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Inhibition of *Rumex crispus* L. seed germination under natural solar radiation conditions

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Abstract. Inhibition of germination by solar radiation is a reaction of phytochrome mechanism, called High Irradiance Response (HIR). Depending on their response to light, seeds are usually divided into three groups: photoblastic positive (germinating in light, but not germinating in darkness), photoblastic negative (giving opposite response) and indifferent (germinating both in light and darkness). The division is based on studies conducted in laboratory conditions, where low irradiance was used. The aim of manuscript is to learn the reaction of *Rumex crispus* L. seeds, belonging to the group of positive photoblastic seeds, to solar radiation under natural radiation conditions. It was found that the response of seeds depended on the fluence rate of solar radiation. Relations between germination and irradiance, photoperiod, and temperature were described using the stepwise regression method. Under high radiation, germination of photoblastic positive seeds of *R. crispus* L. was inhibited, and so these seeds behaved as photoblastic negative that do not germinate in the light. In the high radiation conditions, seeds of *R. crispus* exhibited short-day reactions. A model well describing of changes in three basic factors shaping the germination of *R. crispus* L. seeds was obtained. These studies in the natural conditions of solar radiation present the ecological significance of these reactions.

Key words: germination, photoblastism, *Rumex crispus* L., seeds photosensitivity

INTRODUCTION

Plants use natural or artificial radiation during the process of photosynthesis for the production of biomass, as well as a carrier of information about the changing environment. Non-photosynthetic regulation of plant development by radiation is called “photo morphogenesis”. Among numerous photo morphs, most studies were conducted focusing on flowering induction and seed germination.

Radiation may exert either promotional or inhibitory effect on seed germination. The classic division based on photoblastism was developed in the laboratory conditions, where a relatively low irradiance was applied. Seeds were divided into three groups: PP – positively photoblastic (germinating well in the light, not germinating in the dark), NP – negatively photoblastic (germinating well in the dark, not germinating even under low irradiance), I – indifferent (germinating well both in the dark and in the light) (Barton, 1965; Evenari, 1965).

Plants receive light signals by means of specialized photoreceptors. The most important photoreceptors of higher plants include: phytochromes absorbing far red/red light (FR/R), cryptochromes (Cashmore et al., 1999), and phototropins (Briggs and Huala, 1999; Briggs and Olney, 2001) absorbing blue/ultra violet light from the range of A (B/UV-A) and LOV domains: light (L), oxygen (O), voltage (V) (Devlin et al., 2007). Photoreceptors inform the plant about the surrounding light environment in a very precise way, which is used to optimize the photosynthetic process and to shape the morphology of plants. Seed reactions to light are primarily triggered by the activity of the phytochrome, which responds to the solar radiation intensity and length of the day. The phytochrome mechanism, formed in the course of evolution, is used, among others to optimize reproduction. Thus, it serves as the “observer” of environmental changes, determining the initiation or the termination of the germination of seeds depending on the radiation conditions.

Phytochrome is a molecule occurring in two forms, P_r and P_{fr}, which changes depending on the kind of its treatment with the red or far red radiation. The P_r form absorbs the red light (600–700 nm) with a maximum of 655–665 nm, while P_{fr} – far red (700–750 nm) with a maximum of 725–735 nm. In this way, the FR/R ratio reflects the photostationary state of the phytochrome (P_{fr}/P_{tot}) (Quail et al., 1995; Smith, 1995). The P_r and P_{fr} concentrations depend on the spectral composition of radiation (Smith and Holmes, 1977).

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Light fluence rate gives the radiation incident on a sphere of unit cross section, and expressed per unit surface area (of the sphere) and per unit time (Bjorn, 2010). The corresponding time integrated quantity is light fluence. Depending on the amount of energy involved in the transformation of phytochrome, generally three types of reactions can be distinguished: Very Low Fluence Response – VLFR, Low Fluence Response – LFR, and High Irradiance Response – HIR (Mancinelli, 1994). In VLFR and HIR, the level of P_{fr} response is shaped by phytochrome A, while in LFR – by phytochrome B (Casal et al., 1997; Quail et al., 1995; Smith and Holmes, 1977).

Depending on the response to the daylength, seeds were distinguished into the short-day, including *Lepidium, Epilobium cephalostigma* (Isikawa, 1954), *Tsuga canadensis* (Olson and Nienstaedt, 1957) and long-day ones, incl. *Betula pubescens* (Black on Wareing, 1954), *Begonia evansiana* (Nagao et al., 1959).

Phytochrome is encoded by the five genes (*PHYA, PHYB, PHYC, PHYD* and *PHYE*) (Briggs and Olney, 2001; Casal, 2000; Clack et al., 1994; Fankhauser, 2001; Sharrock and Quail, 1989; Whitelam and Devlin, 1997).

Temperature plays an important role in seed germination beside modulating phytochrome. Although it does not directly affect the reconfiguration of the phytochrome, it significantly modifies the effects of radiation (Probert, 1992; Probert et al., 1987; Probert and Smith, 1986).

