

Spectral composition of the applied radiation as a factor affecting the development, habit and yield of spring barley

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Abstract. The aim of the conducted experiments was to determine the impact of the differentiated composition of spectral radiation on the development of spring barley. The experiment was conducted in laboratory conditions using artificial sources of radiation. The habit of the barley was dependent on the spectral composition of the radiation in the growth chambers in which the red to far-red values were in the range of 0.92-10.0. Barley grown with an increased share of far red light produced decidedly longer internodes and taller shoots than the plants radiated with a smaller amount. The leaves of the barley grown in a high red to far-red ratio were positioned less vertically and the plants formed a more dense canopy than in the chambers with a lower red to far-red ratio. The plants grown in the chamber with a low red to far-red ratio produced a greater mass of stems with ears and a lower mass of infertile stems in comparison with the plants grown in radiation with a lower share of far-red. In summary, in these condition it was found that an increase in the number and mass of grains, in the grain weight to stem weight ratio, in the total mass of straw and plants as well as in an increase in the 1000 grain weight. A low red to far-red ratio is an indicator of the existence of competition but observed differences in barley development and yield showed that in these conditions the plants demonstrated adaptive responses to shading.

Keywords: growth chambers, far red and red radiation, shading, plant habit, grain

INTRODUCTION

Solar radiation plays a major role in the plant world as a source of energy and environmental information. The spectral composition of radiation fulfills an important function in plant signalling process during plant development. Changes

allow plants to detect information concerning the potential competition posed by neighbouring plants and indicate the optimal strategy to adopt in order to overcome it. One such strategy is the creation of some mechanisms to provide information about impending shading and preparing the appropriate response, this will allow the plant to survive in the unfavourable conditions. In the case of the transmission of the radiation and its reflection by the neighbouring plants, a decrease in the R/FR ratio value may be observed (Smith and Whitelam, 1997; Smith, 2000). Radiation from the range of far red (FR), reflected from the neighbouring plants may cause a response known as “shade avoidance syndrome” (SAS) (Smith, 1982; Smith and Whitelam, 1997; Ballaré, 1999) and modify the vegetative development of the plant. The reception of light signals by plants is possible due to photoreceptors such as phytohormones (which participate in photo morphogenesis), crypto hormones and LOV-domains (light, oxygen, tension) (Briggs and Olney, 2001; Casal, 2000; Devlin *et al.*, 2007; Fankhauser, 2001). One such phytohormone is phytochrome A (phyA), which responds to changes in: 1) the intensity of radiation which is affected by the presence of neighbouring plants (Yanovsky *et al.*, 1998), and 2) the photoperiod. It promotes the flowering of plants after irradiation with FR (Lin, 2000) and does not respond to radiation from the range of R (Neff and Chory, 1998). Photo-morphogenetic changes due to shading include: an acceleration of development, an elongation of shoots, the

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reduction of tillering and the number of branches, a lower area and dry matter of leaves (Franklin and Whitelam, 2005; Franklin, 2008; Pierik *et al.*, 2004; Smith, 1992, 1995). One characteristic morphological response to radiation with a low R/FR ratio is the elongation of the shoot, hypocotyl, internodes (Robin *et al.*, 1994), petioles (Pierik *et al.*, 2009), leaves and cotyledons (Robin *et al.*, 1994) as well as the reduction of the leaf to shoot dry mass ratio (Casal *et al.*, 1987a). According to Casal *et al.* (1990) radiation with a low R/FR ratio value inhibits the tillering of grasses. In the dense stands the reduction of branches is observed, there is also an increase in plant height and the development of leaves in the upper levels of the stand. The plant evaluates the presence of a neighbour by monitoring the signal reflected from the green tissues, this is characterized by the greater share of FR in relation to R. The changes in FR intensity are correlated with the density and proximity of the neighbouring plants (Ballaré *et al.*, 1997; Ballaré *et al.*, 1987). Radiation in the field is modified mainly by absorption and reflection, which are dependent on the chlorophyll concentration in plant organs. A decrease in the R/FR ratio in the field is associated with an increase in the density of green plants (Casal and Smith, 1989). Plants determine their current degree of shading through the phytochrome perception of the R/FR ratio. Experiments conducted with *Chenopodium album*, *Datura ferox* and *Sinapis album* showed that changes in the R/FR ratio are perceived in the early developmental phases (just before shading) and a decrease in this ratio indicates upcoming competition (Ballaré *et al.*, 1987). A relatively small increase in FR intensity causes a greater elongation growth and even a negative phototropic response (*i.e.* bending from neighbour plants). However, even small changes in the R/FR ratio cause considerable changes in the photomorphogenesis of plants (Brown *et al.*, 1995).

Combinations of different radiation sources cause diverse spectral compositions and various photomorphogenic effects. The additional participation of FR as a component of photosynthetic active radiation (PAR) causes the affected plants to be taller with a lower number of leaves and a decrease in their area as well as a lower leaves-to-shoot dry matter ratio (Brown *et al.*, 1995). Apart from the photomorphogenic effects caused by radiation in the FR range, a significant role in photo-morphogenesis is also played by radiation in the white range (*e.g.* fluorescent lamps). This radiation causes the area of the leaves to be lower in comparison with the leaves of plants receiving radiation in the yellow and red range which is emitted by sodium lamps (Brown *et al.*, 1995). A lower area of leaves was also the result due to white light with the addition of R in relation to radiation within the blue light range (Frąszczak and Kula-Maximenko, 2021).

In the early phase of plant development the mutual shading of plants is a relatively minor consideration whereas the R/FR ratio on the horizontal and the open area is high. The enlargement of the FR share indicates the presence

of neighbouring plants. As the plants grow, the reflected radiation within the FR range increases and the R/FR ratio decreases. These “early warnings” are the signals sent by the neighbours (a decreased R/FR ratio) and received by a phytochrome which is located mainly in the tissues of the coleoptile. This phenomenon was observed in the etiolated oat seedlings by Verbelen *et al.* (1982). Plants compete with each other, most of all for the best conditions of radiation during ontogenesis. The first phase is the elongation growth of organs which receive the most rapid signals about the plant neighbourhood, *i.e.* about vertically placed shoots, and then about horizontally placed leaves (Ballaré *et al.*, 1987; Libenson *et al.*, 2002). Radiation with a low R/FR ratio causes that the level of FR absorbed by the phytochrome (P_{fr}) is low, and in this way a shading avoidance reaction is triggered, which relies most of all on the promotion of internode lengthening (Casal and Smith, 1989). The growth of the stand causes an increase in the degree of mutual shading, which is expressed as a reduction in the radiation intensity. The low level of radiation which occurs in the blue range is also a factor that increases the shading avoidance response. A greater plant density increases the degree of shading and decreases the photosynthetic active radiation – PAR (Holmes and Smith, 1977a, b).

Shoots of barley, maize and sunflower which were receiving radiation with a decreased R/FR ratio produced a longer main shoot than the plants radiated with higher values of this ratio (Davis and Simmons, 1994a, Kasperbauer and Karlen, 1994; Libenson *et al.*, 2002). Additionally, in the conditions of a decreased R/FR ratio, maize produced shoots with a lower diameter (Kasperbauer and Karlen, 1994). Under the influence of radiation with a lower R/FR ratio, barley developed a lower number of leaves in relation to the plants radiated with a higher R/FR ratio (Davis and Simmons, 1994b). Leaves of barley, wheat, maize, tobacco and fescue treated with an increasing share of FR (lower R/FR ratio) were longer than the plants radiated with a higher R/FR ratio (Davis and Simmons, 1994a, Kasperbauer and Karlen, 1994). However, leaves of maize, tobacco and fescue radiated with a lower R/FR ratio were narrow with a lower area than plants treated with a higher R/FR ratio (Kasperbauer and Karlen, 1994; Wherley *et al.*, 2005).

In controlled conditions it was shown that a lower R/FR ratio can significantly decrease the tillering of fescue (Deregibus *et al.*, 1985) and the branching of clover (Robin *et al.*, 1994). Increasing the sowing density of paspalum (*Paspalum dilatatum*) and ryegrass (*Lolium multiflorum*) causes a considerable reduction in tillering, and also in the number of leaves and the acceleration of flowering, whereas an additional supply of R did not cause the shoot number to increase (Casal *et al.*, 1986). A reduction in tillering at an increased plant density was also observed in some *Gramineae* species, such as wheat (Casal, 1988), barley (Davis and Simmons, 1994b), ryegrass (Casal *et al.*, 1986; 1987b) and fescue (Wherley *et al.*, 2005). However, it is

more complex to make an evaluation of the effect of reduced tillering on plant yield. For instance, the grain yield of sorgo from the branching plants is lower than that from plants with one shoot growing in the dense canopy. This is probably an effect of the large amount of energy used for the production of lateral shoots (Lafarge *et al.*, 2002). The same situation occurred in the experiment with barley where the removal of vegetative shoots improved the yield of grain and straw (Elalaoui *et al.*, 1988). A diverse response was found for rice where high tillering caused a greater yield in comparison to plants with a lower number of shoots (Wu *et al.*, 1998). In most plants SAS causes a decrease in the number of shoots and yield in conditions of high plant density. The way of plant tillering plays also an important role in grass breeding with respect to positive and negative selection, which relies on the limitation (*e.g.* for maize) or on an increase in tillering (*e.g.* for rice) (Fellner *et al.*, 2003; Kebrom and Brutnell, 2007). Doust *et al.* (2004) found that among the various species of grasses many develop multiple mechanisms of tillering regulation which are tolerant of shading resulting from the closeness of the plants in the stand.

