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Temperature and photoperiod effects on photosynthetic indices of radish (*Raphanus sativus* L.)

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Abstract

The experiments were performed in 2010 at the Institute of Horticulture, Lithuanian Research Center for Agriculture and Forestry in the phytotron chambers, under controlled environment conditions.

The aim of this study was to investigate the effect of different temperatures and photoperiod conditions on photosynthetic pigments accumulation, carbohydrate distribution and assimilative indices of radish (*Raphanus sativus* L. 'Faraon'). The day/night temperature and photoperiod were maintained at 4ºC and 8 hours (F1), 4ºC and 16 hours (F2) in freezer chambers and 18/14°C and 8 hours (F3), 18/14°C and 16 hours (F4) in phytotron chambers, respectively. Just after cotyledons formation radishes were transferred to freezer chambers F1 and F2 for low positive temperature further (low-temperature) treatment, other plants were treated under F3 and F4 conditions. 14 days later radishes were moved from F1, F2 and F3 to the F4 conditions till the end of experiment (29 days).

Our investigation revealed that low-temperature (4ºC) influenced the development of radishes by increasing biomass accumulation in storage organs further (roots) and accelerating plant growth (relative growth rate, net assimilation rate). Increased shoot-to-root ratio and specific leaf area showed that under ordinary temperature conditions (18/14ºC) radish grew more leaves but accumulated less assimilative products in roots. The lowest photosynthetic pigments concentration was found under long-day photoperiod independent of temperature treatment (F2 and F4). After the 1st measurement, in F2 treatment the highest and in F3 the lowest content of all carbohydrates in roots and leaves further (shoots) were determined but after the 2nd measurement there were no big differences between all treatments, because in 29 days growing under ordinary temperature and long-day period the development level of differently treated radishes equalized. In summary, low temperature had the strongest effect on the carbohydrate accumulation in roots and shoots. At the maturity stage, there were no differences in carbohydrate contents. Moreover, the dry weight of roots increased due to carbohydrates allocation from shoots to roots. Under low-temperature and short-day photoperiod relative growth and net assimilation rates of radishes were higher during all experiment.

Key words: radish, temperature, assimilative indices, carbohydrates, photoperiod.

Introduction

Raphanus sativus is a cool-season plant which grows best in spring and autumn in many European countries. The temperature is a primary environmental factor influencing the rate of plant development. Plants can acclimate to their light environment at several integration levels. Firstly, they can change the fraction of biomass invested in leaves, stems and roots. Secondly, they are able to modulate the leaf area per unit biomass invested in leaves, by altering their anatomy. Thirdly, they can change the relative investment of nitrogen between photosynthetic components (Evans, Poorter, 2001). Environmental conditions play a significant role in the regulation of root and shoot biomass. It is especially important that plant growth response in the course of adaptation to treatments implies the coordination of shoot and root growth aimed at the optimization of resource consumption (Hsiao, Xu, 2000).

Since leaf development has a strong relationship with growth, knowing changes in biometrical parameters (Montero et al., 2000), and chlorophyll meter could be useful for estimating radish growth and prediction of production (Le Bail et al., 2005). Also, plant growth can be defined as the increase of dry materials in plant or increase of plant parts numerically. One of the most useful indices of plant growth is the relative growth rate (RGR). It assumes that new growth is related to existing biomass and is therefore exponential (Odabas et al., 2005). Firstly, they can change the fraction of biomass invested in leaves, stems and roots (Evans, Poorter, 2001). The aim of this study was to investigate the effect of different temperatures and photoperiod conditions on chlorophyll accumulation, carbohydrate distribution and assimilative indices of radish.

Materials and methods

The experiments were performed in 2010 at the Institute of Horticulture, Lithuanian Research Center for Agriculture and Forestry in the phytotron chambers, under controlled environmental conditions. The day/night temperature and photoperiod were maintained at 4ºC and 8 hours (F1), 4ºC and 16 hours (F2) in freezer chambers and 18/14°C and 8 hours (F3), 18/14°C and 16 hours (F4) in phytotron chambers. The radish (*Raphanus sativus* L. 'Faraon') was sown in peat substrate, pH 6. Just after cotyledons formation radishes were transferred to freezer chambers F1 and F2 for low-temperature treatment, other plants were treated under F3 and F4 conditions. 14 days later radishes were transferred from F1 and F2 to the F4 till the end of experiment (29 days). At the end of experiment radishes were in the 2nd stage of organogenesis.

