Planta 144, 121–124 (1979)

Planta

Inhibitory Effects of Full Daylight on the Germination of *Lactuca sativa* L.

T. Górski and K. Górska

Department of Agrometeorology, Institute of Soil Science and Plant Cultivation, 24-100 Puławy, Poland

Abstract. Using glass filters that transmit various spectral bands and different intensities of natural daylight, experiments with achenes of lettuce *cv.* Vanquard were performed. Germination during prolonged treatment depended both on the far red/red radiation ratio and on the irradiance. The promotive effect of red radiation present in natural light prevailed at low irradiances, the inhibitory effect of far red radiation at high irradiances. The dormancy imposed by prolonged white light of high intensity can be cancelled by transferring the achenes to darkness or to diffuse weak white light. The effects are obviously of the "high irradiance response" type; they are exerted by the same mechanism that causes seed dormancy under leaf canopies. Some considerations on the ecological significance of seed behaviour are given.

Key words: Germination (seeds) – *Lactuca* – Light (high irradiance response).

Introduction

In a former report (Górski, 1975) it was stated that the direct solar radiation exerts an inhibitory effect on germination of normally non-photoblastic (i.e., germinating in darkness as well as in diffuse white light) lettuce achenes; a good negative correlation between germination and total energy of direct solar radiation received during treatment has been found. Since these achenes were also inhibited by prolonged FR transmitted through a leaf canopy, and since this effect was considered as an HIR, one cannot exclude the fact that inhibition in full sunlight is also a kind of photoresponse, although the opposite hypothesis, as action of temperature rise and/or moisture stress, should also be considered.

The aim of the presented experiments was to determine the main factor involved in inhibition of seed germination in the direct sunlight.

Abbreviations: FR = far red radiation; R = red radiation; HIR = high irradiance response; P_{fr} = the far red absorbing form of phytochrome; P_r = the red absorbing form of phytochrome

Materials and Methods

Germination Test

The achenes of lettuce *cv.* Vanquard were obtained from Centrala Nasienna Inc. (Lublin, Poland). Twenty achenes were sown per 5 cm Petri dish on four layers of white flannel and a Whatman filter, moistened with distilled water. The dishes were exposed in an open stand under glass filters (Jena, GDR) transmitting various bands of natural radiation. To compensate for total irradiance under glass filters, mat glass and neutral plastic filters (Cinemoid, England) were used. To eliminate partly the shading by the dish edge, the desk with the dishes was arranged at 20° angle to the horizontal level and was displaced three times a day into the direction of the sun. The dishes were carefully observed, and water was added, twice a day, if necessary. The control dishes were located in a wooden framework box, permitting no sunflecks. Germination was evaluated 72 h after exposure. There were no replicates of experimental dishes, but the presented results are averages of at least four unrelated experiments, performed during different periods.

Radiation Measurements

The spectral composition of the light under the filters and in the framework box was determined by means of a spectroradiometer (OBRTS, Warsaw, Poland), half-band width, 20 nm. The total irradiance on the level of achenes was measured with a Moll-Gorczyński pyranometer (Kipp and Zonen, Delft, Netherlands); an identical device was used to record total and diffuse radiation in an open stand. The direct radiation on the horizontal surface was determined as the difference between total and diffuse radiation. All irradiance measurements under the filters are valid for the horizontal position of the filters and 45° sun angle in bright weather. FR refers to the spectral band 715–735 nm; R, to the band 645–665 nm.

0032-0935/79/0144/0121/$01.00

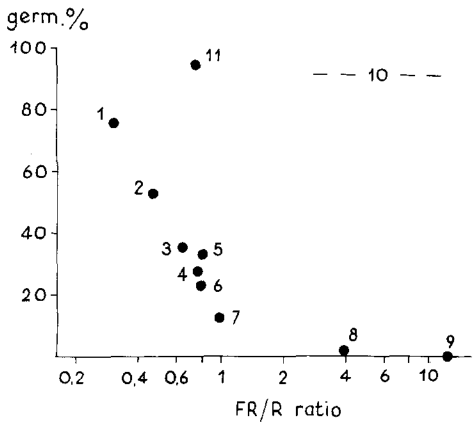

Fig. 1. Germination of lettuce achenes (cv. Vanquard) in natural daylight under filters giving different FR/R ratios. Filters: *1* 12-mm BG 17, *2* BG 19; *3* 3-mm BG 17; *4* WG 8; *5* OG 3; *6* window glass; *7* RG 2; *8* RG 5; *9* RG 8; *10* UG 6. *11* diffuse white light control. Under filter UG 6 no measureable R or FR is found. Except for 12-mm BG 17 the total irradiance under all filters was compensated to the level measured under filter UG 6 (about 30% of full daylight). During 72 h exposure, the energy received in the open stand was around 5010 J cm^{-2}. The results are averages of 4 unrelated experiments

