a lower dry weight to length ratio (Casal et al., 1994), which corresponds to a decreased stem diameter. Leaf growth (area, dry weight) and root growth are concomitantly reduced. The situation can be different in plants exposed to treatments of low R:FR that are restricted to the stem. In an experiment with *Amaranthus quitensis*, a low R:FR treatment applied to the stem increased stem length and dry weight but *did not* affect leaf or root growth (Ballaré et al., 1991c). Consequently, plants of this weed receiving low R:FR in the internodes accumulated more dry matter than the high R:FR controls. Apparently, the low R:FR stimulus increased stem sink strength, and indirectly enhanced photosynthesis. In *S. alba*, the same treatment increased stem length but hardly affected stem dry matter (Casal et al., 1995). In the latter species, stem dry weight is enhanced by low R:FR when this signal also reaches the leaves. When only one leaf of the pair attached to the first internode is exposed to low