Plants were illuminated by high-pressure sodium lamps "SON-T Agro" ("Philips", USA).

Photosynthetic pigments were measured by spectrometric method of Wetshtein (Гавриленко, Жигалова, 2003). Pigments were extracted with 100% acetone. A "Genesys 6" spectrophotometer was used for the analysis ("Thermospectronic", USA).

Carbohydrates were measured by a high performance liquid chromatography (HPLC) method. About 1 g of fresh weight of plant tissue (leaves) was ground and eluted with 70ºC bi-distilled water. The extraction was carried out for 24 h. The sample was filtered through cellulose and cellulose acetate (pore diameter 0.25 μm) filters. The analyses were performed on "Shimadzu HPLC" (Japan) chromatograph with refractive index detector ("RID 10A"); oven temperature was maintained at 80ºC. Separation of carbohydrates was performed on "Shodex SC-1011" (Japan) column (300 x 4.6 mm), mobile phase – bi-distilled water.

The leaf area of radish was measured by "WinDias" leaf area meter ("Delta-T Devices", UK). For determination of dry weight shoots and roots were dried in a drying oven at 105°C for 24 h.

Assimilative indices were calculated as follows:

relative growth rate (RGR) – the variation in the RGR can be partitioned into an assimilatory component, net assimilation rate (NAR), and morphological component, leaf area ratio (LAR). It was obtained by the following formula RGR (g d^{-1}) = NAR x LAR (Hunt et al., 2002);

net assimilation rate (NAR) – the net assimilation rate of a plant is defined as its growth rate per unit leaf area for any given time period (day). It can be calculated as: NAR (g^{-1} cm^{-2} d^{-1}) = (1/LA) x (dW/dt), where LA is leaf area (cm^2) and dW/dt is the change in plant dry mass per unit time;

leaf area ratio (LAR) – the total surface area of a plant's leaves (cm^2) divided by the dry weight of the plant (g);

specific leaf area (SLA) – is the ratio of leaf area (cm^2) per plant to leaf dry weight;

leaf weight ratio (LWR) – is the ratio of total leaf weight (g) to total plant weight (g);

shoot root ratio (SRR) – is the ratio of shoot-to-root.

The standard deviation of mean (p = 0.05) of biological (n = 6) and analytical (n = 3) replications calculated by *MS Excel* program are presented in the Table and Figures.

Results and discussion

The outcome of the experiment showed that radish roots grown under low-temperature (F1, F2) were larger, grew faster and accumulated more photosynthetic products than those grown under the ordinary (18°C) temperature (F3, F4) (Table). Besides, it is known that environmental conditions play a significant role in the regulation of root and shoot biomass (Vysotskaya, 2005). It is especially important that plant growth response in the course of adaptation to treatments implies the coordination of shoot and root growth aimed at the optimization of resource consumption (Hsiao, Xu, 2000). SRR values compared with the first and second measurements revealed that two weeks of low-temperature exposure had a positive influence on growth of radishes roots (Table).

It is clear that the highest differences between SRR ratios are among radishes after 2 weeks of low-temperature treatment (F1, F2) and radishes grown at ordinary (18°C) temperature (F3, F4). This difference indicates that radishes after short term of low-temperature accelerate their growth. Differences between photoperiod showed that short-day (8 hours) period was the best for fast growth, but under long day (16 hours) conditions radishes accumulated slightly less dry mass in roots and in leaves (Fig. 1).

Increased SRR ratio also shows that in F3 and F4 treatments radishes formed more shoots than accumulated assimilative products in roots. SLA data confirmed that leaf area was higher than in F1 and F2 treatments (Table). This means that for optimal growth morphological or physiological plasticity in the shoot-to-root ratio is required. In addition to the change in the biomass shoot-to-root ratio, plants could also have alternative ways to change resource allocation to gain limiting resources, by changing the morphology and chlorophyll concentration in leaves (Aikio, Markkola, 2002).