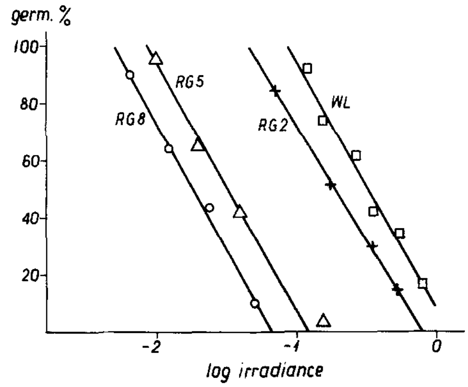

Fig. 2. Germination of lettuce achenes (cv. Vanquard) in natural daylight under filters giving different irradiances, but fixed FR/R ratios. *WL*=white light under window glass. Log irradiance=0 means full daylight (around 3570 J cm^{-2} during 72 h of exposure). For FR/R ratios see Figure 1. The results are means of 6 unrelated experiments

Results

Germination in Various Spectral Bands

The achenes were sown under various filters, transmitting different spectral bands, but equal total irradiance, compensated to the level measured under filter UG 6, transmitting no radiation below 800 nm. The compensation with neutral filters permitted the maintenance of similar temperature and evaporative conditions in all the dishes; only under the 12 mm filter BG 17 was the total irradiation about 60% of that under the other filters. Direct solar irradiance under filter UG 6 was reduced to 30% of that in the open stand; the reduction was greater in diffuse light. During the experimental period the weather was predominantly sunny; the total energy received in the open stand during 72 h of exposure changes in particular experiments within the limits of 3460–6850 J cm^{-2}, and energy of direct radiation on the horizontal level within the limits of 1790–3360 J cm^{-2}. The mean daily temperature of these periods varied between 15° and 21° C.

The results of germination tests are presented in Figure 1. The germination was closely related to the FR/R ratio. Under filter RG 8, which gave a ratio of about 12, we never observed germinating achene; under the 12 mm filter BG 17, the germination rate was around 75% (this result is not fully comparable because of reduced irradiance), under BG 19, where the ratio FR/R was about 0.5, at 53%. Almost full germination (92%) appeared under filter UG 6, where no measurable R or FR was found. Full germination (95%) occurred only in diffuse white light, where the FR/R ratio was about 0.75, but the total irradiance was close to 0.25 of that under the filters. This result suggested that germination not only depends on FR/R ratio, but also on irradiance.

Germination at Various Irradiances

Filters RG 8, RG 5, RG 2, and window glass were supplemented with various numbers of neutral filters to obtain different total irradiances at fixed FR/R ratios. These experiments were performed in the late summer and early autumn. The total radiation received in the open stand during 72 h of exposure changed within the limits of 2560–5760 J cm^{-2}, direct radiation within 900–3940 J cm^{-2}. The mean daily temperature varied between 12° and 20° C. Although the relatively great variability of natural conditions caused some differences in germination in particular experiments, the averaged results of six experiments (Fig. 2) show clear patterns: germination is linearly related to the logarithm of irradiance; it depends both on irradiance and on the FR/R ratio.

Germination of Inhibited Achenes after Translocation to Darkness

If inhibited achenes were transferred to the dark after three days of exposure, germination was dependent on the spectral band previously used. The seeds inhibited under window glass and under filter RG 2 germinated fully during two days in darkness or in diffuse white light; about 60% of those from filter RG 5 germinated, and those from filter RG 8 showed not more than 10% germination in darkness. For those achenes we were not able to observe any significant dependence on irradiance used during inhibition. The achenes from filters RG 8 and RG 5, however, germinated fully during two days after a few seconds of exposure to white light; this stimulation could be easily reversed by a few minutes of exposure under filter RG 8.