Another spectacular response of SAS is the induction of flowering, this is a complex process which integrates external factors, *i.e.* the temperature and the photoperiod with gibberellins as endogenic regulators of the growth and development of plants. According to Thomas (2006) a low R/FR ratio induces the acceleration of plant flowering. Moreover, a decrease in this ratio of radiation causes an increase in the concentration of endogenic plant hormones, *i.e.* gibberellins and auxins, which led to an increase in their activity and contributed to the lengthening of the internodes (Vandenbussche *et al.*, 2005; Kurepin *et al.*, 2007).

The main aim of the studies conducted was the determination of the impact of the spectral composition of the radiation, which was differentiated in the range of R and FR (R/FR), on the growth and development of spring barley cultivated under controlled conditions.

MATERIAL AND METHODS

The experiments were conducted in the Institute of Soil Science and Plant Cultivation – State Research Institute (IUNG-PIB) in Puławy, Poland. The plants were grown in four climatic chambers (HERAEUS, The Netherlands), where artificial sources of light were used. In each chamber a different spectral composition of radiation was used. Bulbs and fluorescent lamps (Philips, The Netherlands) as well as halogen lamps of the PAR30 rosé type (Paulmann, Germany) (Table 1) were used to radiate the plants.

With the aim of obtaining an adequate spectral composition of radiation spectro-radiometric measurements were used, which were made at a 20 cm distance from the source of light. The temperature and humidity of the air as well as the length of the simulated day and night were the same in all chambers. The cycle of day and night which occurs under

Table 1. Sources of the radiation applied in growth chamber tests

| Growth chamber | Type and source of radiation | Distance between the plant and the source of radiation (cm) |
|----------------|--|---|
| A | 20 fluorescent lamps (58 W) – Philips | 55 |
| B | 20 fluorescent lamps (58 W) – Philips + four light bulbs (60 W) – Philips | 65 |
| C | 18 fluorescent lamps (58 W) – Philips + 12 light bulbs (75 W) – Paulmann | 55 45 |
| D | 18 fluorescent lamps (58 W) – Philips + 12 light bulbs (75 W) – Paulmann | 45 35 |

natural conditions was maintained in these studies. These data originated from the weather station of Institute of Soil Science and Plant Cultivation – State Research Institute in Puławy where agrometeorological data concerning the immediate locality are collected every day. The experiments were started under the simulated conditions of sunrise and sunset found for Puławy (51°24'46"N, 21°58'00"E) on the 26th of March, *i.e.* in the optimal time period to sow spring barley (Noworolnik, 2014) when the length of day/night amounted to 12 h and 30 min/11 h and 30 min. In mid-April these values amounted 13 h and 48 min/10 h and 12 min and in mid-May 15 h and 33 min/8 h and 27 min. For the longest day of year – 21st of June, the length of the day/night amounted to 16 h and 38 min/7 h and 22 min and at the end of the vegetation period (July) it reached 15 h and 30 min/8 h and 30 min. During the whole period of this experiment, the air temperature and humidity in the chambers changed with respect to the temperature and humidity occurring under natural conditions in Puławy in the months of the year following March 26. At the beginning of the experiment the mean day/night temperature amounted to 7.5/2.5°C, while in April it was 12/4°C, in May it was 19.4/7.8°C, in June it was 24.0/10.0°C, and in July it amounted to 25.9/11.3°C. Whereas the mean day/night humidity in March, April, May, June and July amounted to 64/81, 56/75, 54/76, 57/77 and 58/79%, respectively.

The spectral composition of the radiation originating from a different source was measured with the use of an LI-1800 spectrometer (Li-COR, USA) working in the range of 350-1100 nm, with a half width of 4 nm. The fluorescent lamps (growth chamber A) which emitted radiation in the photosynthetic active range (400-700 nm) were highlighted by three main and three lower maxima. They covered the following ranges (nm): violet-blue (430-440), green-yellow (540-560), orange (610-620), blue-green

(480-490), yellow (580-590) and red (630) (Doroszewski *et al.*, 2020). The spectral composition of the Philips bulb and the Paulmann halogen lamp shows the significant contribution made by longwave radiation. These sources of radiation are characterized by an increase in irradiation as the wavelength increases from the violet range to near infrared (Doroszewski *et al.*, 2020) (Fig. 1a,b).

By using the appropriate well-matched set of bulbs and fluorescent lamps as well as placing the plants at various distances from the source of radiation, various combinations of radiation exposure were obtained for each chamber (Fig. 1). The same PAR ($300 \mu\text{mol m}^{-2} \text{s}^{-1}$) was obtained in all chambers and therefore the distance between the tops of the plants and the source of light was different. Maxima in the form of peaks originating from fluorescent lamps in chambers C and D were considerably lower than in chambers A and B.

The integrated values of the radiation in the selected spectral ranges used in the growth chambers are presented in the Table 2. Radiation with a wavelength lower than 400 nm was similar in all chambers but certain differences occurred for radiation with a wavelength higher than 400 nm. The highest radiation wavelengths in the spectral ranges 400-499 and 500-599 nm occurred in chambers A and B, respectively while the plants in chambers C and D were exposed to slightly lower wavelengths. As the wavelength increases above 600 nm, the differences in the radiation between the particular growth chambers became greater and greater. The lowest radiation wavelength occurred in chamber A, while the wavelengths were longer in chambers

Table 2. Characteristics of the radiation in selected spectral ranges of the growth chambers

| Range of radiation | Integrated value ($\mu\text{mol m}^{-2} \text{s}^{-1}$) | | | |
|--------------------|---|-----|-----|------|
| | Chamber | | | |
| | A | B | C | D |
| 350-399 | 2 | 2 | 2 | 2 |
| 400-499 | 44 | 40 | 8 | 36 |
| 500-599 | 118 | 128 | 105 | 105 |
| 600-699 | 138 | 140 | 152 | 159 |
| 700-799 | 23 | 41 | 101 | 145 |
| 800-899 | 35 | 43 | 165 | 249 |
| 900-999 | 1 | 42 | 185 | 263 |
| 1000-1099 | 4 | 53 | 215 | 306 |
| 400-700 (PAR) | 300 | 308 | 295 | 300 |
| 700-1100 | 64 | 181 | 677 | 973 |
| 350-1100 | 365 | 489 | 963 | 1265 |

B, C and D, respectively. Therefore, the maximal differences occurred between the A and D chambers, which in the range of 1 000-1 099 nm amounted $302 \mu\text{mol m}^{-2} \text{s}^{-1}$.

In order to obtain a similar amount of Photosynthetically Active Radiation – PAR (400-700 nm) reaching the plants in the four aforementioned growth chambers (the photon flux density of PAR amounted to approximately $300 \mu\text{mol m}^{-2} \text{s}^{-1}$), different lamps and bulbs were used in our experiment, *i.e.* fluorescent lamps, bulbs and lamps

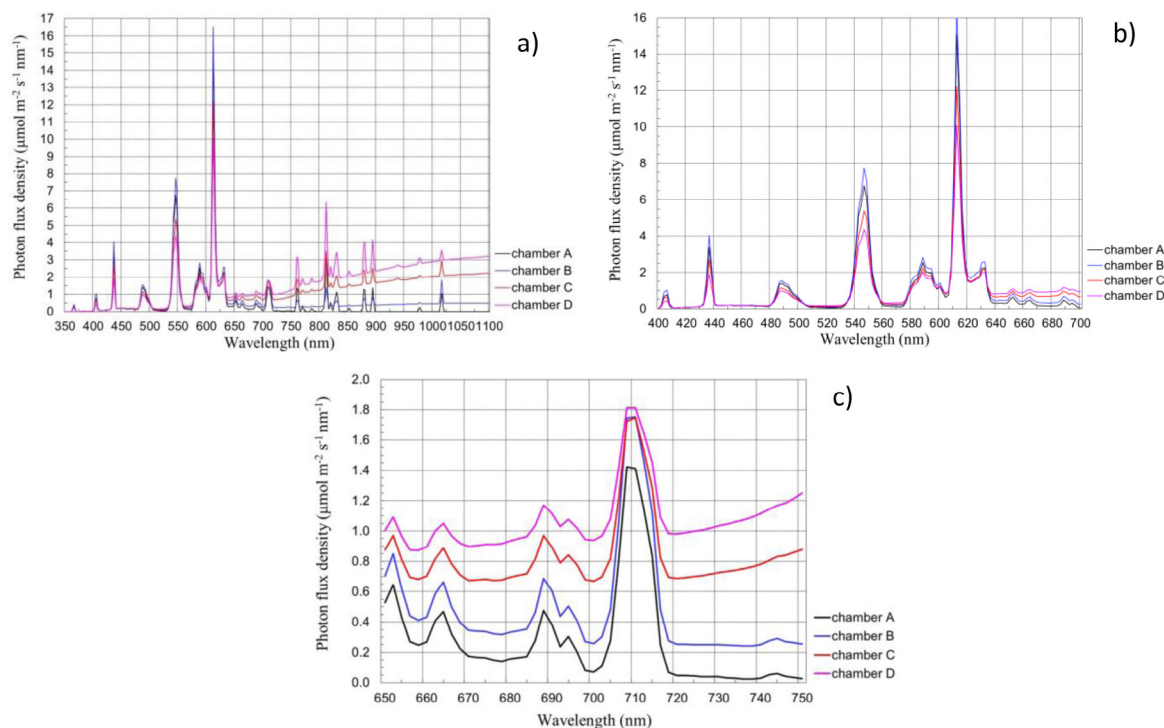


Fig. 1. Spectral composition of the radiation: a) in growth chambers used in the experiment with spring barley, b) in the photosynthetic active range used in the growth chambers, c) in the growth chambers in the range of red (R) and far red (FR).

