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Developmental responses of portulaca seedlings to conflicting spectral signals

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Summary. *Portulaca oleracea* seedlings avoid growing in the direction of neighbouring plants even when they are very small or remote. The present study was designed to determine the relative effect on the development of *Portulaca* seedlings of light availability (i.e. the resource level) as compared with spectral composition (i.e. the signal of future competition for the resource). The plants were subjected to various intensities of photosynthetic light and red/far-red (R/FR) ratios from opposite directions. The seedlings became recumbent preferentially towards the direction with the lower FR light, even when this meant growing towards plastic that absorbed 20 times more photosynthetic light. A preference for the direction with higher photosynthetic light over lower FR was also found, though only under extreme light differences. The response of the seedlings was not absolute: the orientation chosen depended on the light received from other alternative directions.

Key words: Developmental plasticity – Environmental signals – Red/far-red ratios – Plant competition – *Portulaca oleracea* L.

It was recently shown that seedlings of *Portulaca oleracea* avoid growing and branching in the direction of very small and relatively remote neighbours (Novoplansky et al. 1990a). Replacing these neighbours with plastic rectangles of different spectral characteristics suggested that the directional sensitivity of *Portulaca* seedlings is related to the ratio between red light (R; peak at 660 nm) and far-red light (FR; peak at 730 nm). This ratio is known to be changed when light passes through, or is reflected from, neighbouring plants (Smith 1982; Casal and Smith 1989). These results offered a further example of the role of R/FR signals in the sensing of neighbouring plants (Kasperbauer 1971; Smith 1982; Casal and Smith 1989). They also indicated that R/FR sensitivity can be directional rather than merely quantitative. Furthermore, the work with *Portulaca* stressed, more than other cases (e.g. Balleré et al. 1987), the ability of plants to react in ways that reduce the chances of future and not only actual shade.

The earlier work with *Portulaca* raises questions concerning the possible responses of plants that are presented with conflicting or complicated information. In the present study we subjected *Portulaca* seedlings to reduced photosynthetic light from one direction and to low R/FR ratios from another direction. These experiments were meant to compare the relative effects of photosynthetic light with those of specific spectral signals. The latter could predict the growth of large neighbours, and would therefore be relevant to future rather than to present environmental conditions. Thus, a general theoretical topic dealt with here is the relative role in morphogenesis of available resources versus environmental signals which convey information but are of no immediate material or energetic significance. A related question, dealt with in a second set of experiments, concerns the ability of the plants to choose the best available direction: Is a specific light composition preferred or avoided depending on the availability of other, more or less favorable alternatives? Such conditional responses would mean that the plant compares the signals received from various directions and responds as an integrated system.

The experiments were conducted on the Giv'at-Ram campus in Jerusalem, Israel, between June and September 1989. *Portulaca* seedlings were collected and planted in pots as described by Novoplansky et al. (1990a). The seedlings were planted so that their hypocotyl was at the level of the rim of pots with a diameter of 12 cm. These pots were placed on flat open ground 60 cm from each other and were irrigated individually to field capacity every 12 h by a computerized drip system (Gal-Kol, Kfar-Blum, Israel). The water hose entered each pot from beneath and the dripping heads were buried in the soil, so they did not influence the surface of the ground around the plants. Each pot was fertilized every 7 days with 150 ml of 20N:20P:20K solution (2 grL^{-1}).

In the first set of experiments single *Portulaca* seedlings were planted in pots with a strip of plastic, 4 cm

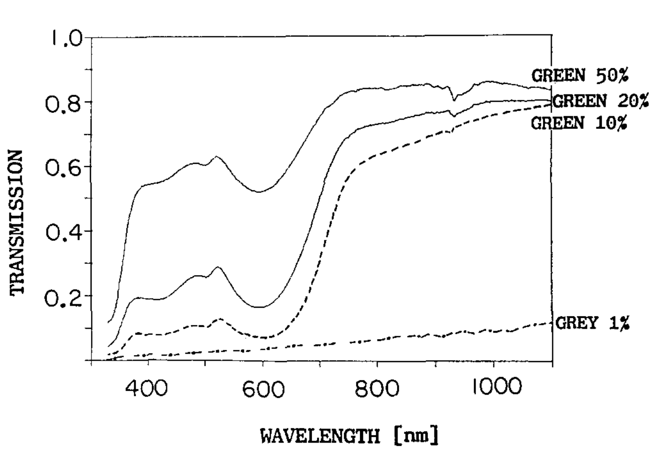

Fig. 1. Transmission of the plastic filters used in the various experiments. All measurements were made with a spectrophotometer (Cary 2300, Varian, Monrovia, CA, USA). The flat curve of "grey 1%" is of "natural shade" film that reduced the light with a minimal alteration of the spectral composition. The other curves are of "vegetative shade" films whose transmission and reflection properties resemble those of leaves (Smith 1982)