The inhibited germination of seeds exposed to sunlight was recorded in the indifferent seeds of *Lactuca sativa* (Doroszewski, 1989; Górski and Górska, 1979) as well as photoblastic positive *Elsholtzia Patrini, Rumex crispus* (Doroszewski, 1989).

Rumex crispus L. is one of the most common uncultivated plants in the world. It occurs in numerous habitats, i.e. in wasteland, roadsides, lanes, balks, meadows, pastures and arable land, with the exception of the most acidic soils. It prefers moisturized, heavy, clay, and nitrogen-rich soils (Pye, 2008). The aim of the work was to study the effect of solar radiation on seeds of *R. crispus* L. (belonging to the PP – positively photoblastic) germinated under natural conditions, as well as to construct a model describing the quantitative relationship between irradiance and the germination of these seeds. Assuming that the reactions of seeds to light are an expression of adaptation to specific environmental conditions during the phylogenies, it should be assumed that these reactions can be best understood in natural conditions. As for their ecological significance, it is doubtful that it can be fully understood on basis of laboratory results. The research provided new knowledge on the biology of seed germination of *R. crispus* L.

MATERIALS AND METHODS

The research material were seeds of *Rumex crispus* L. obtained directly from the pastures in the vicinity of Puławy, Poland. Seed species affiliation was determined by an experienced qualified botanist according to Szafer key (1988), and deposited in a cold store of IUNG-PIB. They were kept in the dark at a temperature of 4 ^{o}C and humidity at 30%. The study, conducted in 2015, was divided into two series. The first series of tests was aimed to verify the viability of seeds. For this purpose, 30 seeds were sown on Petri dishes prepared in advance (lined with three layers of filter paper and moistened with distilled water) having a diameter of 9 cm in 10 repetitions. The seeds germinated at room temperature. The mean number of germinated seeds was 99.7% and standard deviation 0.9.

The main part of the research was carried out in the second series, the aim of which was to test solar radiation as a factor regulating seed germination. In this series in 43 repetitions, 30 seeds were sown in Petri dishes (with a diameter of 9 cm) lined with three layers of flannel and the two layers of filter paper, and moistened with distilled water to prevent seed drying.

The dishes with seeds for a certain number of hours per day were exposed to natural conditions (natural lighting in day), for the rest of the time they were transferred to light proof boxes (night). The length of the photoperiod was:

a) 24 hours (on average for 15 hours with natural solar radiation + 9 hours in night) – dishes with seeds were kept in this treatment day with natural solar radiation and 9 hours in night
b) 12 hours – dishes with the seeds were exposed to sunlight from 7AM and transferred to light-proof boxes at 7 PM.
c) 7 hours – dishes with seeds exposed to light from 7 AM to 2 PM.

The seeds plates (44 plates) were also exposed to the scattered radiation – they were kept for 24 hours in a wooden box which allowed only 20% of the total radiation. Germination of these seeds (kept in a wooden box) was at a satisfactory level of 99.7%, however, the paper describes germination of seeds exposed to total solar radiation. This was a comparison to seeds sown and remaining in complete darkness where complete germination inhibition occurred.

The experiments were carried out in Puławy, Poland ($\varphi = 51^{o}25'$, $\lambda = 21^{o}58'$) in the period April–September.

The values of total, diffused, direct radiation were obtained using a pyranometer the Moll-Gorczyński manufactured by Kipp and Zonen company in Delft, Holland (Podogrocki, 1993) with a continuous registration. Temperature measurements were performed in all the treatments using electric resistors placed in the dishes enclosed only by a clear glass lid, similarly as seeds.

The values of seed germination are shown as probits (Finney, 1952). The advantage of the probit scale is the possibility to accurately present the reactions occurring in seeds under extreme conditions, by significantly increasing the distance between successive points at the beginning and at the end of the scale. The probit scale does not have the values of 0 or 100 (which are rarely found in nature anyway). If germination was zero, it was replaced with 0.1%, and if it was a hundred percent, it was shown as 99.9%. The dependence of germination on irradiance, temperature, photoperiod, is presented by the curves plotted on the basis of the empirical formula obtained using stepwise multiple regression method. Aggregating the independent variables was carried out within such a number of days after sowing which gave the highest coefficient of determination of the searched compounds.

The calculations, which took into account the radiation, were performed using logarithm of the irradiance, which better presents germination under very low levels of irradiance, where changes in the seed germination are particularly high. In order to use the results obtained during the experiments performed in the dark, up to the level of irradiance in kJ cm^{-2} 120 h^{-1}, the constant value of “0.1” was added before logarithming. The values of irradiance taking part in the interaction, were used for calculating in the version without the logarithm.