(Table 1). Because our aim was to obtain the same PAR in all chambers (*i.e.* $300 \mu\text{mol m}^{-2} \text{s}^{-1}$), the distance between the top of the plant and the source of the light (lamps and bulbs) was different (it ranged from 35 to 65 cm) (Table 1). This arrangement was maintained during the growth of the plants, *i.e.* the lamps and bulbs were placed at a higher level relative to the pots to maintain the assumed distance in each chamber and also to maintain the same PAR value. The spectral characteristics of the photosynthetically active radiation in each chamber is presented on the Fig. 1b.

The use of differentiated sources of radiation resulted in very large differences occurring in the radiation wavelength size in the range of 700-1100 nm, with a considerable portion of the radiation in the near infrared (780-1400 nm). The highest intensity of radiation in this range most definitely occurred in chamber D and the lowest in chambers A and B.

Radiation in the range of 620-699 and 700-759 nm was decidedly lower in chamber A while it was greater in chambers B, C and D. Radiation in the red and in the far red range occurred in chamber A, it was about 2 and almost 5 times lower than in the chamber D, respectively. This difference was caused by the very low emission of fluorescent lamps in these ranges of radiation and at the same time the very high emission of Paulmann's halogen lamps in the longwave part of the spectrum.

In the conducted studies, the R/FR ratio (650-670/720-740 nm) ranged from 10.0 to 0.92 in the growth chambers (Table 3). These ranges (650-670 nm/720-740 nm) are frequently taken into consideration in the other studies (El-Keblawy *et al.*, 2019; Magagnini *et al.*, 2018). In the radiation range of 650-750 nm, one high peak occurred with a maximum at 710 nm and four lower peaks at approximately 653, 666, 688 and 695 nm (Fig. 1c).

The subject of the research was spring barley *cv.* Rastik which is characterized by a greater protein content and a lower content of fibre in the grain and due to this, it produces a higher quality fodder and it also belongs among the high-yielding varieties with a high degree of genetic resistance to disease. Five seeds were sown in Mitscherlich pots filled with a peat soil substrate produced on the basis of fine, brown high peat and recommended for use as an appropriate soil for plants which do not require an acidic substrate. The influence of the peat soil substrate (pH 5.5-6.5) and the concentration of macro- and microelements was evaluated. According to Noworolnik (2008) spring barley requires soils

with a pH above 5.5 which is encountered in agricultural practice. The germination of the barley was observed and finally, one properly developed seedling was left in each pot. The moisture content of the soil in all of the pots was maintained at the level of 60% of field water capacity. 24 pots were placed in each growth chamber with a specific spectral composition, these were indicated by the letter A, B, C and D, respectively (Table 3, Fig. 1c). The pots containing plants were rearranged within the chamber once a week. The plant growth rate was observed during the ontogenesis phase and its evaluation was based on Haun's scale (1973). The arrangement of the leaves on the plant was characterized with the help of the mean tilt angle values (MTA), which define the mean angle of the leaves and shoot arrangement. An MTA value equal to 0° describes the horizontal position of the leaves and a shoot whereas a value equal to 90° indicates the vertical position. Observations and measurements during growth and plant development were performed in a non-destructive way, whereas the other measurements were made after the plants were harvested. The following, main morphological features of the plants in the pots were measured: the height of the plants, the number of shoots, the length of the shoots and internodes and the length of an ear. The following characteristics of the matured plants were also evaluated: the number and mass of the grains, the mass of the straw and the total mass of the plants. The plants were harvested 135, 147, 152 and 165 days after their emergence in the D, C, B and A growth chamber, respectively.

A statistical analysis included the parameters of growth, development and the barley yield. For the calculation of averages and the significance of the differences between particular parameters, data from the measurements of the plants in the growth chambers are used. The studies were conducted under controlled conditions and therefore, in the statistical analysis each plant was treated as a replication. Every plant in the growth chamber was a replicate – in all there were 24 plants in 1 chamber (1 plant per a pot).

The shoots of plants with various numbers of internodes together with their yield-generating elements were taken into account. The following factors were included in the analysis: the total number of shoots, the fertile and unfertile shoots as well as the generative elements developed on a particular stem such as: the length of the ear, the number of grains, the mass of all grains, the weight of 1000 grains, the mass of the straw, the total mass of the stem and the ratio of the grain weight as compared to the weight of the straw.

The average values of the tested plant characteristics were compared through the application of an analysis of variance with confidence intervals. The means with their confidence intervals are shown in the Figs 2, 4, 5 and 6. If the confidence intervals for the compared pairs of averages overlap with each other then there was a lack of significant difference. In the opposite case – the averages differ significantly ($\alpha < 0.05$). When the F-test is significant, the

Table 3. Values of the R/FR ratio in the radiation ($\mu\text{mol m}^{-2} \text{s}^{-1}$) applied in the growth chambers

| Growth chamber | Value of R/FR ratio (650-670 nm/720-740 nm) |
|----------------|--|
| A | 10.0 |
| B | 2.08 |
| C | 1.02 |
| D | 0.92 |

differences between the averages were tested using the LSD test with $\alpha = 0.05$. The lengths of these intervals are varied – they depend on the number and standard deviation.

The average values of the tested features of plants were compared with the use of the STATGRAPHICS Plus program, ver. 2.1 for Windows, with the use of Multiple Range Tests.

RESULTS

The barley that was grown in growth chambers C and D with a low R/FR ratio (1.02 and 0.92, respectively) showed a considerably faster development as measured by Haun's scale (Haun, 1973) than the plants grown in chambers A and B, where this ratio amounted 10.0 and 2.08, respectively (Fig. 2a). The differences in the spectral composition of the

radiation, and especially in the R/FR ratio between growth chambers C and D were relatively small and amounted 0.1. However, the development of the plants in chamber D was accelerated by about 1-2 days. The difference between plant development in chambers A and B and the plants from chamber D amounted to between 5 and 50 days. There was a particularly significant difference in the heading stage (indicated by the number 9 according to Haun's scale) (Haun, 1973), when the peduncle of the plants in growth chambers A and B developed very poorly or failed to develop at all, as opposed to the plants grown in chambers C and D.

Although the R/FR ratio for the radiation applied in chamber A was almost 5 times higher than in chamber B, this factor not cause any differences in the development of the plants grown in these chambers.

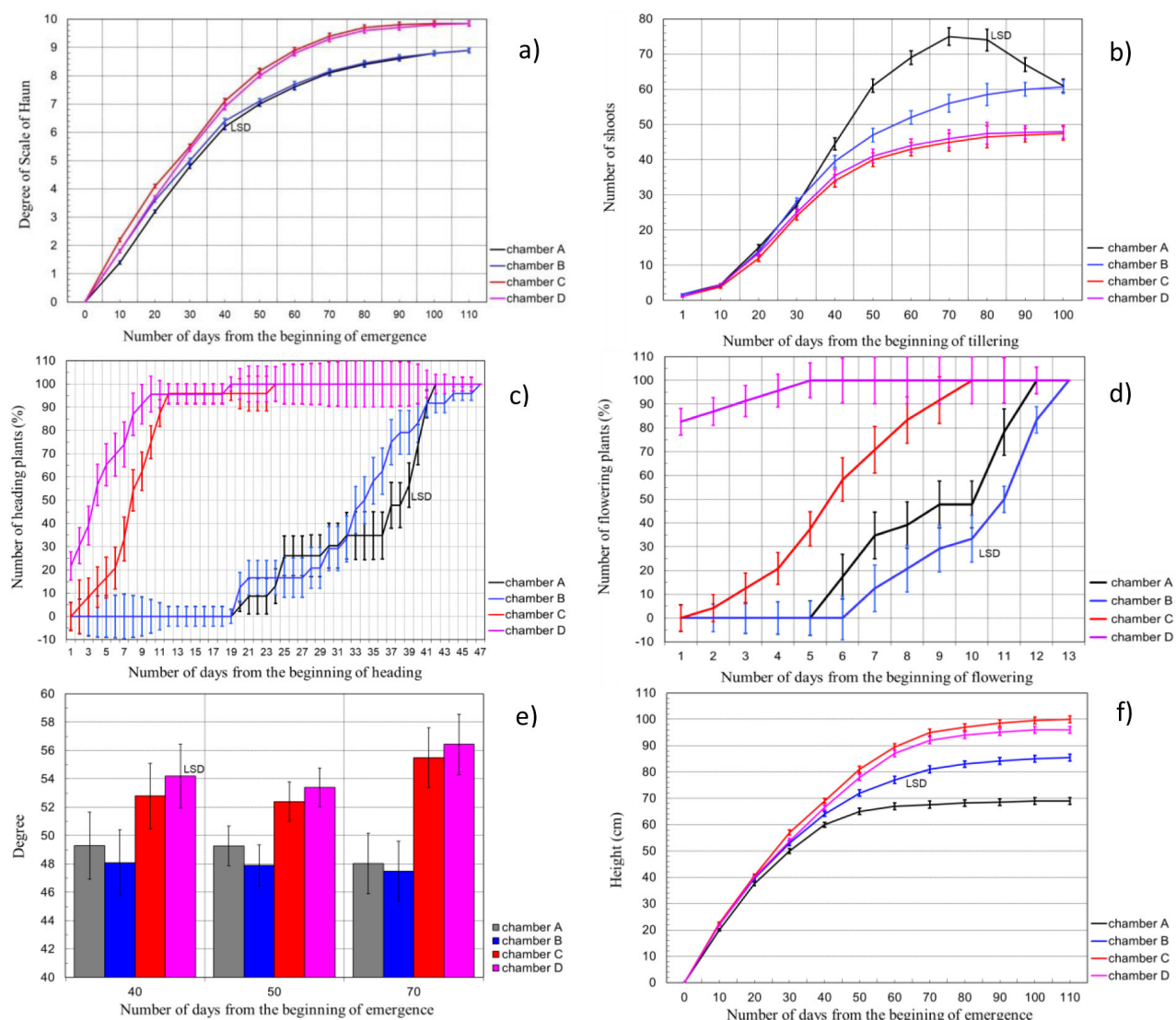


Fig. 2. Development of spring barley in growth chambers with different radiation being applied: a) the rate of the development of spring barley, b) the course of the tillering of spring barley in the growth chambers with different radiation being applied, c) the rate of heading of spring barley plants, d) the rate of flowering of spring barley, e) the angle of barley leaves arrangement ($^{\circ}$), f) the height of the spring barley plants depending on the applied radiation and the time of emergence. *Confidence intervals of the average non-overlapping means that a statistically significant difference occurs between the averages with a level of significance $\alpha < 0.05$.