Table 1. Spectral characteristics of the plastic films that were used for the experiments. Photosynthetic light transmission (PAR) is on a photon basis and refers to all photons between 400 and 700 nm. Red/far-red – R/FR – refers to the ratio of 660 ± 12 nm to 730 ± 12 nm. All films were prepared from polyethylene in Ginnegar Plastics, Israel. They were 100 μm thick, U.V. resistant and optically stable. Measurements were carried out with a portable photospectroradiometer (LI 1800, Li-Cor, Lincoln, Nebraska)

Film	PAR transmission [%]	R/FR modification [%]
"Green 10%"	11.20	−75.7
"Green 20%"	22.50	−66.3
"Green 50%"	54.60	−29.6
"Grey 1%"	1.04	− 3.1

high, bound to their rim. Half of the plastic strip was green ("green 10%", "green 20%" or "green 50%"; Fig. 1 and Table 1) and the other half was grey "grey 1%"; Fig. 1 and Table 1). In this way, the seedlings were subjected to relatively high photosynthetic light levels with a low R/FR ratio from one direction and to reduced photosynthetic light levels with an essentially unchanged R/FR ratio from the other. It should be noted that most of the direct light received by the plants was not influenced by the plastic in any way: Direct sunlight was transmitted through the plastic films for less than 2.3 h after sunrise and before sunset.

As seen in Fig. 2, the *Portulaca* seedlings became recumbent preferentially in the direction of the grey plastic (R/FR ratios similar to that in direct sunlight) and avoided developing in the direction of the green plastic (lower R/FR ratios typical of the shade cast by leaves). Avoidance of low R/FR predominated even when the plastic on the opposite side absorbed 20 times more photosynthetic light (Fig. 2b). Yet the availability of photosynthetic light did have an effect on *Portulaca* development: A 50 fold difference in photosynthetic light transmission of the plastic reversed the preference of the plants and caused most of them to develop in the direction of the higher photosynthetic light and the lower R/FR ratios (Fig. 2c).

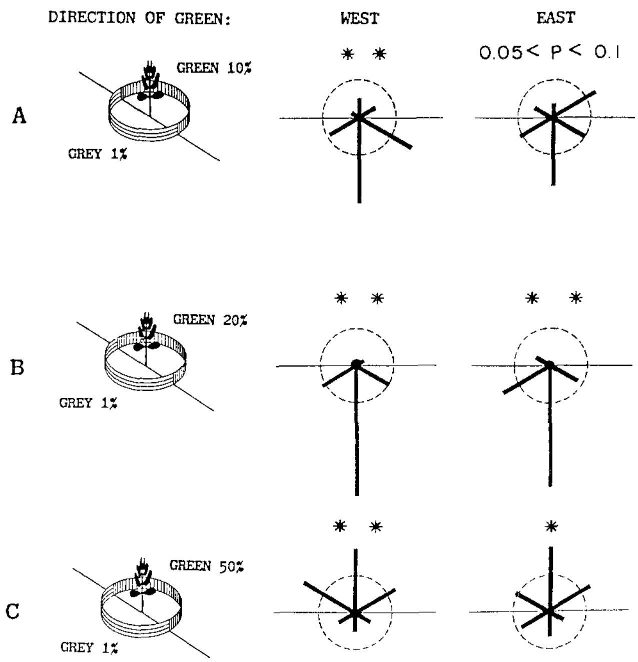

Fig. 2. Frequency distribution of plants whose main shoot became recumbent to various directions when confronted with "Grey 1%" on their east or west and with either "green 10%", "green 20%" or "green 50%" on the opposite direction. The sectors (60 degrees each) to which the main shoot became recumbent were determined 14 days after the beginning of the experiments. The broken line in each scheme represents the expected random frequency. Every experiment was conducted twice, using 45–50 plants each time. The differences between the number of plants that became recumbent to the east and the west were tested for statistical significance using the Chi-square method (Sokal and Rohlf 1981); * $P<0.025$, ** $P<0.001$

The results (Fig. 2) show that the development of *Portulaca* seedlings is sensitive both to R/FR signals and to the level of photosynthetic light. In the seedlings and conditions that were used, however, the effect of spectral signals appears to be very large: the low R/FR ratios had a larger effect than a 20 fold decrease of photosynthetic light during 2.3 h after sunrise and before sunset.

