

Low UV-B radiation and substrate acidity impact on photosynthetic parameters of *Brassica napus*

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The aim of this study was to assess combined effect of $1 \text{ kJm}^{-2}\text{d}^{-1}$ UV-B radiation and substrate acidity (pH 4.8) on photosynthesis and growth of summer rape (*Brassica napus*) in a controlled environment. Rape were sown in a neutral (pH 6.0–6.5) peat substrate, when 2nd true leaf unfolded, growth substrate was acidified using $0.07 \text{ mM H}_2\text{SO}_4$ concentration solution and UV-B radiation exposure was started. Duration of the experiment: five days. Gas exchange parameters were measured with portable photosynthesis system LI-6400. Content of chlorophyll was evaluated spectrophotometrically. The results showed that the highest inhibition on *Brassica napus* growth and photosynthetic parameters was under combined effect of $1 \text{ kJm}^{-2}\text{d}^{-1}$ UV-B radiation and pH 4.8 substrate acidity. The impact of single $1 \text{ kJm}^{-2}\text{d}^{-1}$ UV-B radiation on investigated parameters was low and statistically insignificant, except transpiration rate and water use efficiency. Single substrate acidity affected in 58.6% ($p < 0.05$) decrease in photosynthetic rate, almost twofold decrease of transpiration rate, and 3.8% ($p < 0.05$) decrease in intercellular CO_2 concentration, and 27.1% ($p < 0.05$) increase in water use efficiency, compared to the reference treatment. Combined substrate acidity and UV-B radiation effect on photosynthetic rate was the highest, when the decrease was 80.6% ($p < 0.05$), compared to the reference treatment. The changes of transpiration rate under combined effect of investigated stressors compared to the reference treatment were insignificant ($p > 0.05$). The increase (by 2%, $p < 0.05$) of intercellular CO_2 concentration of *Brassica napus* affected by combined impact of investigated stressors shows that higher negative impact was on enzymatic reactions of photosynthesis than on transpiration. The highest negative effect on content of photosynthetic pigments and biomass accumulation also was of combined effect of investigated stressors.

Key words: net photosynthesis, intercellular CO_2 concentration, transpiration, water use efficiency, photosynthetic pigments, dry biomass, *Brassica napus*

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INTRODUCTION

Abiotic and biotic stresses cause alterations in normal physiological processes of all plant organisms. Recently, along natural stress factors plant organisms are imposed to a large scale of new stressors related to human activity. All these stresses decrease the biosynthetic capacity of plant organisms, alter their normal functions and cause damages which may lead to plant death [1, 2].

During the later part of the 20th century the average of UV-B irradiances in the biosphere has increased. Ultraviolet wavelengths greater than 280 nm (UV-B radiation) are an ubiquitous component of the solar radiation, but their levels considerably vary in the biosphere spatially and temporally [3]. UV-B causes damage to DNA, proteins and membranes, impedes photosynthetic activities, and disturbs plant growth [4]. Other studies demonstrate that increased levels of UV-B mainly affect PS II in the thylakoid membranes, specifically the functionality of the D1 protein, decreasing the electron transport efficiency [5]. UV-B has been also shown to affect the activity of enzymes of the carbon reduction metabolism, mainly Rubisco, and in this way directly involved in the CO₂ assimilation and biomass production [6]. UV-B radiation decreases plant height, stem length and leaf area in a number of species including wheat, rice, pea, sunflower, tomato and lettuce [7]. Since UV-B induces general stress responses in plants, the syntheses of a broad variety of metabolites regarding growth, development and defence may be affected [8]. Plant tissues respond to UV-B by inducing cellular protective processes that include changes in phenylpropanoid metabolism with increased synthesis of UV-B absorbing compounds, mostly flavonoids and other related phenolics [9]. Although UV-absorbing compounds primarily protect the DNA molecule [3]. Also, the effects of UV-B radiation on photosynthesis vary among species. In some species, UV-B radiation can negatively affect leaf photosynthesis [10, 11], but in some others it has little or no effect [12].

The problem of soil acidification resulting from the acid rains and application of fertilizers has been known for many years. The acidification can result in negative impact on root metabolism and decrease plant growth and yields when soil pH falls to less than critical thresholds (usually less than 5.5) which leads to increased activity of aluminum (Al) and manganese (Mn) [13, 14]. Increased concentration of aluminium ions (Al³⁺) in soil inhibits root elongation by disrupting the function of the plasma membrane, cell wall, Ca homeostasis and signal transduction pathways [15]. This reduces the capacity of roots to explore soil for moisture and nutrients [16]. Soil acidification can also lead to leaf yellowing and whole plant net photosynthetic rate decrease [17], because of all the mentioned negative impacts on root [15, 16] and reduced content of chlorophylls [17].