A temperature that was too low inhibited seed germination in all the treatments. For this reason, only the experiments with thermal conditions sufficient for germination were taken into account in this study. After analyzing 44 experiments, a thermal threshold was determined with an average temperature of 6 °C (in 5 days after seeding). The results of experiments with a temperature below 6 °C were not taken into account. After such a selection, the germination of seeds of 132 plates were taken for data analyses. The calculations determining the impact of direct and total radiation on seed germination were performed. Due to the fact that higher coefficients of determination were obtained using the values of total radiation, the results of our calculations show the data for this type of radiation.

In Figures from 1a to 2b the areas outside the borders (drawn with a curves dotted line) of the actual conditions in the experiments, where the image of correlations was created based on an extrapolation, are shown in gray.

RESULTS AND DISCUSSION

The biggest differences in germination among individual treatments occurred in five days after seed sowing. The largest effect (the largest coefficient of determination) of the impact of solar-thermal conditions on seed germination was visible with a one-day delay. The activity of factors from the five-day period was the most visible in six days after seed exposure.

Seed germination was dependent on air temperature, solar radiation and the length of the day, hence this phenomenon can be explained in a satisfactory manner only by a complex exposure to all the most important factors.

Using the method of stepwise multiple regression, we obtained the following correlations between germination conditions and thermal-solar conditions for the seeds of *R. crispus* L.:

$$y = 2.23 + 0.577\,t - 0.000318\,t^3 + 1.61\ln(E+0.1) +$$
$$+ 0.00723\,f^2 - 0.000788\,t \cdot E - 00496\,f\,E$$
$$R^2 = 0.63$$

where:
y – germination (in probits)
t – mean temperature of the 5-day period (in °C)
f – mean photoperiod of the 5-day period (in hours)
E – radiation (in kJ cm^{-2} 120 h^{-1})
ln (E+0.1) – logarithm of natural radiation (in kJ cm^{-2} 120 h^{-1})

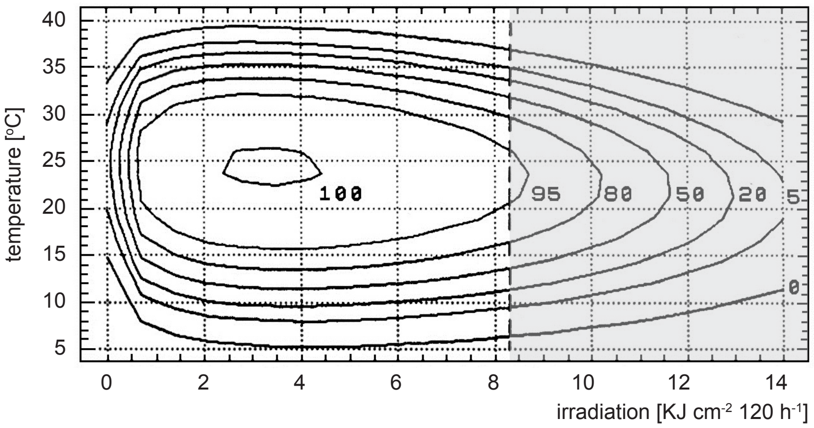
Using the above formula graphs were drawn to show the germination of the seeds of *R. crispus* L. depending on light, temperature and photoperiod.

Under low light, the seeds of *R. crispus* responded to the increase of radiation with a rapid increase of germination (Figure 1 a–c). Maximum germination of this species overlapped with a very wide range of light, especially at the 7-hour day (Figure 1a). Under favorable thermal conditions (20–25 °C), we did not observe the decrease of germination under the increased radiation, as opposed to the treatments with a 12- or 15-hour photoperiod (Figure 1b, 1c) which showed a rapid germination decrease, especially the 15-hour treatment. Despite the occurrence of very favorable thermal conditions for germination (20–25° C), at about 13 kJ cm^{-2} 120 h^{-1} at the 12-hour, and about 11 kJ cm^{-2} 120 h^{-1} at the 15-hour day, there was the total inhibition of germination. The graphs in Figure 1 show the existence of a very explicit correlation between the level of seed germination of the seeds of *R. crispus* and temperature. It was found that both low and high temperature inhibits seed germination.

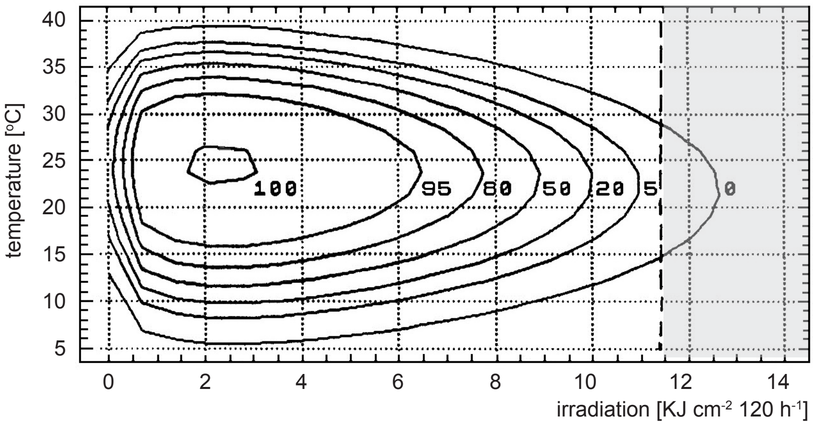
The graphs showed the germination of the seeds of *R. crispus* depending on the radiation and the daylength for the temperature of 15 °C (Figure 2a) and 22 °C (Figure 2b). The shapes of the isolines showing seed germination for both temperature values are very similar, with a significantly higher germination (for the same light conditions, daylength + irradiance), when the temperature was 22 °C. In both cases, under low irradiance, the impact of the photoperiod on the germination of seeds of *R. crispus* was small; but under relatively large irradiance, it was higher (above 5 kJ cm^{-2} 120 h^{-1}). Under very high irradiance and a very long day, there was an interaction between the both factors.