The highest SLA was obtained from F3 treatment after both measurements. SLA represents the mean leaf area per unit of leaf weight. It measures leaf density or relative thickness. In plants the higher SLA, the thinner the leaf is. Our results evidence that SLA ratio increased more than 3-fold after second measurement, but LWR did not change at all (F3, F4). In F1, F2 treatments LWR decreased more than twice.

Table. The influence of different temperature and photoperiod conditions on radish assimilative indices

Treatments	SRR	SLA $cm^2\ kg^{-1}$	LWR $g\ kg^{-1}$	RGR $g\ d^{-1}$	NAR $g\ cm^{-2}\ d^{-1}$	LAR $cm^2\ kg^{-1}$
1st measurement (after low-temperature treatment, 14 days)						
F1	5.26 ± 2.81	592.38 ± 35.11	0.89 ± 0.06	0.08 ± 0.02	0.15 ± 0.03	9.54 ± 0.96
F2	7.02 ± 0.57	329.95 ± 8.84	0.87 ± 0.01	0.04 ± 0.01	0.01 ± 0.00	80.03 ± 10.59
F3	9.21 ± 1.68	1268.16 ± 508.47	0.05 ± 0.01	0.03 ± 0.01	0.01 ± 0.00	90.82 ± 20.04
F4	8.55 ± 1.18	361.96 ± 280.59	0.05 ± 0.04	0.03 ± 0.01	0.02 ± 0.01	70.94 ± 14.39
2nd measurement (after experiment, 29 days)						
F1	0.61 ± 0.22	537.87 ± 59.47	0.36 ± 0.07	0.03 ± 0.01	0.13 ± 0.02	41.15 ± 14.71
F2	0.44 ± 0.08	591.55 ± 23.50	0.30 ± 0.04	0.02 ± 0.01	0.01 ± 0.00	209.14 ± 21.15
F3	8.39 ± 2.26	4624.83 ± 555.04	0.05 ± 0.02	0.01 ± 0.00	0.01 ± 0.00	99.20 ± 17.36
F4	5.98 ± 1.04	1384.41 ± 786.49	0.05 ± 0.04	0.02 ± 0.01	0.01 ± 0.01	233.49 ± 41.53

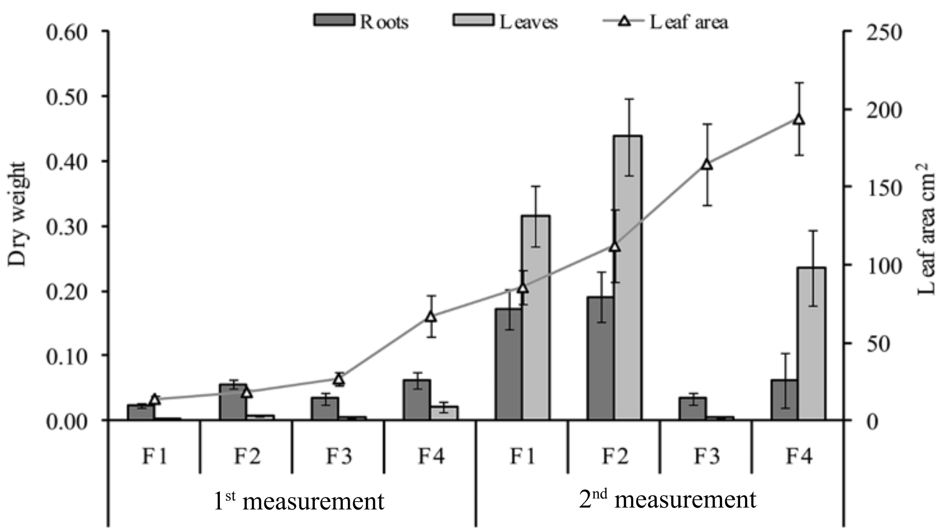

Figure 1. The dry mass distribution in radish roots and leaves, and leaf area per plant