Several studies have demonstrated that other environmental factors can influence the effect of UV-B on plants, which may explain the inconclusive results of many field studies. For example, water supply has been shown to influence the effect of supplemental (1.2 kJm⁻²d⁻¹ UV above ambient) UV-B on the growth and photosynthetic electron flow of several *Arctic bryophytes* [18]. Paoletti [19] has studied UV-B and acid rain effects on beech (*Fagus sylvatica* L.) and holm oak (*Quercus ilex* L.) leaves. Beech leaves were more sensitive to UV-B radiation and to acid fog spraying than those of holm oak. The combined treatment of UV-B radiation and acid fog induced the highest level of necrosis in leaf tissues, but of the two factors it was the acid fog that caused the most severe damage [19]. While our earlier experiments with radish showed a slightly different plant response to combined effect of the mentioned stressors, i. e. the decrease of photosynthesis of radish plants treated with substrate acidity and UV-B radiation was lower compared to the single impact of the substrate acidity. And UV-B radiation stimulated both enzymatic reactions of photosynthesis and water use efficiency of radish plants grown in acidified peat substrates [20]. So this

study focused on the combined impact of low UV-B radiation and substrate acidity on photosynthesis and growth of summer rape (*Brassica napus*) plants.

MATERIALS AND METHODS

Summer rape (*Brassica napus*; cv. 'Landmark') was chosen for investigation. Experiments were carried out in a vegetation room with controlled environment: photoperiod – 14 h, average temperature of 20–25 °C, relative humidity – 60%. "Philips Master Green Power CG T" 600 W lamps, light intensity at the level of plants 14000 Lx, provided light.

Rape (10 per pot) were sown in a neutral (pH 6.0–6.5) peat substrate in 5 L pots (21 cm in diameter). In each treatment there were three pots of replication. When 2nd true leaf unfolded, i. e. at leaf development stage (BBCH-12) [21] rape plants were divided into four groups: I) reference treatment group (substrate pH 6.5) was watered with distilled water all the time; II) rape plants were exposed to 1 kJm⁻²d⁻¹ UV-B radiation; III) growth substrate of rape plants was watered with 0.07 M concentration H₂SO₄ solution and growth substrate acidified till pH 4.8; IV) plants growth substrate was acidified as mentioned above till pH 4.8 and rape plants exposed to 1 kJm⁻²d⁻¹ UV-B radiation. The treatment variants were chosen according to earlier experiments at the Environmental Department of the VMU [20]. Duration of the experiment was five days.

Investigated indices net photosynthetic rate, intercellular CO₂ concentration, transpiration, water use efficiency, photosynthetic pigments and leaf area, fresh and dry biomass of shoot (foliage) of rape were measured at the end of the experiment.

Gas exchange parameters were measured with portable photosynthesis system LI-6400 (LI-COR, USA). Net photosynthetic rate (Pn) (μmol CO₂ m⁻²s⁻¹), intercellular CO₂ concentration (Ci) (μmol CO₂ mol air⁻¹), transpiration (Tn) (mmol H₂O m⁻²s⁻¹) and water use efficiency (WUE) (μmol CO₂ mmol H₂O⁻¹) of second

fully expanded leaves were registered every 3 seconds for 10 minutes; from these data were calculated a mean of day of measured indices. Environment conditions during experiments were as follows: air flow rate – 400 μmol s⁻¹; block and leaf temperature – 23 °C; CO₂ concentration in sample cell – 380–400 μmol CO₂ mol⁻¹; relative humidity in sample cell – 30%; lightness in quant – 110 μmol m⁻² s⁻¹.

The second fully expanded leaves were harvested and photosynthetic pigments were analysed using a spectrophotometer (Genesys 6, ThermoSpectronic, USA) in 100% acetone extracts prepared according to Wettstein's method [21]. Photosynthetic pigments were expressed in mg g⁻¹ of fresh weight.

The leaf area was determined using millimeter graph paper method. The leaves of five randomly taken plants from each variant were cut and spread over millimeter graph paper, and the area of the leaf was counted. The leaf area was expressed in cm² plant⁻¹.

At the end of the experiment the plants were harvested and dried in an oven at 60 °C until constant dry foliage biomass was obtained. The biomasses were expressed in mg plant⁻¹.

ANOVA was used to determine the effects of substrate acidity and UV-B. For the comparison of independent variables Student's t and U tests were used. All analyses were performed by STATISTICA and the results were expressed as mean values and their confidence intervals (CI) (p < 0.05).