No differences were found in terms of the tillering of the plants at the beginning of this phase (Fig. 2b) however, significant differences occurred after 20 days. The tillering of the plants grown in chambers C and D was decidedly lower than in chambers A and B. In spite of this, the number of lateral shoots of the plants grown in chamber B was lower than in chamber A, where the high and constant growth of the barley lateral shoots was noted. Maximum tillering in growth chamber A occurred on day 70 from the beginning of this phase. The barley plant in this chamber produced an average of approximately 75 shoots but some of them achieved 90 lateral shoots and maximal tillering in this chamber amounted to 98 shoots. After achieving the highest level of tillering among all of the plants in this growth chamber, a rapid decrease in the number of lateral shoots was observed. In contrast to the plants from chamber A, the tillering of the plants from the other chambers was longer and at the end of this phase the increase in the number of shoots was not very significant. However, a significant difference in the number of shoots was found between the plants growing in chambers A and B and the plants from chambers C and D. Finally, the barley that was grown at a high R/FR ratio (growth chambers A and B) produced about 9-10 shoots more than the plants grown under conditions of a low R/FR ratio (chamber C and D).

Barley heading in the experiments with different spectral compositions of the applied radiation was differentiated with respect to the time of the commencement of the phase, its duration and the time of its ending. The greatest difference in the rate of heading occurred among plants grown in chamber D and plants from chambers A and B. The most rapid heading took place in growth chamber D with the lowest R/FR ratio (*i.e.* 0.92).

The most rapid rate of this phase course occurred decidedly in chamber D, and to a lesser extent in growth chamber C, and finally to the least extent in chambers A and B (Fig. 2c). In the case of the barley grown in chamber D the heading phase lasted for 19 days, in chambers A and C – 23 days and in chamber B this phase lasted for the longest time, *i.e.* 28 days. Therefore, at the time when the heading phase commenced in chambers A and B, in chamber D it was just ending. When the process of heading in chamber C had ended, in chambers B and A about 16 and 14% of the plants had just headed, respectively. The end of the heading phase of the plants in chamber D took place about 23 days earlier than for the plants grown in chamber A, and by just 28 days earlier than in chamber B. While in growth chamber C the end of the heading phase occurred between 18 and 23 days earlier than in chamber A and B, respectively.

Similar to heading, the earliest process of barley flowering commenced in the experiment where the R/FR ratio amounted 0.92 (Fig. 2d). On the first day of flowering about 83% of the plants from chamber D were already in this phase while in the other chambers flowering had not yet begun. When the experiment with the highest amount of

FR for all plants was in its flowering phase, in chamber C this phase amounted to 36%, and in the experiments with a small amount of radiation (chamber A and B) the plants had not yet flowered. This process commenced in these plants on the next day. A significantly more rapid barley flowering rate occurred in chamber D and this continued from the first to the seventh day of this phase in comparison with the plants from chambers A and B. Also, in the second experiment with a low R/FR ratio of radiation (chamber C), the process of plant flowering was approximately 2-4 days more rapid than in plants from chambers A and B.

An important element of plant habit is the leaf angle and shoot arrangement. In the thirty days from the beginning of tillering the leaves of the plants from all of the experiments were arranged at an angle of 48-50° and showed no significant differences in this feature. In the forty days from the beginning of emergence (*i.e.* during tillering) differences were observed but they were not statistically significant (Fig. 2e). Significant differences in the arrangement of the barley leaves occurred under different R/FR ratios in the growth chambers until day 50 and 70 from the beginning of emergence. While on day 50 (*i.e.* during barley heading) in the growth chambers C and D (where the R/FR ratio amounted respectively to 1.02 and 0.92) the leaves and shoots were more vertically arranged than for the plants growing in the chambers with high values of this ratio (R/FR=10.0 and 2.08) because they were set at an angle of 52-53° and 48-49°, respectively. Even larger differences in the leaf and shoot arrangement among the experiments occurred on day 70 from the beginning of emergence. In the experiments with radiation characterized by a significantly large number of FR (C and D chambers) the arrangement of the angle of leaves and shoots amounted to about 56°, and in the experiments with small and very small concentrations of FR (A and B chambers) this angle amounted to about 48° (Figs 2e, 3).

The effect of the radiation conditions on the length of particular internodes was also analysed in the presented studies. Each group of shoots with a differentiated number of internodes was considered individually. Research has shown that as the R/FR ratio decreased, the length of the internodes increased. In particular, for chambers C and D the barley internodes were significantly longer in comparison with the shoots of the plants grown in chambers A and B (Table 4).

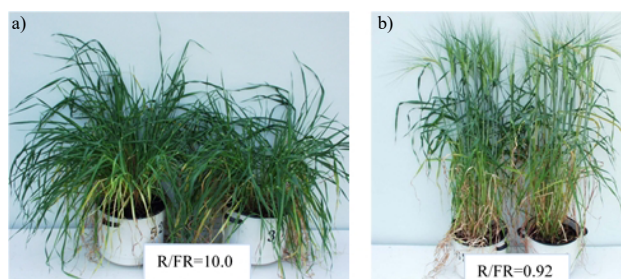


Fig. 3. Habit of spring barley plants grown in chambers A (a) and D (b).

Table 4. Average length of the internodes of spring barley shoots (cm)

| Internode | Stem with the number of internodes | Growth chamber | | | |
|-----------|------------------------------------|----------------|-------|-------|-------|
| | | A | B | C | D |
| I | 4 | 4.5a | 4.6a | 5.2a | 5.5a |
| | 5 | 3.7a | 3.8a | 4.4b | 4.2b |
| | 6 | 2.6a | 2.6a | 2.8a | 2.5a |
| | 7 | 1.5ab | 1.4a | 1.6b | 1.4a |
| | 8 | 1.0a | 1.4b | 0.9a | 0.9a |
| II | 4 | 8.3a | 8.5a | 10.5b | 9.1ab |
| | 5 | 6.7a | 6.7a | 9.1c | 8.2b |
| | 6 | 5.7a | 6.0a | 8.4c | 7.0b |
| | 7 | 4.0a | 3.9a | 5.4b | 4.9b |
| III | 4 | 9.5a | 9.8a | 14.6b | 13.6b |
| | 5 | 8.2a | 8.2a | 10.4b | 10.2b |
| | 6 | 7.3a | 8.6b | 10.2c | 9.6d |
| | 7 | 6.0a | 6.1a | 10.1c | 8.6b |
| IV | 4 | 12.2a | 12.0a | 14.0b | 15.5c |
| | 5 | 10.7a | 10.4a | 12.7b | 13.5c |
| | 6 | 8.0a | 8.3a | 11.3c | 10.3b |
| | 7 | 7.0a | 6.9a | 10.5c | 9.2b |
| V | 4 | 5.2a | 6.3b | 9.4d | 8.5c |
| | 5 | 12.6a | 12.6a | 14.3b | 15.3c |
| | 6 | 10.5a | 10.2a | 13.4b | 13.3b |
| | 7 | 7.3a | 7.2a | 10.1b | 9.6b |
| VI | 4 | 5.6a | 7.3b | 9.5c | 8.6bc |
| | 6 | 12.1b | 11.5a | 15.4c | 16.2d |
| | 7 | 9.7a | 9.8a | 13.0b | 12.9b |
| VII | 6 | 6.2a | 8.1b | 9.7c | 10.4c |
| | 7 | 11.9a | 12.0a | 16.8b | 17.2b |
| VIII | 8 | 9.3a | 9.4a | 12.7b | 13.1b |
| | 8 | 11.2a | 11.7a | 15.5b | 15.2b |

Numbers in lines marked with the same letters do not differ significantly. In the opposite case averages differ significantly (at a significance level $\alpha < 0.05$).

The barley grown in chamber C produced the longest second internode among the various shoots with four, five and seven internodes. Moreover, the plants from this chamber produced the longest fifth and sixth internodes among the shoots with these numbers of internodes, respectively.

The plants grown in the chambers with the lowest R/FR ratios produced the longest shoots (Table 5). However, plants from the C and D chambers formed shoots that were about 9 cm longer with 4 and 5 internodes in contrast to plants cultivated in chambers A and B. The length of the

Table 5. Dependence of the average length of the spring barley stems on the type of irradiation applied and the construction of the stem (cm)

| Stem with the number of internodes | Growth chamber | | | |
|------------------------------------|----------------|-------|-------|-------|
| | A | B | C | D |
| 4 | 34.5a | 34.9a | 44.5b | 43.8b |
| 5 | 42.0a | 41.8a | 51.0b | 51.4b |
| 6 | 46.4a | 47.3a | 61.4b | 58.4c |
| 7 | 47.5a | 47.4a | 67.6b | 63.8c |
| 8 | 45.7a | 53.9b | 69.3c | 65.4c |

Explanations as in Table 4.

shoots with 6 internodes was more differentiated and the differences amounted to 11-15.6 cm. Among the shoots with 7 internodes this difference was more than 16-20 cm.