The impact of radiation on the germination of the seeds of *R. crispus*, at the daylength of 7, 12, 15 h under the temperature of 12, 17, or 22 °C is presented in the form of graphs in Figures 3 a–c, whereas the effect of radiation on the germination of the seeds of *R. crispus*, under temperature of 15 and 22 °C at the daylength of 7, 12, or 15 h is shown in Figures 4 a, b. Optimal radiation is about 2 kJ cm^{-2} 120 h^{-1}, but at a short daylength, this value becomes higher (about 4 kJ cm^{-2} 120 h^{-1}).

a **7 hour daylength**



b **12 hour daylength**



c **15 hour daylength**

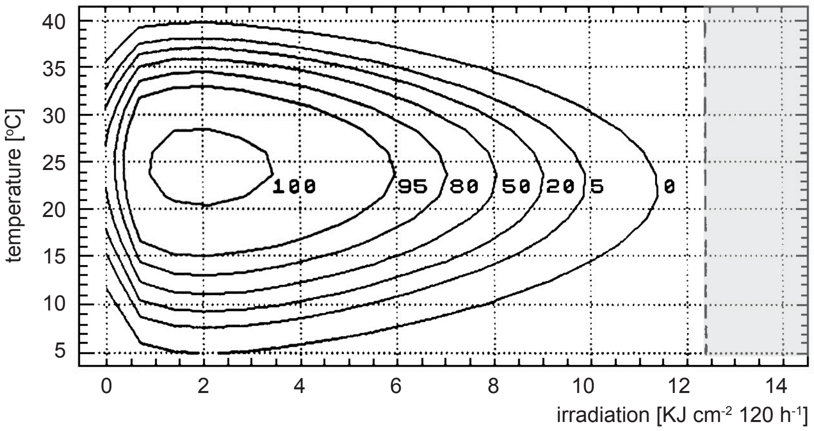
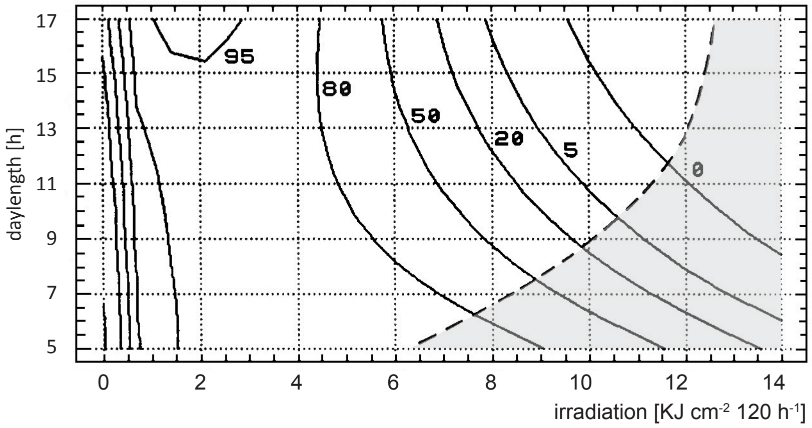


Figure 1. Dependence of germination of *Rumex crispus* seeds on irradiance and temperature (in percentage terms) under the: a) 7 hour daylength, b) 12 hour daylength, c) 15 hour daylength

a **temperature 15 °C**



b **temperature 22° C**

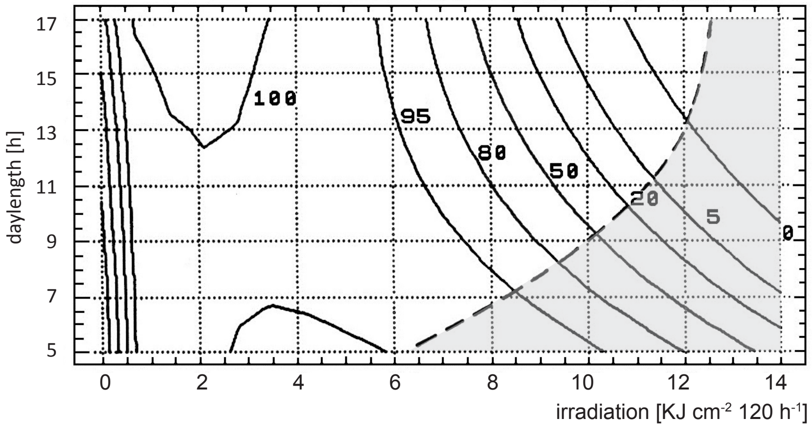


Figure 2. Dependence of germination of *Rumex crispus* seeds on irradiance and photoperiod (in percentage terms) at a) 15 °C and b) 22 °C.