RESULTS

Single 1 kJm⁻²d⁻¹ UV-B radiation had no statistically significant effect on net photosynthesis of rape plants, while substrate acidity decreased it markedly (Fig. 1). On the last day of the experiment the substrate acidity (pH 4.8) decreased the net photosynthesis of *Brassica napus* by 58.6% (p < 0.05) compared to the reference treatment (substrate pH 6.5). The inhibition of net photosynthesis of rape plants treated with both investigated factors (UV-B and substrate acidity) were the highest compared to the single impacts of the substrate

acidity and UV-B radiation, when 4.8 pH substrate and $1 \text{ kJm}^{-2}\text{d}^{-1}$ UV-B radiation dose decreased the net photosynthesis by 80.6%, compared to the reference treatment (pH 6.5). Compared to the combined impact of the investigated factors on photosynthesis of rape with single impact of UV-B radiation the net photosynthesis decreased by 76.4% ($p < 0.05$) and with pH 4.8 substrate – by 21.9% ($p < 0.05$).

Single $1 \text{ kJm}^{-2}\text{d}^{-1}$ UV-B radiation had no statistically significant effect on intercellular CO_2 concentration of *Brassica napus* (Fig. 2). Intercellular CO_2 concentration of rape leaves grown in pH 4.8 acidified substrate decreased by 3.8% ($p < 0.05$), but it increased by 1.6% ($p < 0.05$) under the combined impact of pH 4.8 and UV-B radiation (Fig. 2).

The changes of transpiration rate under investigated factors varied a slightly different tendency as net photosynthesis (Fig. 1), i. e. single $1 \text{ kJm}^{-2}\text{d}^{-1}$ UV-B radiation caused statistically significant increase in Tn of rape plants, while single substrate acidity decreased it 2.2 times (Fig. 3). The combined substrate pH 4.8 and $1 \text{ kJm}^{-2}\text{d}^{-1}$ UV-B radiation dose impact decreased the Tn only by 4.5% ($p > 0.05$) compared to the reference treatment (pH 6.5).

Both investigated factors affected water use efficiency of rape too (Fig. 4). Single $1 \text{ kJm}^{-2}\text{d}^{-1}$ UV-B radiation decreased WUE by 24.9% ($p < 0.05$) of rape plants, while single substrate acidity increased it by 27.1% ($p < 0.05$) (Fig. 4). The combined substrate pH 4.8 and $1 \text{ kJm}^{-2}\text{d}^{-1}$ UV-B radiation impact affected the decrease of WUE by 72.6% ($p < 0.05$) compared to the reference treatment (pH 6.5).

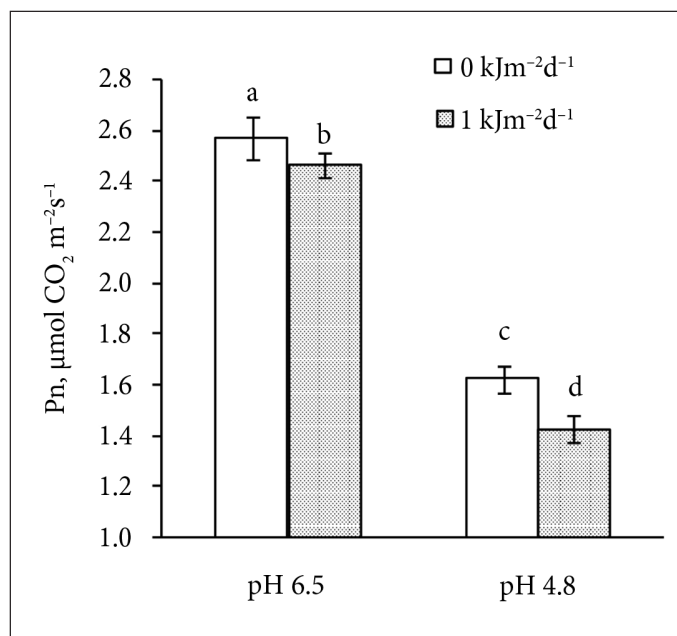


Fig. 1. The effects of $1 \text{ kJm}^{-2}\text{d}^{-1}$ UV-B radiation and different (pH 6.5 – reference treatment, pH 4.8) substrate acidity on net photosynthetic rate (Pn) of *Brassica napus*. The values are means $\pm \text{CI}_{0.05}$. Significant differences ($p < 0.05$) between treatments are denoted with different letters