Plants grown in chambers with the lowest R/FR ratio produced the longest shoots (Table 5). However, the plants from chambers C and D formed shoots about 9 cm longer with 4 and 5 internodes as opposed to plants cultivated in chambers A and B. The length of the shoots with 6 internodes was more differentiated and the difference amounted to 11-15.6 cm. Among the shoots with 7 internodes this difference was greater than the 16-20 cm in the plants from chambers C and D in relation to plants from chambers A and B. However, the greatest difference in shoot length (it amounted to 15.4-23.6 cm) occurred between plants from chambers C and A and B which had shoots with 8 internodes. Significant differences in the length of the shoots (11.5-19.7 cm) were also noted between chambers D and A and B. Moreover, an 8 cm difference in the length of the shoots with 8 internodes was found between the plants from chambers A and B. Longer shoots were produced by plants grown in the B chamber. Generally, it was found that the combination of an increase in the internode number and a decrease in the R/FR ratio produced an increase in the mean length of the barley stem.

The differences in the height of the highest shoots were not significant in the first three weeks after germination (Fig. 2f). However, significant differences occurred in the month from the beginning of emergence in the plants from chamber C in comparison with plants from chamber A. During the forty days from the beginning of emergence, the differences in the heights of the shoots among the plants grown in the chambers with various spectral compositions were significant. The tallest plants grew in chamber C, they were about 4 cm lower in chamber D, and 10-15 cm lower in chamber B, while the plants grown in chamber A were lower by about 10-30 cm as compared to the tallest barley. The intensive growth of barley plants in chambers B, C and D continued until the 90th day from the beginning of emergence while in chamber A this process finished after 60-70 days from the start of emergence. In the experiment where the R/FR ratio amounted to 1.02 the tallest plant was 110 cm tall and the shortest one was 91 cm

Table 6. Average length of spring barley ears (cm)

| Stem with the number of internodes | Growth chamber | | | |
|------------------------------------|----------------|------|------|-------|
| | A | B | C | D |
| 4 | 4.6a | 5.0a | 7.4b | 4.9a |
| 5 | 5.1a | 4.8a | 7.1c | 5.6ab |
| 6 | 5.7a | 5.9a | 8.2c | 6.8b |
| 7 | 5.9a | 7.1b | 9.1c | 8.5d |
| 8 | 5.6a | 7.9b | 9.7c | 7.3b |

Explanations as in Table 4.

tall. In the chamber where the R/FR ratio amounted 0.98 the tallest and the shortest plant amounted 103 and 84 cm, and where this ratio = 2.08 these values amounted to 93 and 73 cm, while in the chamber with the highest R/FR ratio (*i.e.* 10.0) the plants were 79 and 63 cm tall, respectively.

The barley grown in chamber C produced the longest ears among all of the shoots (Table 6). While the ears of the plants grown in chamber D were longer than those on the plants from chambers A and B. A slightly longer and the longest ears were produced by plants in chambers B and D, respectively. The shortest ears were produced by the plants grown in chamber A, *i.e.* in conditions with the highest R/FR ratio. This observation concerned the shoots with five, six and seven internodes because these differences were not found among shoots with four and eight internodes. The mean length of the ears was longer in the plants with a greater number of internodes.

Most plants in the experiments had 5, 6 and 7 internodes. However, the R/FR ratio was not found to influence the total number of shoots and fertile shoots (Table 7). The barley grown in chamber D with the lowest R/FR ratio produced the greatest amount of shoots with ears as compared to the plants grown in the other chambers. On the other hand, there were no differences found in the number of these shoots among the plants grown in chambers A, B and C (Fig. 4a).

The barley grown in conditions with a greater share of FR (chamber C and D) produced the least unfertile stems in relation to the plants grown in radiation with a small share of FR, *i.e.* in chamber A and B (Fig. 4b). A particularly substantial difference (15 and 17 infertile stems) occurred among the plants

from chamber D and chambers A and B. A significant difference in the number of sterile stems amounted to almost 10, this was also noted between the plants from chambers A and C.

The largest number of all barley stems (both fertile and sterile) was produced in conditions with a high R/FR ratio (chambers A and B) and was 9-10 times greater than in plants from chambers with a low ratio (chambers C and D). However, this difference was not statistically significant considering the wide range of LSD (Fig. 4c).

The greatest number of grains were produced by plants from chamber C relative to the other chambers. The exception was a shoot with 7 internodes which showed no differences in the number of grains as compared to plants from chamber B (Table 8). Slightly less grains were produced by the plants grown in chamber B but a greater number than were obtained from chambers A and D. Apart from that, there was a significant difference in the number of grains produced by the stems with 5, 6 and 7 internodes which occurred between the plants from chambers A and D.

The largest number of grains were produced by plants grown in chamber C with a relatively low R/FR ratio, and the least – in conditions with the highest R/FR ratio, *i.e.* in chamber A (Fig. 5a).

The greatest mass of grain was achieved by the plants grown in chamber C, and the least in chambers A and D (Table 9). The grain yield from chambers B and C was similar in the case of the stems with 5 and 6 internodes. However, with reference to the stems with other numbers of internodes, the mass of barley grain from chamber C was greater than that from chamber D.

The lowest yield of grain was produced by plants grown in chamber A, and the greatest was found in chamber C (Fig. 5b). The highest mean weight of grain was achieved by plants with 7 internodes which also had the highest weight of 1000 grains -TGW (Table 10).

The weight of 1000 grains on particular stems of barley with 4 internodes was not differentiated (Table 10). Among the stems with 5 internodes the greatest TGW originated from plants from chamber C whereas in chamber D – this occurred on plants with stems consisting of 6, 7 and 8 internodes. The lowest TGW was produced by plants from chamber A with the highest R/FR ratio while the greatest

Table 7. Number of plant shoots in the growth chambers included in the measurements

| | Number of shoots with internodes | | | | | | | | | | | | | | | | | | | |
|--------------------------|----------------------------------|-----|-----|-----|--------------|------|------|------|--------------|------|------|------|--------------|------|------|------|--------------|-----|-----|-----|
| | 4 internodes | | | | 5 internodes | | | | 6 internodes | | | | 7 internodes | | | | 8 internodes | | | |
| | Growth chambers | | | | | | | | | | | | | | | | | | | |
| | A | B | C | D | A | B | C | D | A | B | C | D | A | B | C | D | A | B | C | D |
| Total number of shoots | 8a | 31b | 22c | 39d | 106a | 211b | 180c | 332d | 507a | 498a | 414b | 493a | 184a | 180a | 213b | 135c | 22a | 18a | 24b | 10c |
| Number of fertile shoots | 8a | 27b | 20c | 39d | 106a | 163b | 174b | 332c | 507a | 368b | 402b | 493a | 184a | 147b | 207c | 135d | 22a | 14b | 22a | 10c |

Explanations as in Table 4.

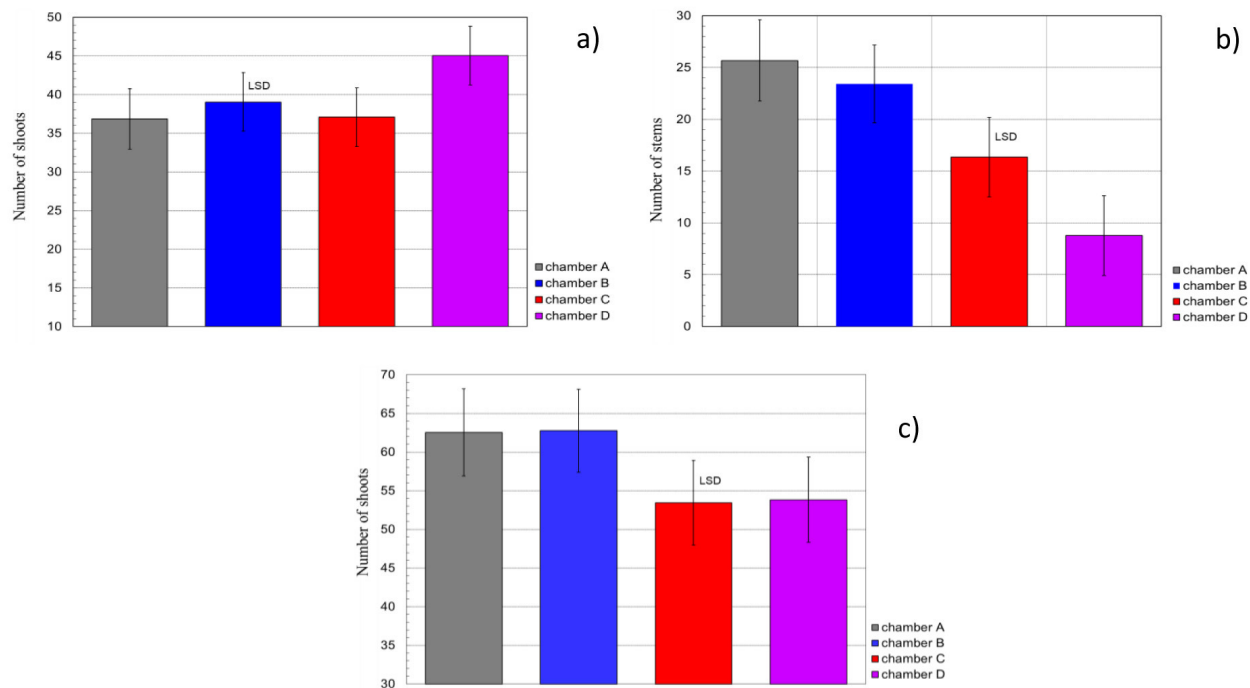


Fig. 4. Dependence of the number of shoots of spring barley on the type of radiation applied: a) fertile, b) infertile, c) all shoots. Explanations as in Fig. 2.