Germination of Other Seeds

Additional experiments (without replication) were performed with *Lactuca sativa* L. cultivars May's Queen, Grand Rapids and Nochowska, *Lactuca serriola* L., *Arabis pumila* Jacq., *Hordeum vulgare* L., *Sinapis alba* L. and *Mesembryanthemum cristallinum* L. All the lettuce cultivars, *Lactuca serriola* and *Arabis pumila*, previously classified as FR dormant (Górski et al., 1977), demonstrated spectral and irradiance dependence similar to that of cv. Vanquard. The seeds of three other species, which showed no inhibition under leaf canopy, germinated equally well in all spectral bands, independently of the FR/R ratio chosen, although a slight inhibition in full sunlight was observed.

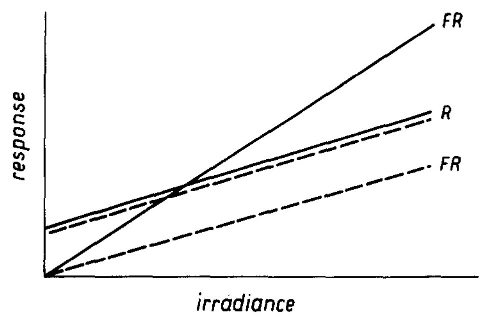

Fig. 3. An operational scheme of action of R and FR. The effects of FR are inhibitory to germination, R-promotive. *Straight lines*= immediate responses during exposure to light; *Dashed lines*=late effects in subsequent darkness. At high irradiances R must be much stronger than FR to promote germination during exposure; FR must be much stronger than R to inhibit germination in darkness

Discussion

The inhibitory effects of prolonged white light on seed germination are known from laboratory experiments with many "insensitive" (i.e., germinating in darkness as well as after short white or red irradiation) and positively photoblastic seeds (i.e., requiring short white or red light for germination; for review see Evenari, 1965; Toole, 1973). To our knowledge, however, direct evidence for the inhibitory action of FR present in natural white light has not been demonstrated.

It is obvious that the inhibition of germination in our experiments is of the HIR type. The achenes of lettuce cv. Vanquard are normally insensitive to light; they germinate in darkness as well as in diffuse white light and after short FR. In the former experiments (Górski, 1975), inhibition was obtained only by prolonged artificial or natural (under leaf canopy) FR. The results presented here showed an excellent intensity dependence; moreover, the FR band is the most effective. It seems that the operational criteria for the HIR are fulfilled. The dependence on the FR/R ratio is often ascribed to the classical phytochrome mechanism; however, the experiments of Hartmann (1966) clearly demonstrated that in HIR, although R given alone has no effect, R given simultaneously with various bands of longer FR may cause responses similar to those of FR at the peak of action (720 nm). The intensities in two cooperating bands may differ drastically in such cases; the important point is to establish an appropriate steady state of phytochrome (Mohr, 1972). The spectral bands used in our experiments were very broad, and the results may be regarded as integrated effects of many particular bands, given simultaneously. Identical responses can be obtained by manipulating various spectral compositions and intensities (Fig. 2).

Our results can be summarized in one simple operational scheme (Fig. 3). With the increase of irradiance the inhibitory effect of FR increases more than the stimulatory effect of R (another rate constant). If the irradiances of FR and R are equal, the germination stimulatory effect of R will prevail at low irradiances, and the inhibitory effect of FR at high irradiances.

After transferring the seeds from filter RG 8 to the dark, they demonstrate R-FR reversion, and thus we can assume that phytochrome is present in these seeds; since untreated seeds readily germinate in darkness, phytochrome must be mainly in the P_{fr} form (Rollin, 1972). During the prolonged FR treatment, phytochrome reverts to the P_r form, because the seeds do not germinate in the following darkness without supplementary red or white light.

The inhibition of germination in strong white light could be interpreted as a result of cycling between P_r and P_{fr}, leading to accumulation of physiologically inactive intermediates. The amount of intermediates is irradiance dependent; in open sunlight they constitute the substantial part of the total phytochrome. In the dark the intermediates are subjected to relaxation to the active P_{fr} form (Kendrick and Spruit, 1977). Our results agree with this model but do not justify any speculations on the nature of the molecular mechanisms. However, it should be noted that P_{fr} may be transformed to intermediates only in the presence of those wavelengths that are absorbed by it, i.e., mainly FR. Anyway, the inhibition of germination is related to the amount of FR present in natural white light (Fig. 1). The secondary peak of action may be expected in the blue region of the spectrum; in fact, the filter OG 3, transmitting no blue radiation, caused somewhat higher rate of germination than window glass, although the FR/R ratios were similar under both filters.