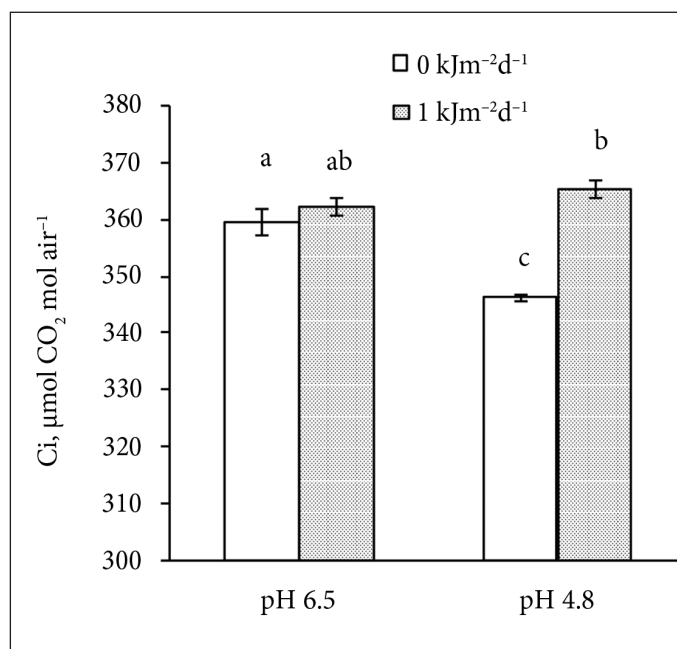


Fig. 2. The effects of $1 \text{ kJm}^{-2}\text{d}^{-1}$ UV-B radiation and different (pH 6.5 – reference treatment, pH 4.8) substrate acidity on intercellular CO_2 concentration (Ci) of *Brassica napus*. The values are means $\pm \text{CI}_{0.05}$. Significant differences ($p < 0.05$) between treatments are denoted with different letters

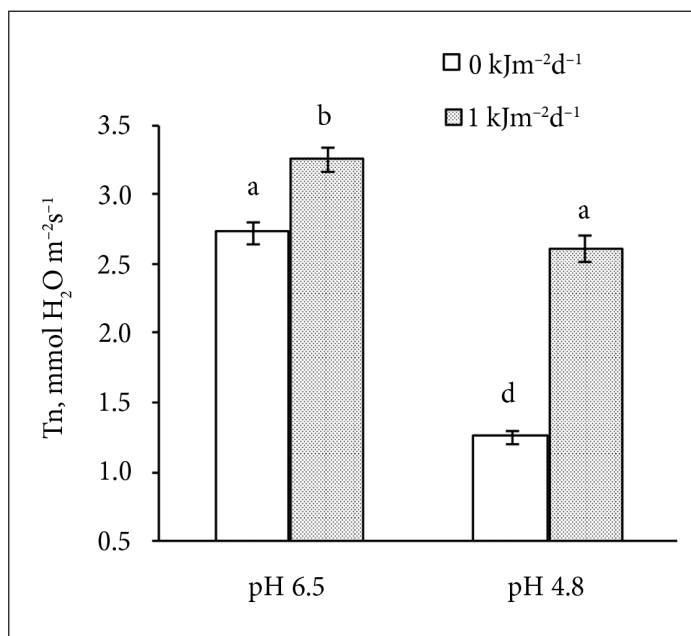


Fig. 3. The effects of 1 kJm⁻²d⁻¹ UV-B radiation and different (pH 6.5 – reference treatment, pH 4.8) substrate acidity on transpiration rate (Tn) of *Brassica napus*. The values are means \pm CI_{0.05}. Significant differences ($p < 0.05$) between treatments are denoted with different letters

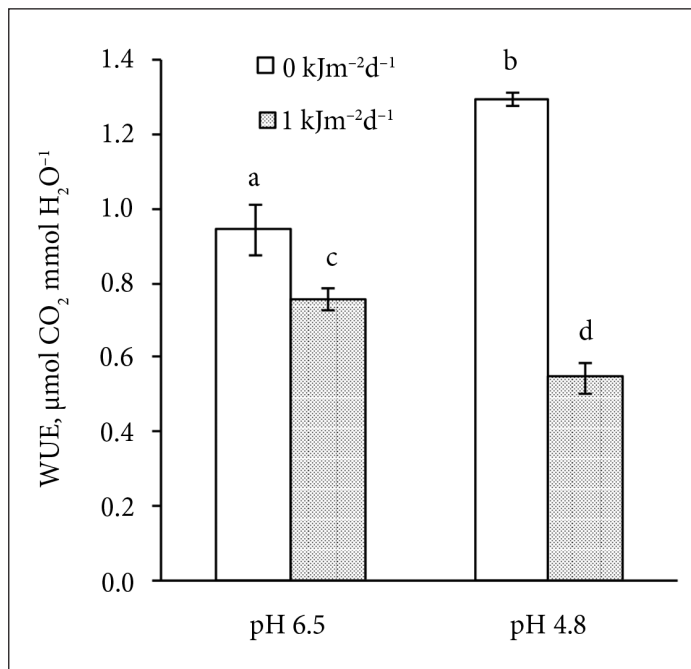


Fig. 4. The effects of 1 kJm⁻²d⁻¹ UV-B radiation and different (pH 6.5 – reference treatment, pH 4.8) substrate acidity on water use efficiency (WUE) of *Brassica napus*. The values are means \pm CI_{0.05}. Significant differences ($p < 0.05$) between treatments are denoted with different letters