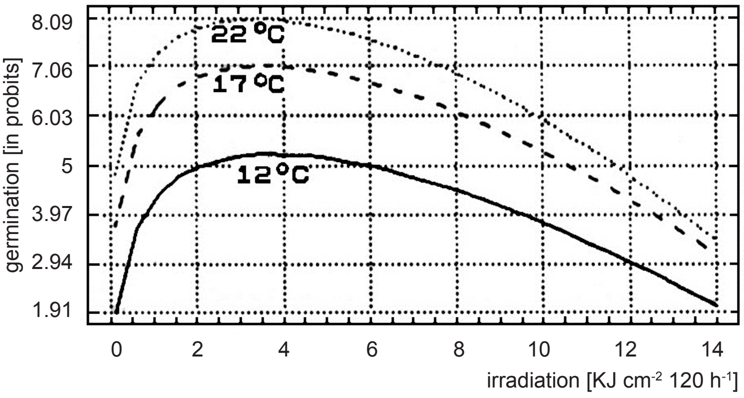
The impact of temperature on the germination of the seeds of *R. crispus* at the day: 7, 12, 15 h for the relatively low: 1 kJ cm^{-2} 120 h^{-1}, average: 6 kJ cm^{-2} 120 h^{-1} and high: 11 kJ cm^{-2} 120 h^{-1} radiation is presented in Figure. 5. Under low and medium irradiance, maximum germination occurred at approx. 25 °C, while under high irradiance (11 kJ cm^{-2} 120 h^{-1}) , at 22–23 °C.

For the temperatures of 15 °C and 22 °C, and the irradiance of 1, 6, and 11 kJ cm^{-2} 120 h^{-1} (Fig. 6a, b), we presented the impact of daylength. For both temperatures, under high (6 kJ) and very high radiation (11 kJ cm^{-2} 120 h^{-1}), the highest germination occurred at the 7-hour photoperiod, while the day elongation contributed to the decrease of the level of germination, which was especially large under irradiance of 11 kJ cm^{-2} 120 h^{-1}. There was a strong correlation between the daylength and radiation. Under low irradiance, germination increased along with the daylength, while under high irradiance, germination decreased.

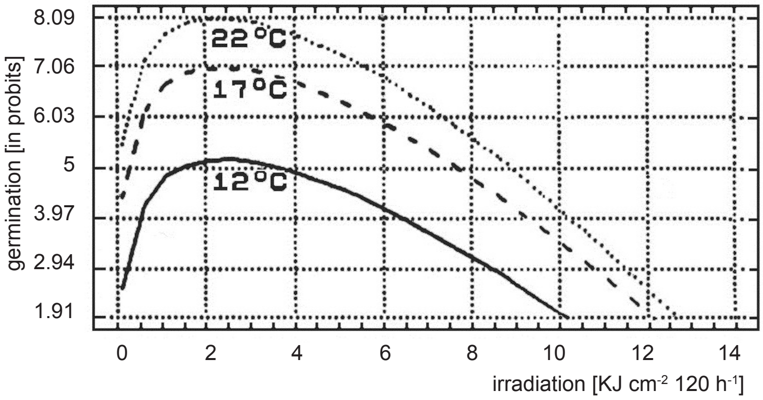
The graphs showing the germination of the seeds of *R. crispus* (Figures 1-6) were provided for the highest differences between treatments. Under the influence of a number of unfavorable conditions (primarily with high radiation), germination was inhibited. In the following days, in which low radiation was noted, the germination inhibition resolved. The highest germination was recorded for the seeds under a 7-hour, lower under 12-hour, while the lowest – under 15-hour natural radiation. After 45 days, the seeds of *R. crispus* under all day exposure germinated 96.2%, under 12-hour exposure – 98.1%, while under 7-hour – 99.9%. In the treatments where the seeds were subjected to all day long dispersed irradiance, the germination was 99.1%.