The highest NAR and RGR were obtained from F1 treatment after both measurements (Table). Net assimilation rate (NAR) is one of the most important growth parameters. It describes the net production efficiency of the assimilatory apparatus. The RGR is the product of NAR and LAR, where NAR is largely the net result of carbon gain (photosynthesis) and carbon losses (respiration, exudation) expressed per unit leaf area (Poorter, Remkes, 1990). The highest RGR value in F1 (Table) suggests that treatment with low temperature and short-day photoperiod is the best conditions for fast root growth. An increase in NAR also requires an increased rate of photosynthesis, which can be realized by extra investment in photosynthesis apparatus, thus decreasing SLA. Alternatively, the balance between the amount of roots and the amount of leaf area could influence the water status of leaves and hence the rate of photosynthesis (Poorter, Remkes, 1990). Ushio et al. (2008) observed that the change in NAR was similar to our results of RGR, and NAR between both measurements (Table).

The increase of LAR indicates that after second measurement leaves were thinner than after first one because of the influence of short-day photoperiod (Table). Poorter (2002) observed that an increase in SLA implies that leaves invest less biomass per unit area. This will come, at least partly, at the expense of the photosynthetic machinery. Therefore a lower rate of photosynthesis per unit leaf area can be expected.

The highest LAR was obtained in F3 treatment after 1st measurement (after low-temperature) and in F4 at the end of experiment (Table). The

LAR is the ratio of leaf area to total plant weight and is the product of morphological component (SLA), the ratio of leaf area to leaf weight, and the LWR, indicating the fraction of total plant weight allocated to the leaves (Poorter, Remkes, 1990). In F3, after 1st measurement the increase of LAR was caused by increase of SLA, or after 2nd measurement in F4 treatment LAR increase was influenced by long-day photoperiod (Table). The change in leaf area ratio depends on the light and temperature, and it is observed that the leaf area ratio is in inverse proportion with them (Kaneko, Suzuki, 2006). It is known that there is a linear relationship between the specific leaf area and light intensity (Caliskan et al., 2010). The increase of temperature also increases the specific leaf area (Table).

Our results showed the different effect of low-temperature and different photoperiod on photosynthetic pigments accumulation and chlorophyll ratio (Fig. 2). After F1 and F2 treatments photosynthetic pigments levels were lower than in plants grown under F3, F4 treatments (Fig. 2). It indicates that radish leaves responded to low temperature by accumulating less chlorophyll *a* and *b*. Krol and co-authors (1999) also stated that exposure to low temperature inhibited chlorophyll *a* and *b* accumulation, and according to LWR, leaf weight and RGR, NAR were measured the highest (Table).

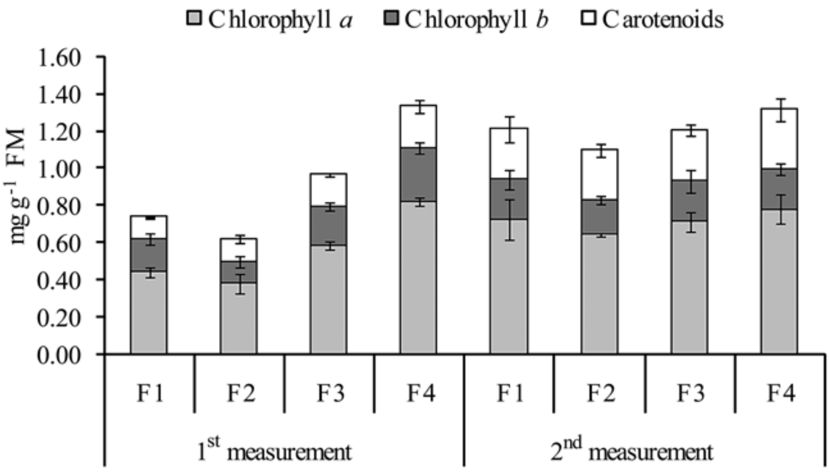

Figure 2. The content and ratio of photosynthetic pigments in radish leaves under F1, F2, F3, F4 treatments

The lowest chlorophylls content was found in F2 and the largest in F4 after both measurements (Fig. 2). This suggests that the highest influence on chlorophyll accumulation was exerted by different temperature and photoperiod treatments. Our findings suggest that low-temperature decreased photosynthetic pigments levels in shoots (Fig. 2), but increased growth rate of roots (Table). The combination of short-day (F1) and low-temperature treatment had the biggest influence on radish root growth. The opposite result was obtained under long day (F3) and 18°C temperature treatment.