Single 1 kJm⁻²d⁻¹ UV-B dose impact decreased chlorophyll *a* and chlorophyll *b* content by 23.2% ($p > 0.05$) and 26.5% ($p > 0.05$) respectively, compared to the reference treatment (Fig. 5). While the single pH 4.8 substrate acidity effected in chlorophyll *a* and *b* content increase by 25.0% and 15.4% respectively, but also statistically insignificant compared to the reference treatment (pH 6.5). Chlorophyll *b* was more sensitive to combined UV-B radiation and substrate acidity impact than chlorophyll *a* and carotenoids. Thus the combined UV-B and substrate acidity effect caused 91.7% ($p < 0.05$), 2.1 times ($p < 0.05$) and 82.6% ($p < 0.05$) decreases of chlorophyll *a*, chlorophyll *b* and carotenoids respectively, compared to the reference treatment.

Combined impact of UV-B radiation and substrate acidity on biomass accumulation followed the same tendency as on other investigated indices, i. e. the decreases were higher compared to the single impact of the investigated factors. Leaf area, fresh and dry foliage biomasses of *Brassica napus* plants exposed to single UV-B radiation increased by 11.3, 14.3 and 22.6% respectively, but statistically insignificant (Fig. 6a, b, c). Single and combined substrate acidity effect decreased leaf area by 77.6% ($p < 0.05$) and 73.2% ($p < 0.05$) respectively, compared to the reference treatment. Only combined impact of substrate acidity (pH 4.8) led to statistically significant decrease of dry biomass of foliage, when it decreased by 70.6%, compared to the reference treatment (pH 6.5) ($p < 0.05$).