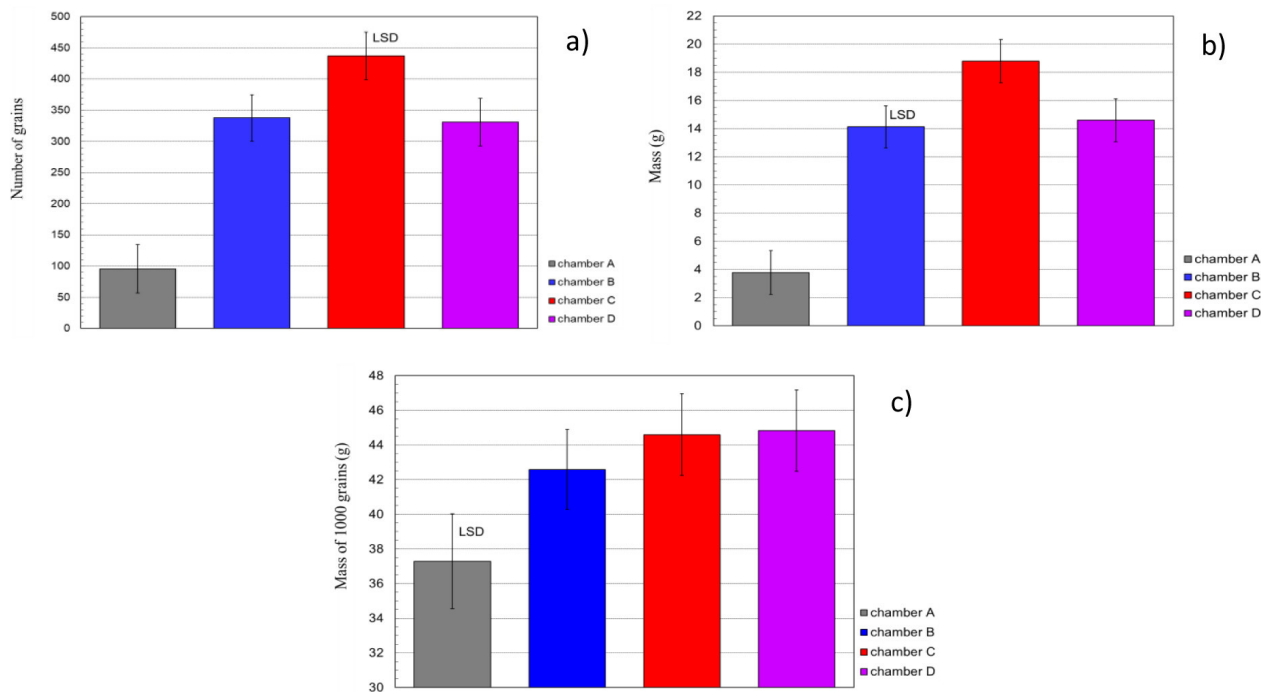


Fig. 5. Features of the grain produced by a single plant of barley depending on the light conditions: a) number of grains, b) weight of grain (g plant^{-1}), c) mass of 1000 grains (g). Explanations as in Fig. 2.

TGW was found under conditions with the lowest R/FR ratio – chambers C and D (Fig. 5c).

Among the stems with 4 and 8 internodes, the greatest weight was achieved for plants from chamber C, and a greater mass of stems with 5 internodes were produced in

chambers C and D (Table 11). However, the biggest mass of straw was produced by stems with 6 and 7 internodes which grew in chamber D. In general terms, the biggest mean mass of straw was achieved by plants with 8 internodes and harvested in chamber C.

Table 8. Dependence of the number of grains of spring barley plant on the radiation applied and also on the number of internodes

| Stem with the number of internodes | Growth chamber | | | |
|------------------------------------|----------------|-------|-------|-------|
| | A | B | C | D |
| 4 | 1.5a | 8.9c | 14.8d | 3.8b |
| 5 | 2.3a | 9.4c | 10.6c | 5.4b |
| 6 | 2.6a | 11.1c | 12.0c | 8.0b |
| 7 | 2.8a | 12.9c | 13.9c | 10.2b |
| 8 | 4.9b | 15.4c | 21.6d | 2.4a |

Explanations as in Table 4.

Table 9. Grain mass of the barley stem (g stem⁻¹)

| Stem with the number of internodes | Growth chamber | | | |
|------------------------------------|----------------|-------|-------|-------|
| | A | B | C | D |
| 4 | 0.08a | 0.38b | 0.55c | 0.14a |
| 5 | 0.09a | 0.41c | 0.44c | 0.22b |
| 6 | 0.10a | 0.46c | 0.50d | 0.35b |
| 7 | 0.11a | 0.50b | 0.84c | 0.48b |
| 8 | 0.16a | 0.54b | 0.88c | 0.10a |

Explanations as in Table 4.

Significant differences were not found in the mass of straw from plants grown in differentiated conditions of radiation (Fig. 6a), although a slight decrease in straw mass was observed for the plants grown in chambers C and D (with a lower and the lowest R/FR ratio, respectively).

The greatest total mass of stems (grain + straw) with 4, 5, 6 and 8 internodes was produced by plants grown in

Table 10. Dependence of the weight of 1000 grains on the radiation applied and on the number of internodes on the stem (g)

| Stem with the number of internodes | Growth chamber | | | |
|------------------------------------|----------------|--------|---------|--------|
| | A | B | C | D |
| 4 | 40.20a | 41.89a | 37.77a | 38.34a |
| 5 | 40.11ac | 43.01b | 45.50c | 40.15a |
| 6 | 38.10a | 41.84b | 42.82bc | 43.88c |
| 7 | 39.81a | 39.96a | 43.79b | 46.64c |
| 8 | 34.06a | 36.96b | 41.11c | 42.78c |

Explanations as in Table 4.

Table 11. Yield of barley stems (g stem⁻¹)

| Stem with the number of internodes | Growth chamber | | | |
|------------------------------------|----------------|-------|-------|-------|
| | A | B | C | D |
| 4 | 0.47a | 0.47a | 0.71b | 0.40c |
| 5 | 0.52ab | 0.44c | 0.51a | 0.56b |
| 6 | 0.61a | 0.55b | 0.68c | 0.78d |
| 7 | 0.69a | 0.76b | 0.86c | 1.13d |
| 8 | 0.75a | 0.93b | 1.41c | 1.02b |

Explanations as in Table 4.

chamber C. Only among the stems with 7 internodes was a greater mass produced by plants grown in chamber D (Table 12). However, stems with 6 and 7 internodes grown in chamber D produced a greater mass than the plants from chambers A and B. A greater mass of stems with 5, 6 and 7 internodes were also found in plants grown in chamber B as opposed to chamber A.

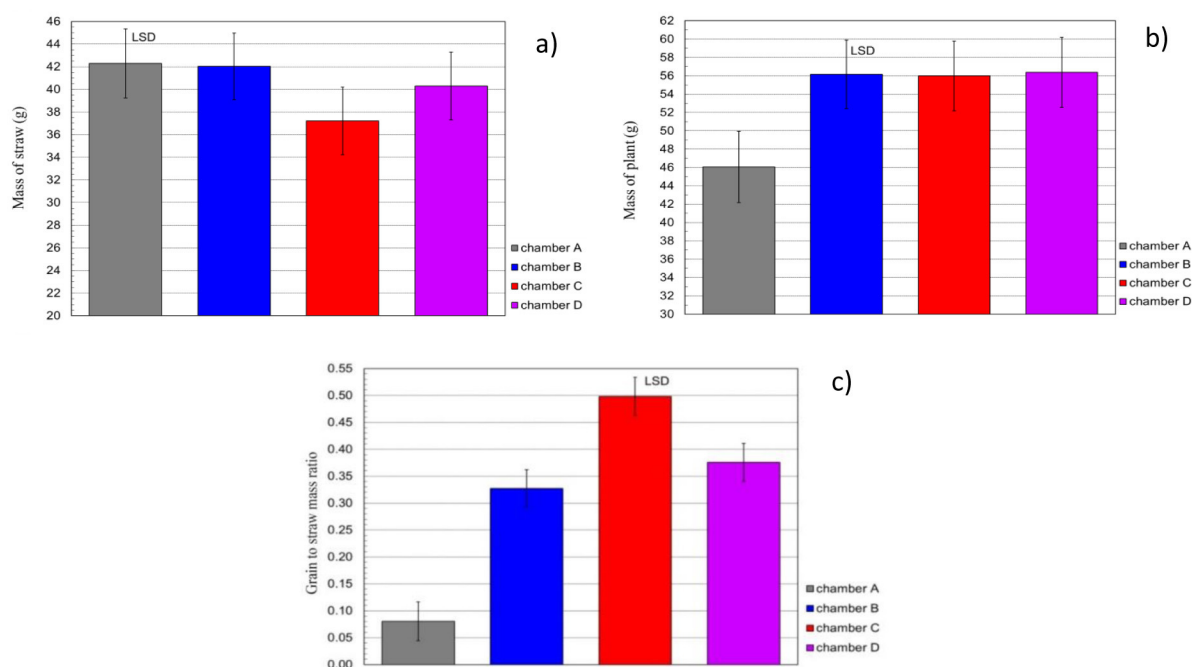
**Fig. 6.** Dependence of the yielding features of a single plant of spring barley on the radiation applied: a) mass of straw (g plant⁻¹), b) total mass of the plants (g), c) the grain-to-straw weight ratio. Explanations as in Fig. 2.