The highest in F2, and the lowest in F3 contents of raffinose, sucrose and glucose in roots and shoots were determined after 1st measurement. It is clear that F3 conditions are the worst for growth of radishes. RGR, NAR had the lowest values and SRR the highest (Table). This shows that short-day photoperiod was not sufficient for normal plant growth. In F2 treatment, long-day photoperiod and low-temperature influenced the accumulation of carbohydrates and almost all values were higher compared with other treatments (Fig. 3). This indicates, that high content of carbohydrates, particularly that of glucose, not only displays a higher activity of photosynthesis (Smeekens, 2000), but also has nutritional importance, since in vegetable food, they are more valuable sugars than disaccharides.

At the end of experiment, an increase in glucose, mannose and fructose content in radish roots was observed under all treatments. While in leaves only a slight increase in raffinose in F2 and sucrose in F3, F4 (Fig. 4) was detected. The distribution of dry mass in roots and shoots increased in F1 and F2 treatments. In F3, there were no differences between both measurements, or in F4 the increase in shoots was observed (Fig. 1). Sucrose is the transport carbohydrate most widely distributed in the plant kingdom. It forms the interface between photosynthetic ally active source tissue serving as an energy source for growth and development or supplying the accumulation of storage reserves such as glucose and fructose. Beyond its role in energy metabolism, sucrose and its metabolites have been shown to effect the expression of genes involved in a number of metabolic pathways (Koch, 1996).

It is clear that after 1st measurement the content of carbohydrates was mainly influenced by the combination of low-temperature and long-day photoperiod, but at the end of experiment (2nd measurement) the content of carbohydrates was similar, because after 29 days in the same F4 treatment radishes reached the same level of development.

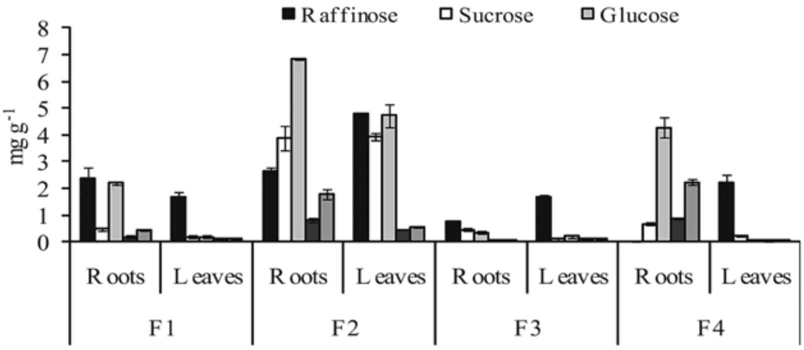

Figure 3. The content of carbohydrates in fresh mass (FM) of radish leaves and roots after different temperature and photoperiod treatments (1st measurement)

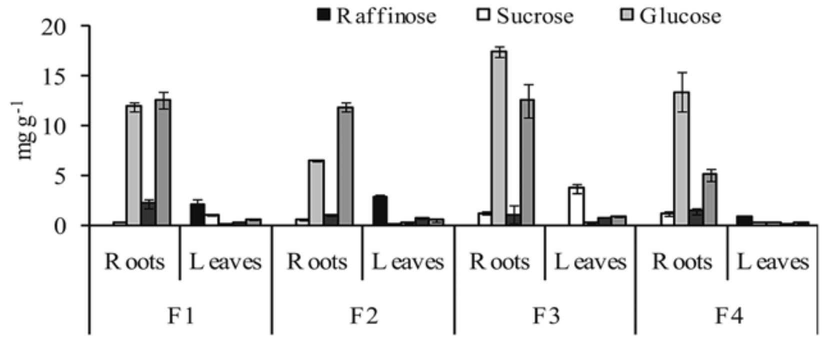

Figure 4. The content of carbohydrates in fresh mass (FM) of radish shoots and roots at the end of experiment (2nd measurement)