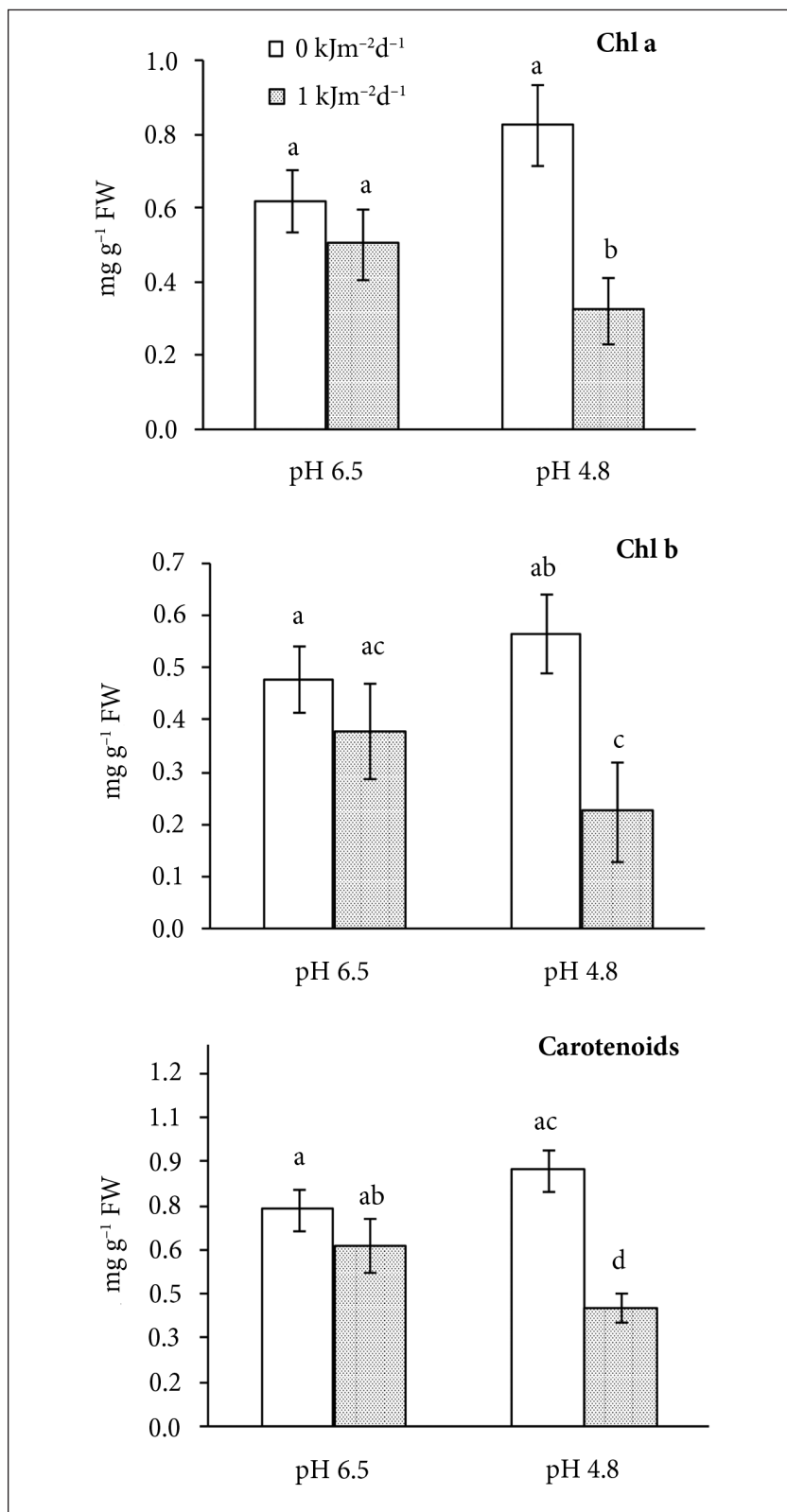


Fig. 5. The effects of 1 kJm⁻²d⁻¹ UV-B radiation and different (pH 6.5 – reference treatment, pH 4.8) substrate acidity on content of chlorophyll *a* (Chl *a*), chlorophyll *b* (Chl *b*) and carotenoids in *Brassica napus* leaves. FW – fresh weight. The values are means \pm CI_{0.05}. Significant differences ($p < 0.05$) between treatments are denoted with different letters