Undoubtedly, the correlation between seed germination and radiation can be interpreted in the context of environmental adaptation. The inhibition of germination under strong sunlight prevents the growth of seedlings, which would otherwise immediately wither from exposure to the

a **7 hour daylength**



b **12 hour daylength**



c **15 hour daylength**

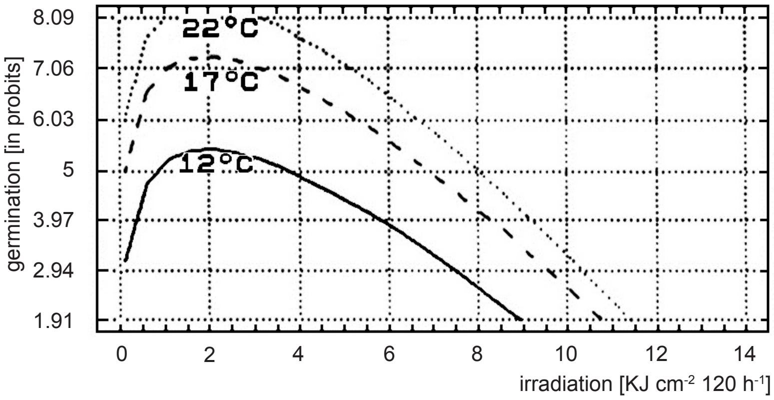


Figure 3. Dependence of germination of *Rumex crispus* seeds on irradiance and temperature (12, 17 and 22 ^{o}C) under the: a) 7 hour daylength, b) 12 hour daylength, c) 15 hour daylength

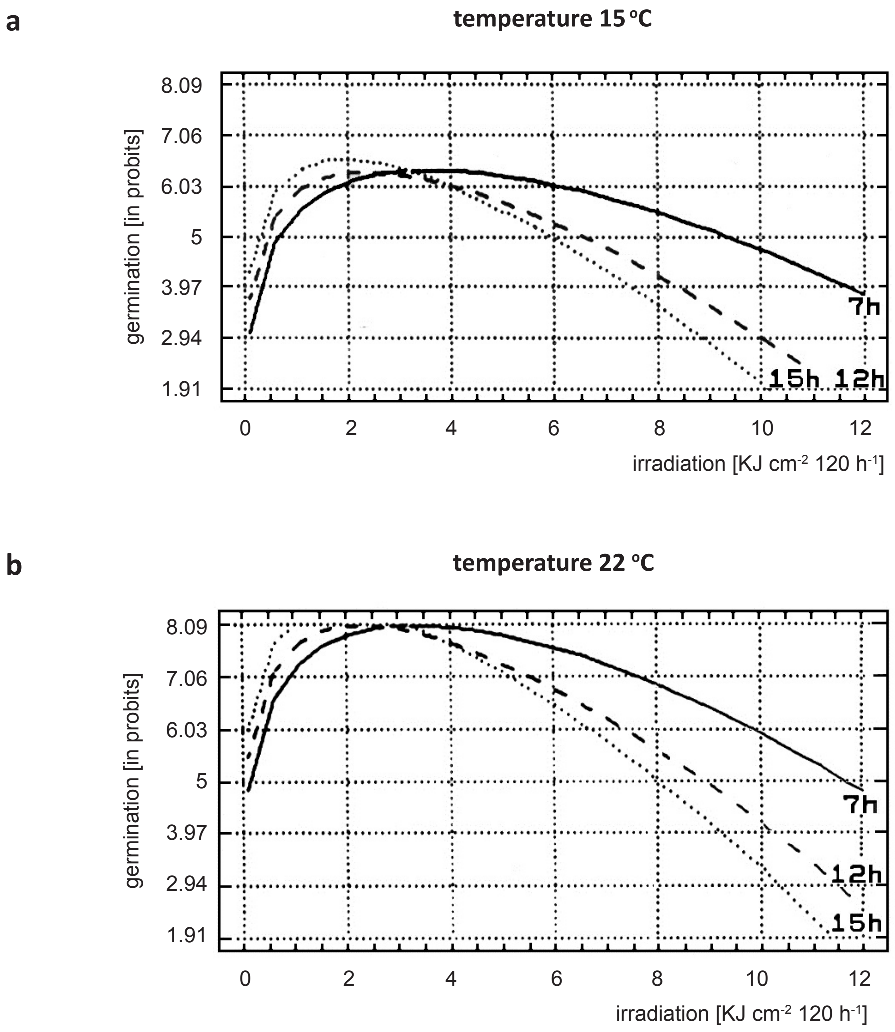


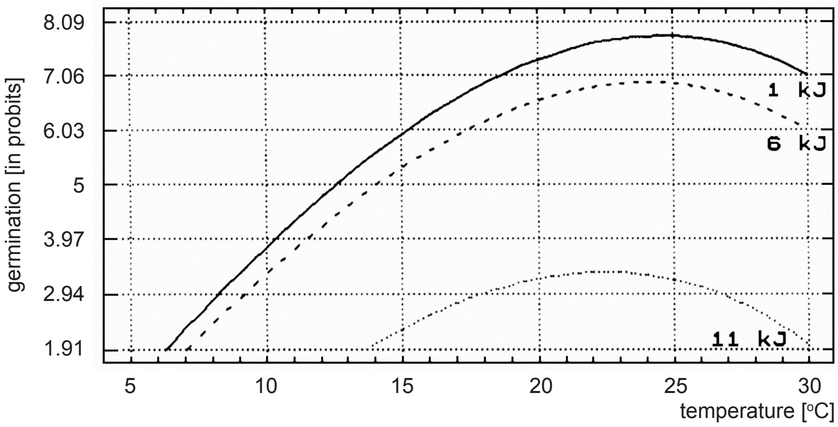
Figure 4. Dependence of germination of *Rumex crispus* seeds on irradiance and photoperiods of 7, 12 and 15 hours of daylenth and temperature a) 15 °C and b) 22 °C

fast-drying topsoil. In contrast, low irradiance "allows" the germination process, because under these conditions, the emerged seedlings have a higher chance of survival. Research conducted by Dechaine et al. (2009) indicates that phytochromes regulate seed germination reactions to light and temperature indicators during seed maturation in different ways. An experiment conducted by Hartmann (2016) shows that plants are able to modify the irradiance of the light spectrum by selective filtering by assimilation organs.