Table 12. Dependence of the total mass of spring barley stem (grain and straw) on the radiation applied and on the number of internodes (g)

| Stem with the number of internodes | Growth chamber | | | |
|------------------------------------|----------------|-------|-------|--------|
| | A | B | C | D |
| 4 | 0.55ac | 0.80a | 1.19b | 0.54c |
| 5 | 0.61a | 0.76b | 0.93c | 0.78b |
| 6 | 0.71a | 0.89b | 1.17c | 1.13c |
| 7 | 0.80a | 1.17b | 1.46c | 1.61d |
| 8 | 0.91a | 1.35b | 2.19c | 1.12ab |

Explanations as in Table 4.

Table 13. Dependence of the barley grain-to-straw weight ratio on the radiation applied and on the number of internodes

| Stem with the number of internodes | Growth chamber | | | |
|------------------------------------|----------------|-------|-------|--------|
| | A | B | C | D |
| 4 | 0.12a | 0.77b | 0.81b | 0.63bc |
| 5 | 0.56a | 0.91b | 0.90b | 0.60a |
| 6 | 0.40a | 0.84b | 0.74b | 0.55c |
| 7 | 0.40a | 0.66b | 0.69b | 0.53c |
| 8 | 0.33a | 0.55b | 0.57b | 0.19a |

Explanations as in Table 4.

The lowest total mass was produced by plants grown in the chamber with a high R/FR ratio, *i.e.* in chamber A. Whereas, in the other chambers, the values of total mass were significantly higher and very similar to each other (Fig. 6b).

The highest grain-to-straw weight ratio was found among plants grown in the B and C chambers (Table 13). An especially low grain-to-straw weight ratio was noted among the plants that grew in the experiment with the highest R/FR ratio in comparison to the plants that were grown in conditions with low values of this ratio (Fig. 6c). In addition, the highest ratio occurred in barley radiated with an R/FR = 1.02.

DISCUSSION

The research conducted showed that the spectral composition of radiation has an effect on the photo-morphogenesis of plants and causes a variation in their response. Different radiation conditions caused various effects including a different rate of growth and development in the barley. The plants which were subjected to the greatest values of radiation, *i.e.* from the range of FR, developed more rapidly than those grown under considerably lower radiation values in this spectral range. This was proven by the more rapid occurrence of the developmental phases, their course and conclusions, with a particular emphasis on the underlying heading and flowering. The conditions of low R/FR caused an acceleration in flowering due to the light quality – the sensing pathway was mediated by phytochromes to regulate the floral activator FT (Franklin and Whitelam, 2005; Thomas, 2006). The studies of Tan *et al.* (2022) showed

that far red light not only accelerates flowering but also regulates plant nutrition and shapes plant morphology. Moreover, a low R/FR ratio may be a signal to promote CO₂ assimilation by increasing photosynthetic capacity (Yang *et al.*, 2020) and in effect promoting energy transfer from PSII to PSI (Tan *et al.*, 2022).

The tillering of barley in various radiation conditions was similar until the 35th day. Then the most stems were produced in plants that were grown in conditions with a small share of FR, and the least – were produced by plants from experiments with a greater share of this kind of radiation. After 100 days from the beginning of tillering, the differences between the particular experiments were already lower. However, it was found that the plants from chambers with a low R/FR ratio (C and D) produced a lower number of stems than those from the chambers with a higher ratio (A and B). According to Doroszewski (2011) the reduction in the lateral shoots of wheat in these conditions was lower and this was observed in all plants.

The effect of an increased share of FR in the radiation (low R/FR ratio) reflected by the grass surface was manifested by a decreased tillering of the rye, and by a branching of the buckwheat studied (Doroszewski, 1997, 2003). The plants which received an increased amount of FR in radiation reflected from grass produced on average two shoots less than plants which were grown on black fallow. These differences were considerably greater in the growth chambers. In the case of barley and wheat the differences amounted to 10 and 13 shoots, respectively (Doroszewski, 2011) but more shoots were produced by the plants grown in high R/FR ratio radiation. The possibility of the occurrence of unfavourable conditions caused a reduction in plant tillering to 4-5 shoots, whereas the plants surrounded by grass started growing in the dense stand. In turn, the plants grown on the fallow or in the growth chambers, where the R/FR ratio was high had no limit in tillering. They received a signal concerning the lack of any threat posed by their competition and in effect could produce considerably more shoots. In the experiment with red fescue the number of shoots was found to be reduced as a response to the increased share of FR in the radiation transmitted by maple and ash trees in comparison with the shoots of plants grown in an open space (Wherely *et al.*, 2005). The clover plants grown in the shade of three grass species also responded to the radiation with a reduction in the R/FR ratio by decreasing the number of branches (Marcuvitz and Turkington, 2000). In another experiment with clover, where the R/FR value amounted to 0.33, the number of branches of degree I and II was the lowest (Lötscher and Nösberger, 1997; Robin *et al.*, 1994). Already at the end of the last century, Casal *et al.* (1986, 1987b) paid attention to the role of the signal of a lowered R/FR ratio, which clearly reduces tillering in grasses. A phytochrome is also responsible for the control of tillering and the growth of leaves in grasses, it responds to changes in the R/FR ratio (Bahmani *et al.*, 2000; Casal, 1988). The research of Xie *et al.* (2016) has

also confirmed that plants can sense R/FR at the early stages of tillering. According to these authors a low R/FR value not only inhibits tiller bud outgrowth, but also promotes the abortion of young tillers that have already been initiated. However, the underlying mechanism is not yet clear. One important theory is the competition for carbohydrates. The reducing effect of increased the FR amount on tillering was found, among others, in wheat (Casal, 1988), barley (Skinner and Simmons, 1993), sorghum (Childs *et al.*, 1997) and ryegrass (Casal *et al.*, 1985). Similar effects of reduced tillering as a result of the R/FR ratio decrease were observed by Casal *et al.* (1990). However, the experiment with amaranth and different R/FR ratios did not result in differences in the number of branches (Rajcan *et al.*, 2002). The barley cultivated in growth chambers with a high R/FR ratio did not limit tillering, because the plants were not threatened in any way. This caused the plants to produce more shoots than in chambers C and D. One example of plant adaptation in order to optimize radiation is *Lolium multiflorum*, which adapts to radiation with a low R/FR ratio by assuming a more elevated and upright position and leaf blades at a higher location. As a consequence, the plants were able to make better use of radiation in the upper levels of the stand (Casal *et al.*, 1990). Similar results were achieved in the experiment with barley which received radiation with a low R/FR ratio, and when compared to plants grown with a high R/FR ratio they had leaves located at a wider angle. Therefore, in general terms it may be concluded that, in conditions of shading by a green mass, the plants reduce their number of lateral shoots and at the expense of lower tillering, redirect the assimilates to increasing plant height, striving for apical dominance in relation to neighbouring plants.

It should be emphasized that the observed changes in plant habit did not occur as a result of existing competition but only occurred prior to the preparation for it. This phenomenon may be explained by the existence of a stimulus in radiation with an increased share of FR which signalled the occurrence of the possibility of potential competition. One effect is that plants seek to overgrow neighbouring plants over a whole period of growth, because they perceive in them a potential threat in the struggle to receive photosynthetic active radiation (PAR). Information concerning the environment in the form of radiation intensity and spectral radiation composition is provided by the phytochrome. It regulates many metabolic transformations and influences plant habit ensuring that the expected competition is met. The obtained results concerning plant morphology also indicate that this response is caused by a dense stand characterized by the transmission of radiation with a low R/FR ratio. Moreover, Ballaré *et al.* (1987, 1988) indicated that it is a reaction induced by radiation reflected from the plant neighbours, even before direct shading occurs. According to Ballaré *et al.* (1987) the reflected radiation signals the presence and proximity in the neighbourhood of other plants. The changes in the amount of FR in the reflected radia-

tion may be correlated with the density and proximity of the neighbouring plants (Ballaré *et al.*, 1997; Kasperbauer, Karlen, 1986; Ballaré *et al.*, 1987). Whereas, the elongation response does not occur when the neighbouring plants are white (Ballaré *et al.*, 1987) or when the plants have grown surrounded by a filter containing CuSO_4 which absorbs FR (Rajapakse *et al.*, 1993). Similar morphological effects occur in plants receiving information which is evidence of a lack of competition. In this situation they produce more branches and tillers as well as transporting more nutrients to their roots which causes a greater production of biomass. In summary, they behave like plants which are grown in conditions without the presence of other neighbouring plants (Antonious and Kasperbauer, 2002; Kasperbauer, 2000a, b, 2001; Kasperbauer and Karlen, 1994; Loughrin and Kasperbauer, 2001; Libenson *et al.*, 2002).

The heading of barley which received greater doses of radiation from the range of FR also occurred about one month sooner compared to plants grown in radiation with a low share of FR. Doroszewski (2011) found that wheat plants grown under similar conditions also showed a more rapid rate of heading in experiments with a low R/FR ratio of radiation as compared to plants receiving radiation with a low share of FR (and a high R/FR ratio).