The R/FR ratios which are relevant to the chance that the plants will encounter future shade need not be correlated with the intensity of the light which is of immediate significance for photosynthesis. It is possible that the large effects of the spectral signals on development are related to the young age of the plants used for the experiments; relatively mature plants have been shown to be less sensitive to the R/FR signals and to respond more clearly to light availability that is of immediate functional significance (Novoplansky et al. 1990a). It is suggested that the sensitivity of young plants to R/FR ratios may be a part of a "long-run strategy" which need not, at least in some cases, lead to the maximization of the use of the available photosynthetic light. This

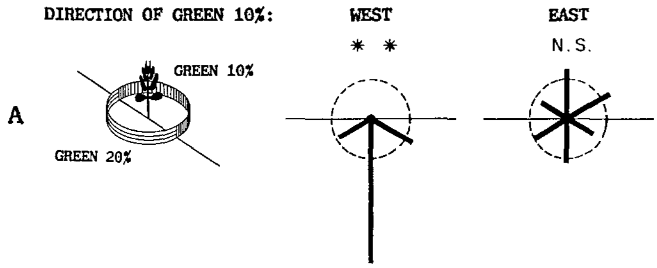

Fig. 3. Frequency distribution of plants whose main shoot became recumbent to various directions when confronted with "Green 10%" on their east or west and with "green 20%" on the opposite direction. Spectral characteristics of the plastic films are summarized in Fig. 1 and Table 1. The sector (60 degrees each) to which the main shoot became recumbent was determined 14 days after the beginning of the experiments. The broken line in each scheme represents the expected frequency of plants in each sector if they would have became recumbent in a random manner. Every experiment was conducted twice, using 45–50 plants each time. The significance of the differences between the number of plants that became recumbent to the east and the west were tested by the Chi-square method (Sokal and Rohlf 1981); ** $P<0.001$, N.S. $P>0.1$

hypothesis should be further investigated by comparing the performance of plants that avoid neighbouring plants with plants that would be forced to grow towards their neighbours.

A second set of experiments was similar to the first in every way, except that both halves of the plastic film bound to the pot's rim were green (Fig. 3): one half of the plastic was "green 10%" (75.7% reduction in R/FR of transmitted light; Table 1) and the other was "green 20%" (66.3% reduction in R/FR of transmitted light; Table 1). In this experiment the *Portulaca* plants had to "choose" between two sides, both of which had been avoided when the seedlings had a "better" alternative (Fig. 2a–b). The results were that none of the 48 seedlings became recumbent towards "green 10%" when it was on the western side.

In spite of the differences in the spectral characteristics, there was no clear directional preference when "green 10%" was on the east and "green 20%" was on the west (Fig. 3). This result suggests that the plants are more sensitive to spectral signals from the west than from the east. Other evidence for a similar sensitivity to "end of the day" signals has been reported (e.g. Kasperbauer 1971; Novoplansky et al. 1990a), but its ecological meaning is not yet understood.

A general conclusion from this last experiment is that *Portulaca* plants act as integrated systems: they respond not to specific signals but rather to the balance of the various directional signals received from the environment. The plants are able to "select" what appears to be the best alternative available at any given situation, avoiding conditions which would have been preferred in other circumstances. It is suggested that this behaviour enables the plants to develop optimally in heterogeneous environments, rather than merely to develop in "appropriate" light combinations, a possibility that requires further, longer tests. An integration of the responses of pea seedlings with two shoots has been demonstrated (Snow 1931; Novoplansky et al. 1989), but in *Portulaca* the integration is more subtle, as it involves different signals perceived by the very same shoots.

Additional evidence concerning the importance of R/FR signals as compared with photosynthetic light availability comes from recent work on spectral signaling in agricultural greenhouses (Novoplansky et al. 1990b–c). Increases of the R/FR ratios was achieved by adding stable fluorescent dyes to the plastic covers of the greenhouses; these dyes converted part of the yellow-green light (500–600 nm) into red light (600–700 nm). This changed plant morphogenesis in ways that enhanced the production of flowers and fruits. The yields of greenhouse grown rose flowers, for example, were increased by such plastic covers by 26%. The response to the R/FR signals indicating future shade could be part of a competitive "arms race" between the plants. In this race the only ESS (sensu Maynard-Smith 1982; Givnish 1982; Iwasa et al. 1985) for an individual plant is to allocate a relatively large fraction of its resources to structures whose only contribution is in competition with neighbours. The fluorescent covers prevent this competitive development, which is wasteful from an agricultural point of view, and thus promote the production of higher yields even though they have a small adverse effect on the available photosynthetic light.

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