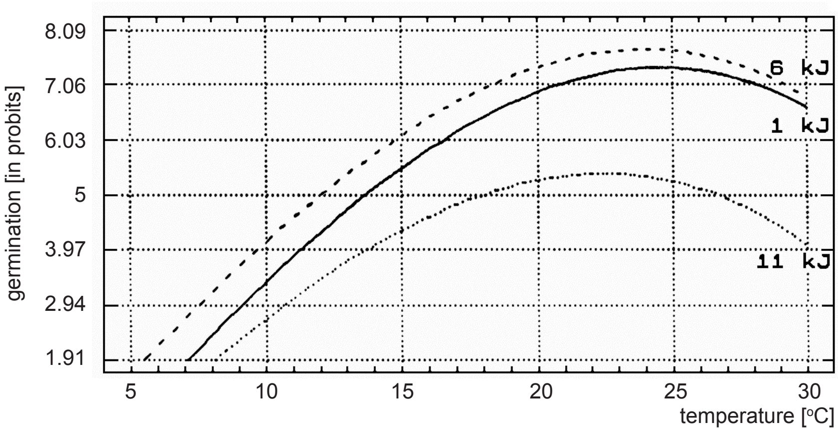
The inhibition of germination in the full light can be, probably, due to the adaptation to the changing moisture conditions (Górski and Górska, 1979). The seeds lying on the ground may be temporarily wet (for example, after a fleeting rain) and could geminate under the appropriate temperature. High radiation indicates that the seedling is in danger of drying out before the roots reach deeper layers of soil. This interpretation is also confirmed by the fact that in the high-energy phytochrome transformation HIR, the maximum activity occurs under approx. 720 nm, which is exactly in the alpha band of water vapor absorption (Doroszewski et al., 2015; Górski, 1973). Hence, irradiance in this band is particularly strong in dry air, when evapotranspiration is high, and the probability of precipitation is small.

The ecological role of seed response to light in natural conditions, and in particular, seed photoblasticity looks largely different than it was suggested by the results of laboratory experiments, typically conducted under relatively low irradiance. The seeds of *R. crispus* turned out to

a **7 hour daylength**



b **12 hour daylength**



c **15 hour daylength**

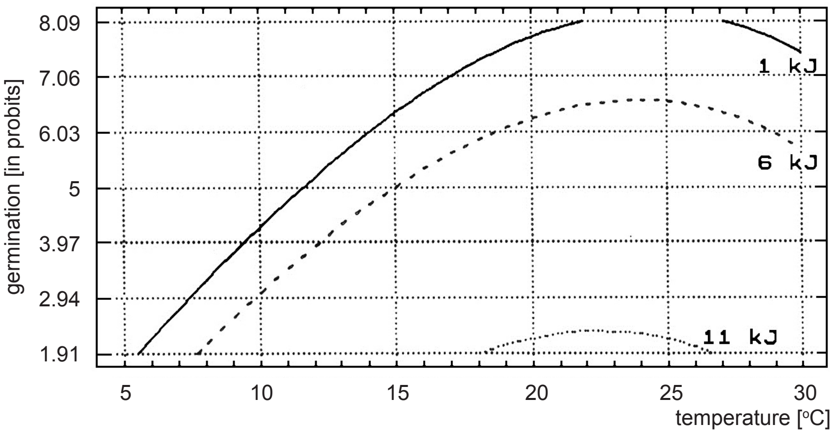


Figure 5. Dependence of germination of *Rumex crispus* seeds on temperature and irradiance (1, 6 and 11 kJ cm^{-2} 120 h^{-1}) under the: a) 7 hour daylength, b) 12 hour daylength, c) 15 hour daylength.