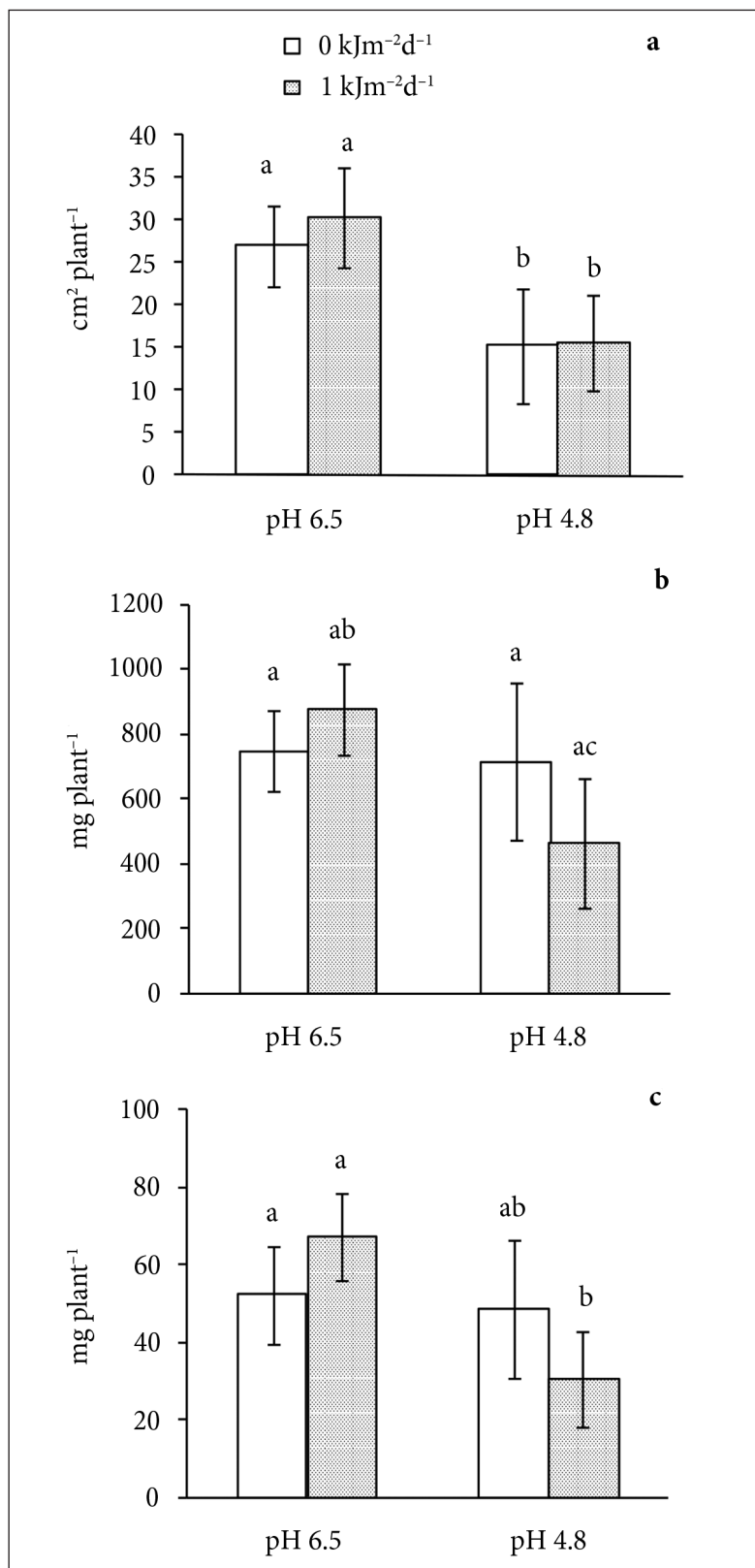


Fig. 6. The effects of 1 kJm⁻²d⁻¹ UV-B radiation and different (pH 6.5 – reference treatment, pH 4.8) substrate acidity on leaf area (a), content of fresh (b) and dry (c) shoot biomasses of *Brassica napus* plants. The values are means \pm CI_{0.05}. Significant differences ($p < 0.05$) between treatments are denoted with different letters

DISCUSSION

The combined influence of different stress factors can lead to death of a plant or can increase its resistance to subsequent unfavourable impacts. The effects vary among species [22]. Some plants respond positively to the ambient levels of UV-B radiation, but the majority react negatively. Enhanced levels of UV-B radiation can commonly negatively affect plant physiological processes and growth [24]. Decrease in plant growth is considered to result from damage of DNA [25] to photosynthetic apparatus [12]. In our research, the investigated $1 \text{ kJm}^{-2}\text{d}^{-1}$ UV-B radiation caused photosynthetic rate decrease (Fig. 1), but stimulated transpiration rate (Fig. 3); compared to non-exposed *Brassica napus* plants. Qaderi and Reid [26] got similar results, when low $4.2 \text{ UV-B kJm}^{-2}\text{d}^{-1}$ radiation affected decrease of photosynthetic rate and water use efficiency and increase of transpiration rate for *Brassica napus* plants [26]. Single substrate acidity resulted in a high (58.6%, $p < 0.05$) photosynthetic rate inhibition and in the highest (2.2 times, $p < 0.05$) decrease of transpiration rate, compared to the reference treatment (Figs. 1 and 3). This shows that stomata were closed, WUE increased (Fig. 4), and this resulted in 27.1% ($p < 0.05$) decrease of C_i (Fig. 2) as CO_2 did not reach the intercellular area. In the study of Izuta et al. [27], photosynthetic rate was also significantly reduced in the seedlings grown in the acidified soils. The highest inhibition of net photosynthesis and the highest intercellular CO_2 concentration of *Brassica napus* plants grown in pH 4.8 acidified peat substrate and exposed to UV-B shows that stress had intense effect on reactions of dark phase of photosynthesis. The net rate of CO_2 assimilation is determined by biophysical processes, which include CO_2 transport through the leaf and stomata, and biochemical processes located in the cells of plants. In this research, under combined impact of investigated factors stomata were not closed, because transpiration rate changed statistically

insignificantly (Fig. 3), hence CO_2 transport into leaf was normal. Soil acidification inhibits biosynthesis of Rubisco in leaves [27], and the increase in intercellular CO_2 level indicates that net photosynthesis is reduced by reducing CO_2 fixation by Rubisco, or can also include conditions in which enzymes of the Calvin cycle were affected negatively [28].

Single UV-B radiation affected the non-significant decrease of content of chlorophyll *a*, chlorophyll *b* and carotenoids compared to the reference treatment (Fig. 5). In some studies UV-B radiation increases chlorophyll content [29], in others – decreases [12, 30], or has no effect [31]. UV-B radiation may be attenuated in leaves by leaf cuticles, or by UV-absorbing compounds produced and deposited in leaf epidermal cells or hairs [32] or by antioxidant systems [33, 4]. The single pH 4.8 substrate acidity affected also in statistically insignificant increase of chlorophyll *a* and *b* content compared to the reference treatment (Fig. 5). In most studies with increasing soil acidity, chlorophyll contents linearly decreases [34], but there are also different results reported earlier by Shan et al. [35] when chlorophyll contents of the seedlings linearly increased with increasing acidity of stimulated acid rain; while the combined UV-B and substrate acidity effect caused very high decreases of chlorophyll *a*, chlorophyll *b* and carotenoids. UV-B radiation can negatively affect plant physiological processes [24] because of the damage of DNA [25] and photosynthetic apparatus [12] as also shown in Figs. 1, 2, 4 and 5 of this research. Additional impact of substrate acidity increased this negative effect.