The flowering phase of barley also occurred 6-10 days sooner at a low R/FR ratio as compared to the plants grown under the influence of a high R/FR ratio. The same dependencies on the course of the rate of flowering were obtained in the experiment with wheat (Doroszewski, 2011). Studies conducted by Mobini *et al.* (2016) also prove this observation. According to these authors, the R/FR ratio occurred due to flower induction in lentil plant and the ratio stood at a level of 1.9 which resulted in a reduced time of flowering. However, an R/FR ratio of above 3.1 delays the flowering time and therefore this ratio should be maintained as a critical threshold which is suitable for flower induction.

Plants grown both in natural conditions, surrounded by grass and in growth chambers with a low R/FR ratio responded to FR emissions by shortening their developmental phases relative to plants grown on black fallow or in conditions of radiation with a higher R/FR ratio. The developmental phases of plants were dependent on the value of their R/FR ratios and when these occurred more rapidly, the R/FR ratio was found to be lower. These responses are probably caused by the plant "striving" for the most rapid possible reach in their generative phase development, *i.e.* seed production, and outpacing the competing plants. This behaviour is characteristic of plants grown in conditions requiring the avoidance of shading.

The acceleration of the developmental phases, such as flowering in the case of *Arabidopsis*, as a response to shading avoidance was already indicated at an earlier date by Halliday *et al.* (1994). *Arabidopsis* or tomato plants which received radiation with a low R/FR ratio, started to flower sooner in conditions of white light (*i.e.* light similar to the

daylight, a mixture of light with different lengths of electromagnetic waves) with additional FR than in conditions with white light alone (Whitelam and Smith, 1991). Similarly, the plants of rough amaranth began their flowering phase sooner in conditions with a lowered R/FR ratio than in radiation conditions with a high R/FR ratio (Rajcan *et al.*, 2002).

The response of the plants to accelerate the flowering process promotes a more rapid production of seeds in shaded conditions, and increases the probability of reproductive success, as a consequence the preservation of future plant generations is enabled. However, it should be stated that reaching the flowering stage is determined by many regulators of plant development. One of them is the *phyB* gene. In *Arabidopsis*, the presence of a meristematic regulator of flowering such as the *LFY* (Simpson and Dean, 2002) and *FT* genes (Cerdán and Chory, 2003) were found, but the main role in this process is attributed to the *ptfl* gene, which interacts with the *phyB*, *phyD* and *phyE* genes (Cerdán and Chory, 2003).

Franklin and Whitelam (2005) found that the occurrence of unfavourable conditions for plant development (sufficient shading or the reflection of radiation from neighbouring plants) is a factor which causes the acceleration of heading and flowering, this is connected with the production of a higher mass of grain. In the case of barley grown in chambers with a low R/FR ratio a high mass of grain and a high grain-to-straw mass ratio were obtained. This development strategy is directed towards species preservation as well-developed grains with a large amount of reserve material increase the chances of the germination and development of a plant with greater competitive possibilities. Such natural properties are known as “last chance” options because they ensure the preservation of the species by the more rapid production of seeds. It may therefore be concluded that the acceleration of development probably occurs in all plants to avoid shading. The acceleration of heading, flowering or seed setting in conditions with low R/FR ratio radiation is at the same time connected with the high mass of a single grain which was observed in barley grown in growth chambers. The research of Halliday *et al.* (1994) as well as Whitelam and Smith (1991) indicate that seedlings of *Arabidopsis* and tomato responded with more rapid development to early warnings, these were supplied by radiation with a low R/FR ratio, and originated from neighbouring plants. The lack of a *phyB* mutant response to far red reflection was shown repeatedly by Smith (1992). The responses of deficient mutants *phyB*, *phyA* or *hy4* in cucumber and *Arabidopsis*, indicate that they do not play a direct role in the perception of the R/FR ratio. This means that phytochrome B is responsible for the perception of radiation in FR and R. Another indicator of more rapid plant development in the conditions of a low R/FR ratio is for instance, the accelerated growth of *Arabidopsis thaliana* leaves (McNellis and Deng, 1995) or the rotting of onions (Mondal *et al.*, 1986). The phytochrome is also credited with control over starting

and also the duration of the flowering process that is found in sorghum (Childs *et al.*, 1997), rice (Izawa *et al.*, 2000) and barley (Hanumappa *et al.*, 1999).

The obtained results of the studies conducted in artificial (stimulated by the respective lighting sets) or natural conditions (originating from reflections produced by the land) confirm that these plants respond very robustly to the spectral composition of the radiation (Doroszewski, 1997, 2011). Among the studied species of cereals, rye and buckwheat showed the most substantial response to the increased share of radiation in the FR range (Doroszewski, 1997). In summary, the observed responses of cereals can with full justification be described as “shade avoidance syndrome – SAS”, which occurs in plants grown in dense stands. The conditions of a low R/FR ratio triggers SAS, it is characterized by a decrease in the branch number (Lei *et al.*, 2022).

The determination of the mutual interaction between neighbouring plants led to the adaptation of a level of competitive conditions for photosynthetic active radiation (PAR) through the appropriate development and morphology of plants (Casal and Smith, 1989; Schmitt and Wulff, 1993; Schmitt *et al.*, 1999). The hypothesis of plastic adaptation indicates that a phytochrome mediates in the sensitivity concerning the R/FR ratio and that this reaction originated as a result of natural selection, as an evolutionary adaptation. It enables plants to participate in the avoidance of competition with the aim of a more effective use of solar radiation in dense plant sites (Ballaré *et al.*, 1987; Casal and Smith, 1989; Schmitt and Wulff, 1993). This strategy led to plants which had an increased potential to remain alive. However, it should be noted that genetic determinants also have a great influence over plant responses.

The acceleration of flowering and a decrease in the number of branches, the number of grains and the yield was the result attained through research with winter and spring wheat, spring rye and barley grown in noncompetitive conditions but with an increased amount of FR in comparison with experiments with black fallow (in the natural conditions) or with a low R/FR ratio (in the artificial conditions) (Doroszewski, 2011). These were similar to the results which occur in the dense stands of cereals, where the constant adaptation of the plants to competitive conditions takes place (Noworolnik, 2003).

The plants were able to monitor red and far-red light due to their photoreceptors, *i.e.* phytochromes (Tan *et al.*, 2022). The main function of a phytochrome is the perception of radiation, especially from the range of R (*phyB*) and FR (*phyA*), and the response of the plants to this signal is the activation of metabolic pathways, which allow, most of all, for an increase in the probability of species preservation (Casal and Smith, 1989). In order to increase this probability, the plant receiving the reflected radiation with the lowest R/FR ratio showed a considerably more rapid rate of development in comparison with plants grown in experiments with high R/FR ratio radiation. According to

Doroszewski (2011) this result was visible in the process of tillering, heading and in the flowering of wheat. In experiments with a low R/FR ratio, the various plant development phases were found to occur at the fastest rate and last for the shortest time.

Most plants are very sensitive to changes in the quality of the radiation they are exposed to and they detect neighbouring competitive plants through a signal in the form of FR reflected from them. Based on own research it may be stated that this signal was an element that determines the developmental dynamic and causes differences in barley morphology such as: the longevity of the internodes, shoots and ears, plant height as well as the number of: 1) shoots with ears, 2) shoots without ears and 3) the total number of shoots. Previous studies by Doroszewski (1997, 2003) that were conducted in natural conditions with rye and buckwheat showed that the limit of the impact of FR on plants originated from reflection from the surface of the soil (grass) and amounted to about 50 cm. This distance was just sufficient, because for plants growing in conditions of reflected radiation with a low R/FR ratio, adaptation responses to competitive conditions occurred, these included the acceleration of development and longer internodes. The research conducted to date with mustard and tobacco showed that the mutual impact of plants took place at a lower distance, *i.e.* 30 cm (Casal and Smith, 1989; Smith *et al.*, 1990; Ballaré *et al.*, 1987).

The results of Doroszewski's research (2001, 2020) also suggest that physiological processes, *i.e.* a decrease in the level of stomatal conductance and transpiration as well as the formation of a lower number of stomata were the effect of the specific composition of spectral radiation. It may be supposed that the physiological and photomorphological processes in plants were directed towards a particular final effect – the optimization of the adapted processes to the existing conditions of radiation and as a consequence, the promotion of survival for the production of seeds (progeny).

Similar results concerning the more rapid development of plants surrounded by grass (low R/FR ratio) in comparison with fallow (high R/FR ratio) were also observed in experiments performed with rye and buckwheat (Doroszewski, 1997, 2003). In addition, in the presented studies, it was found that the spectral composition of the radiation was the factor which differentiated the development of the barley in the growth chambers. In natural conditions of radiation, particular developmental phases of plants also occurred earlier in those experiments where the neighbouring grass emits more FR in comparison with the fallow with lower amounts of FR radiation (Doroszewski, 2011).

The development of plants in the whole period of vegetation occurred more rapidly in growth chambers D and C with a low R/FR ratio in comparison with plants grown in a high R/FR ratio which is present in chambers A and B. Similar dependencies were observed in the development of wheat plants (Doroszewski, 2011).

CONCLUSIONS

1. The spectral composition of the radiation was found to be a factor which differentiated plant development. Barley grown under control conditions with a low red to far-red ratio developed more rapidly in comparison with plants grown under the conditions of a high red to far-red ratio.
2. The acceleration of plant development was caused by far-red originating from the transmission and reflection of light from the green tissues of neighbouring plants. It plays an informative role enabling the adjustment of plant existence to real or expected competition.
3. The observed differences in the development, habit and yields of barley showed that due to radiation with a low red to far-red ratio, plants were prepared for the anticipated competitive (shading) conditions and showed some adaptive responses.

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