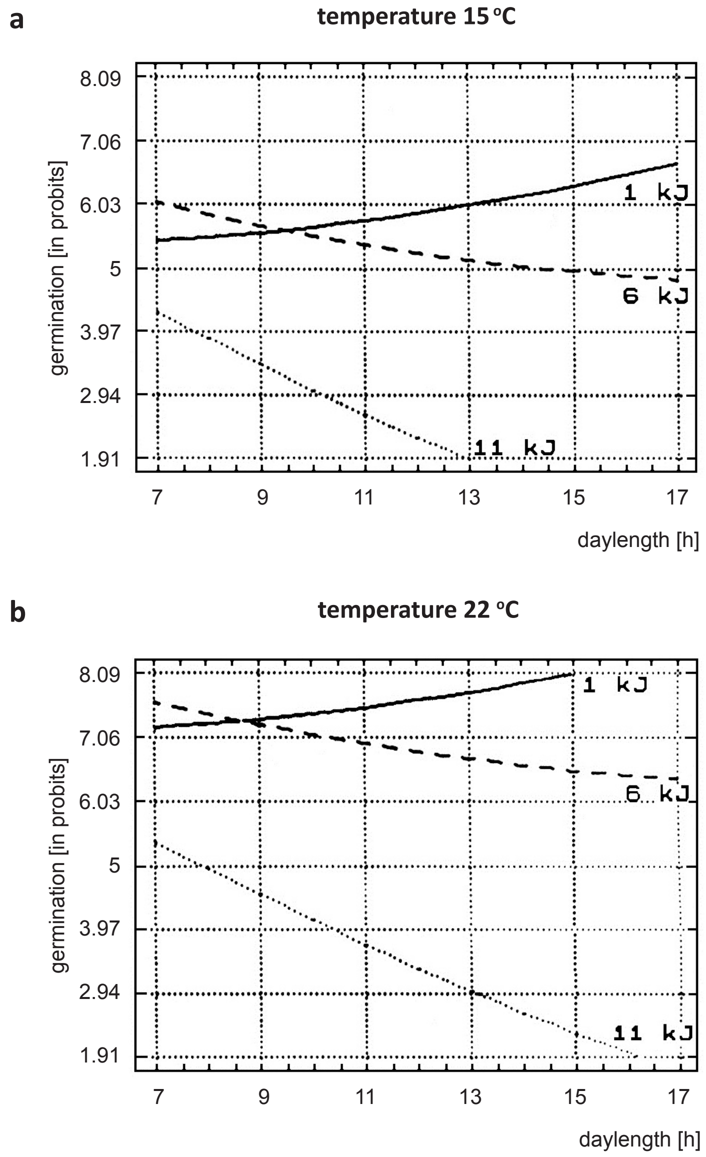


Figure 6. Dependence of germination of *R. crispus* seeds on length of the day and irradiance (1, 6 and 11 kJ cm^{-2} 120 h^{-1}) at temperature of: a) 15 °C and b) 22 °C.

germinate well under such irradiance (in the laboratory), so they were considered to be photoblastic positive. Under strong solar radiation, there was a significant inhibition of germination so the seeds act as photoblastic negative for which irradiance is the limiting factor in seed germination.

It turns out that seed germination under natural conditions is governed by the principle of non monotonicity of ecological functions, which states that there is an optimum range of action of a given factor, limited on both sides; where both deficit and excess bring negative effects. As in the case of photosynthesis (Czarnowski, 1991) and in photomorphogenetic regulation of seed germination, we can identify an optimal range of irradiance, supported by a background, including photoperiod and temperature. It turns out that also the excess light is a significant limiting factor in the seed germination of *R. crispus*.

The studies in open locations showed that the inhibition of seed germination under full solar radiation is dependent on the light intensity and photoperiod, but it cannot be calculated using a simple law of multiplication ($i \cdot t$ = const) as in the case of low-energy phytochrome transformation LFR, known as the Bunsen-Roscoe law, where: i – radiation intensity, and t – exposure time (Mohr, 1972; Smith, 1975).

The obtained results of studies on seed germination indicate that under natural radiation both low- and high-energy responses (LFR and HIR) are occurring. The correlations between the LFR and HIR were explained by the concept of Kendrick and Spruit (1977), which assumed the formation of the physiologically inactive forms of phytochrome under strong light conditions. Currently, a view prevails that phytochrome A (phyA) is involved in the high-energy responses (HIR), also with far red light, while phytochrome B (phyB) is engaged in the classic photoreversible FR/R reactions (Smith, 1995).

The aim of developing the model, using the method of stepwise regression, to describe the correlations among seed germination, irradiance, photoperiod and temperature, has been achieved. The model describes well the dynamics of changes in the seed germination of *R. crispus* depending on three basic factors that modulate germination in this species. The obtained results indicate that the most important factors in seed germination of *R. crispus* are: irradiance and temperature, while a slightly lower role is played by photoperiod. Batlla and Benech-Arnold (2003, 2005) built models that described the seed germination of *Polygonum aviculare* depending on irradiance and temperature. New models concerning seed germination can be used to, among others, build programs to combat weed infestation based on the knowledge of the plant photoreactions.

CONCLUSIONS

1. Under high irradiance at about 13 kJ cm^{-2} 120 h^{-1} at the 12-hour, and about 11 kJ cm^{-2} 120 h^{-1} at the 15-hour day, seed germination of *R. crispus* is inhibited.
2. Under high irradiance, the seeds of *R. crispus* exhibit short-day reactions.
3. The phytochrome mechanism optimizes seed germination in different environmental conditions.

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