We think that we are able to present some considerations on the ecological significance of the described responses. The seeds of three additionally tested species showed no dependence on the spectral composition of prolonged light (the slight retardation of germination in full sunlight probably can be attributed to the supraoptimal temperature). These seeds were previously characterized as completely insensitive to the FR transmitted through the leaf canopy (Górski et al., 1977); this suggests that the same mechanism causes the inhibition under the leaf canopy and in sunlight. The lack of any phytochrome-mediated responses in some seeds is known, as for example in mustard (Mohr, 1972) and maize (Toole, 1973). Among 240 species examined by us thus far (in press), 62 species (mainly cultivated) showed no inhibition by prolonged FR. However, the majority of species, especially the wild-grown ones, demonstrate phytochrome-mediated responses in seed germination. Among them a greater part germinates in the dark as well as in diffuse white light and therefore is often classified as "insensitive"; this is the case for lettuce *cv.* Vanquard (and many other lettuce cultivars). However, they do not germinate in darkness (in nature: when buried) if during the few days before burial the FR prevailed, which is the normal condition in plant canopies. After recovery they require white light to germinate, i.e., they will not germinate until the canopy is thinned.

At irradiances of one order of magnitude smaller than full sunlight, the imbibed seeds lying on the ground will germinate, depending on the FR/R ratio; it is the irradiance range in which white light causes full germination and filter RG 8 (Fig. 2) or dense leaf canopy causes full inhibition. The ecological significance of these responses for species survival is obvious and was discussed in previous papers. It is also probable that other phytochrome-mediated responses appearing in developed plants enable the plants to follow physiological pathways appropriate to mutual shading (Holmes and Smith, 1977).

Further increase of irradiance to the level measured at open stands in bright weather causes inhibition of germination even in white light; natural FR *not transmitted* through the leaves becomes inhibitory to germination. We cannot interpret this response in relation to mutual shading. It seems that the ecological significance is different: The seedlings developed from seeds germinating in full sunlight will have little chance to survive, because of rapid drying before the lower, moister level of soil is reached by the roots. This kind of secondary dormancy enables the seeds "to wait" for cloudy weather, when the evapotranspiration is much lower and the probability of rainfall greater.

One more interesting feature of FR was presented (Górski, 1976): The intensity of the natural FR (about 725 nm) depends on the quantity of water vapour in the atmosphere. Perhaps the interpretation of this and related facts will approach an answer to the question of why the plants "chose" this particular band of spectrum in the course of evolution. We suppose that this interpretation, if verified, will be of general importance.

References

Evenari, M.: Light and seed dormancy. In: Encyclopedia of Plant Physiology. Vol. XV, pt. 2, pp. 804–847, Ruhland, W., ed. Berlin-Heidelberg-New York: Springer 1965

Górski, T.: Germination of seeds in the shadow of plants. Physiol. Plant. **34**, 342–346 (1975)

Górski, T.: Red and far red radiation at sunset: Annual cycle and dependence on precipitable water. Naturwissenschaften **63**, 530 (1976)

Górski, T., Górska, K., Nowicki, J.: Germination of seeds of various herbaceous species under leaf canopy. Flora **166**, 249–259 (1977)

Hartmann, K.M.: A general hypothesis to interpret "high energy phenomena" of photomorphogenesis on the basis of phytochrome. Photochem. Photobiol. **5**, 349–366 (1966)

Holmes, M.G., Smith, H.: The function of phytochrome in the natural environment. Photochem. Photobiol. **25**, 533–557 (1977)

Kendrick, R.E., Spruit, C.J.P.: Phototransformations of phytochrome. Photochem. Photobiol. **26**, 201–214 (1977)

Mohr, H.: Lectures on Photomorphogenesis. Berlin-Heidelberg-New York: Springer 1972

Rollin, P.: Phytochrome control of seed germination. In: Phytochrome. Mitrakos, K., Shropshire, W. Jr., eds. London-New York: Academic Press 1972

Toole, V.K.: Effects of light, temperature and their interactions on the germination of seeds. Seed Sci. Technol. **1**, 339–396 (1973)

Received 21 April; accepted 6 September 1978