The acidification can result in negative impacts on root metabolism and decrease plant growth and yields when soil pH falls to less than critical thresholds ($<5.5 \text{ pH}$) [13, 14]. The combined treatment of UV-B radiation and acid fog affected the highest level of decreases in the research of Paoletti et al. [19]. The results of this research showed the same tendency, however, a significant impact on biomass accumulation was not determined except in case of *Brassica napus* affected by both (substrate acidity and

UV-B radiation) factors (Fig. 6). Under single and combined UV-B radiation impacts the increase of the leaf area of rape was detected, but not statistically significant (Fig. 6). Minimal effects of low UV-B radiation on biomass accumulation of other plants were assessed too [36, 18].

CONCLUSIONS

Single $1 \text{ kJm}^{-2}\text{d}^{-1}$ UV-B radiation impact on most investigated parameters was low and statistically insignificant, except transpiration rate and water use efficiency. UV-B radiation increased transpiration rate by 16.4% and decreased water use efficiency by 24.9% of rape plants statistically significant compared to the reference treatment.

Single substrate acidity affected in 58.6% ($p < 0.05$) decrease in photosynthetic rate, almost twofold decrease of transpiration rate, and 3.8% ($p < 0.05$) decrease in intercellular CO_2 concentration, and 27.1% ($p < 0.05$) increase in water use efficiency compared to the reference treatment.

Combined UV-B radiation and substrate acidity impact affected the highest 80.6% ($p < 0.05$) decrease of photosynthetic rate compared to the reference treatment. The increase (by 2%, $p < 0.05$) of intercellular CO_2 concentration of *Brassica napus* affected by both investigated stressors shows that higher negative impact was on enzymatic reactions of photosynthesis than on transpiration (Tn changed statistically insignificantly compared to the reference treatment).

Also, the highest negative effect on content of photosynthetic pigments and biomass accumulation was of the combined effect of the investigated stressors.

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- (fitokamerose). Iš pradžių rapsai buvo pasėti į neutralaus rūgštumo (pH 6,0–6,5) substratą. Augalams išleidus du tikruosius lapelius jie buvo paveikti UV-B spinduliuote, substratas parūgštintas 0,07 mM H₂SO₄ koncentracijos tirpalu. Eksperimento trukmė – penkios dienos. Fotosintezės parametrai matuoti nešiojama fotosintezės sistema LI-6400. Pigmentų kiekiai lapuose nustatyti spektrofotometriškai. Didžiausius *Brassica napus* tirtų rodiklių pokyčius sukėlė kompleksinis 1 kJm⁻²d⁻¹ UV-B spinduliuotės ir pH 4,8 substrato rūgštumo poveikis. Pavienis 1 kJm⁻²d⁻¹ UV-B spinduliuotės poveikis tirtiems rapsų rodikliams buvo silpnas ir statistiškai nereikšmingas, išskyrus transpiracijos intensyvumą bei vandens naudojimo efektyvumą, kai pokyčiai buvo statistiškai reikšmingi. Pavienis substrato rūgštumo poveikis rapsų fotosintezės intensyvumą sumažino 58,6 % (p < 0,05), transpiracijos intensyvumą – net daugiau nei du kartus (p < 0,05), o viduląstelinį CO₂ kiekį 3,8 % (p < 0,05), taip pat 27,1 % (p < 0,05) padidino vandens naudojimo efektyvumą, palyginti su kontroliniais augalais. Patį didžiausią neigiamą poveikį fotosintezės intensyvumui sukėlė UV-B spinduliuotė ir substrato rūgštumas – nuostoliai siekė net 80,6 % (p < 0,05), palyginti su kontroliniais augalais, o kompleksinis tirtų veiksnių poveikis transpiracijos intensyvumui buvo statistiškai nereikšmingas (p > 0,05). Tad nors tik 2 %, bet statistiškai reikšmingas (p < 0,05) viduląstelinio CO₂ kiekio padidėjimas *Brassica napus* lapuose, esant kompleksiniam tirtų veiksnių poveikiui, rodo stipresnį neigiamą poveikį fermentinei fotosintezės sistemai nei transpiracijai. Kompleksinis UV-B ir substrato rūgštumo poveikis vėlgi buvo didžiausias ir fotosintetinių pigmentų bei biomasės pokyčiams.

Raktažodžiai: fotosintezės intensyvumas, viduląstelinis CO₂ kiekis, transpiracija, vandens naudojimo efektyvumas, fotosintetiniai pigmentai, sausa biomasė, *Brassica napus*

Irena Januškaitienė

SILPNOS UV-B SPINDULIUOTĖS IR SUBSTRATO RŪGŠTUMO POVEIKIS BRASSICA NAPUS FOTOSINTEZĖS RODIKLIAMS

Santrauka

Tyrimo tikslas – ištirti kompleksinį 1 kJm⁻²d⁻¹ UV-B spinduliuotės ir pH 4,8 substrato rūgštumo poveikį vasarinių rapsų (*Brassica napus*) fotosintezės rodikliams bei augimui kontroliuojamoje aplinkoje