Conclusion

Our investigation revealed that low-temperature (4ºC) influenced the development of radishes by increasing biomass accumulation in roots and accelerating plant growth (relative growth rate, net assimilation rate). Increased shoot-to-root ratio and specific leaf area showed that under ordinary temperature conditions (18/14ºC) radish produced more leaves but accumulated less assimilative products in roots. The lowest photosynthetic pigments concentration was found under long-day photoperiod independent of temperature treatment (F2 and F4). After the 1st measurement, in F2 treatment the highest and in F3 the lowest content of all carbohydrates in roots and shoots were determined, but after the 2nd measurement there were no marked differences between all treatments, because in 29 days growing under ordinary temperature and long-day period the development level of differently treated radishes equalized. In summary, low temperature had the strongest effect on the carbohydrate accumulation in roots and shoots. At the maturity stage, there were no differences in carbohydrate contents. Moreover, the dry weight of roots increased due to carbohydrates allocation from shoots to roots. Under low-temperature and short-day photoperiod relative growth and net assimilation rates of radishes were higher during all experiment.

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Skirtingų temperatūrų ir fotoperiodo poveikis valgomojo ridiko (*Raphanus sativus* L.) fotosintezės rodikliams

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Santrauka

Tyrimai atlikti 2010 m. Lietuvos agrarinių ir miškų mokslų centro Sodininkystės ir daržininkystės instituto fitotrono kamerose kontroliuojamomis aplinkos sąlygomis. Tyrimų tikslas – nustatyti skirtingų temperatūrų ir fotoperiodo sąlygų įtaką valgomojo ridiko (*Raphanus sativus* L.) fotosintetinančių pigmentų kaupimuisi, angliavandenių pasiskirstymui ir asimiliaciniams rodikliams.

Dienos/nakties temperatūra ir fotoperiodas buvo 4 ºC bei 8 val. (F1), 4 ºC bei 16 val. (F2) šaldymo kamerose ir atitinkamai 18/14 °C bei 8 val. (F3), 18/14 °C bei 16 val. (F4) fitotrono kamerose. Iškart po skilčialapių suformavimo ridikai (veislė 'Faraon') buvo perkelti į šaldymo kameras, siekiant paveikti F1 ir F2 žemomis teigiamomis temperatūromis, likusieji augalai laikyti F3 ir F4 sąlygomis. Po 14 dienų ridikai iki tyrimo pabaigos (29 dienoms) iš F1, F2 ir F3 buvo perkelti į F4 sąlygas.

Nustatyta, kad žema teigiama temperatūra (4 ºC) lėmė greitesnį ridikų vystymąsi, paskatino biomasės kaupimąsi šakniavaisiuose ir augalų augimą (santykinis augimo greitis ir grynasis fotosintezės produktyvumas). Padidėjęs lapų bei šakniavaisių santykis ir specifinis lapų plotas parodė, kad normalios (18/14 ºC) temperatūros sąlygomis ridikai formavo daugiau lapų nei šakniavaisiuose kaupė asimiliatų. Fotosintetinančių pigmentų mažiausia koncentracija nustatyta ilgos dienos sąlygomis, nepriklausomai nuo temperatūros režimo (F2 ir F4).

Šakniavaisiuose ir lapuose po pirmojo matavimo F2 sąlygomis nustatytas didžiausias, o F3 – mažiausias angliavandenių kiekis, bet po antrojo matavimo didelių skirtumų tarp nevienodų sąlygų nebuvo nustatyta, nes ridikai 29 dienas buvo laikomi normalios temperatūros ir ilgos dienos sąlygomis, todėl jų išsivystymo lygis suvienodėjo.

Taigi galima teigti, kad žema teigiama temperatūra turėjo didžiausią poveikį angliavandenių kaupimuisi šakniavaisiuose ir lapuose. Ridikams pasiekus brandos tarpsnį nebuvo pastebėta skirtumų tarp angliavandenių kiekio. Be to, sausos masės kiekis šakniavaisiuose padidėjo dėl angliavandenių persiskirstymo iš lapų į šakniavaisius. Santykinis augimo greitis ir grynasis fotosintezės produktyvumas esant žemai temperatūrai ir trumpos dienos fotoperiodui buvo didžiausi viso eksperimento metu.

Reikšminiai žodžiai: valgomasis ridikas, temperatūra, asimiliaciniai rodikliai, angliavandeniai, fotoperiodas.