



Physiological responses of microclonally propagated willow to excessive levels of UV-B radiation

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Article info

Received 15.09.2025

Received in revised form

10.10.2025

Accepted 18.11.2025

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Yatsiv, V., Kutsokon, N., & Rashydov, N. (2025). Physiological responses of microclonally propagated willow to excessive levels of UV-B radiation. *Regulatory Mechanisms in Biosystems*, 16(4), e25185. doi:10.15421/0225185

Willow plantations represent a rapidly deployable source of lignocellulosic biomass for bioenergy and a reservoir of bioactive compounds for pharmaceutical use. However, their physiological resilience to increasing ultraviolet-B (UV-B; radiation with a wavelength of 280–320 nm), under current climate change scenarios, remains insufficiently characterised. This study evaluated the physiological responses of the microclonally propagated willow clone ‘Zhytomyrska-1’ to acute UV-B treatments. Our experiments were focused on leaf pigmentation and nitrogen-related status as indicators of stress. Uniform *in vitro*-derived plantlets were acclimatised in greenhouse conditions and divided into four groups: non-irradiated control and three UV-B treatments receiving single acute doses of 5, 10, and 15 kJ/m². Non-destructive leaf measurements were performed with a portable multipigment meter (MPM-100) at seven time points during a two-month period post-exposure to capture short-, medium- and long-term effects. We determined relative chlorophyll, flavonol, and anthocyanin indices, and the nitrogen balance index (NBI) as an integrative parameter for leaf nitrogen status. Data were analysed by both one-way and two-way ANOVA to separate the effects of dose, time and their interaction. Time (developmental stage and seasonal progression) was the dominant factor driving variation in all measured parameters, excluding anthocyanin. The contents of chlorophyll and flavonol were increased at later stages of the vegetation, on days 66 and 70. Meanwhile, the nitrogen balance index tended to decrease at the time points 10–17 days, but this effect was absent after UV-B irradiation at 15 kJ/m², where the nitrogen balance index remained relatively stable during the studied period. Compared to the impact of time, the effects of UV-B radiation were weaker and less consistent, in some cases increasing the levels of chlorophyll and the nitrogen balance index, while decreasing the levels of anthocyanins. Overall, the willow clone ‘Zhytomyrska-1’ demonstrated relative physiological stability across the tested UV-B dose range, suggesting resilience to moderate increases in UV-B comparable to regional annual doses.

Keywords: UV-B radiation; willow; *Salix*; secondary metabolites; chlorophyll; flavonol; anthocyanins.

Introduction

Nowadays, amid global climate change, significant depletion of the stratospheric ozone layer has been observed. Over recent decades, this process has become especially evident due to anthropogenic atmospheric pollution (Fang et al., 2019; Solomon et al., 2020). As a result, the intensity of ultraviolet (UV) radiation reaching the Earth's surface has substantially increased, particularly in the UV-B range (280–320 nm), which is expected to negatively affect plant species and ecosystems. Ultraviolet radiation is a powerful environmental factor for biological systems, as it is readily absorbed by biomolecules such as nucleic acids, proteins, and lipids. UV radiation absorption leads to molecular photoexcitation of the abovementioned macromolecules, resulting in alterations in genetic, biochemical, and physiological processes within cells, thereby influencing many various biological functions (Reisz et al., 2014). Moreover, elevated levels of UV stimulate the formation of reactive oxygen species (ROS), which trigger various secondary metabolites and signalling pathways, including enzyme activation, gene expression, apoptosis, and damage to cellular structures (Rai & Agrawal, 2017).

Numerous studies have reported that additional UV-B radiation adversely affects plant morphology, reproduction, physiology, and metabolism (Kataria et al., 2014; Rai & Agrawal, 2017). Further evidence supports broad physiological and metabolic impacts across taxa (Zlatev et al., 2012). UV-induced stress initiates a range of physiological and metabolic responses in plants, including enhanced synthesis of antioxidant system components, increased activity of antioxidant and DNA-repair enzymes such as photolyases (Hui et al., 2012; Czégény et al., 2016), and activation of genes involved in UV defence and recovery processes (Kataria et al., 2014). Furthermore, UV radiation induces the accumulation of protective compounds that absorb UV light and safeguard cellular components (León-Chan et al., 2017). Elevated UV-B radiation negatively affects the growth of higher

plants, leading to decreased biomass and yield (Salama et al., 2011; Zlatev et al., 2012). It can suppress chlorophyll synthesis (León-Chan et al., 2017) and alter other pigment dynamics too (Yao et al., 2013). UV-B exposure can also impair key photosynthetic processes, including photochemical reactions in thylakoid membranes and enzymatic activities of the Calvin cycle (Hui et al., 2012; Hu et al., 2013). It may additionally affect stomatal function and the structure of photosystem II (PSII) (Lidon & Ramalho, 2011; Singh et al., 2012), and influence photosynthetic performance more broadly (Wang et al., 2010). Altogether, these effects lead to an overall decline in plant physiological performance.

Although elevated UV-B is often considered a stressor, a growing body of evidence shows that moderate UV exposure can exert stimulatory effects on plant physiology, biochemistry and morphology (Jansen et al., 1998). Moderate UV-B activates photoreceptors (notably UVR8) and downstream signalling cascades that induce expression of protective and repair genes, increase photolyase activity and bolster antioxidant systems (Nassour & Ayash, 2021). As a result, plants frequently accumulate UV-absorbing and antioxidant secondary metabolites such as flavonoids, phenolics, anthocyanins, and carotenoids, enhancing photoprotection of leaves and limiting oxidative damage (Jadidi et al., 2023; Ali et al., 2024). In some species, these responses are associated with beneficial phenotypic outcomes – improved photomorphogenic traits and, under controlled conditions, maintenance or even improvement of photosynthetic performance – which can increase resilience to additional abiotic stresses (Nassour & Ayash, 2021; Jadidi et al., 2023).

In the context of climate change and resource depletion, the development of renewable energy sources is gaining importance. An alternative to fossil fuels is the production of biofuels from plant biomass (Amichev et al., 2014; Dimitriou & Mola-Yudego, 2017). Obtaining wood from fast-growing trees, especially willow and poplar, is considered promising for biomass-based bioenergy (Van Slycken et al., 2012; Kutsokon & Khoma, 2025). Members of this family, particu-

larly willows, are promising candidates for bioenergy due to their favourable characteristics for biomass production and environmental remediation (Hangs et al., 2011; Khoma et al., 2021). Willows are known for their high biomass productivity (Stolarski et al., 2013; Kutsokon et al., 2022), which can be utilised for both wood fuel and methanol production (Dou et al., 2016; Volk et al., 2016).

However, the effects of UV-B radiation on woody plants remain understudied, especially within the Salicaceae family. The majority of UV-related plant research has focused on herbaceous crops. Therefore, the aim of our study was to evaluate the influence of UV-B radiation on physiological parameters (relative chlorophyll, anthocyanin, flavonol contents, and the nitrogen balance index) in the leaves of the highly-productive willow clone 'Zhytomyska-1'.

Materials and methods

Plant material. The plant material used in this study consisted of a highly-productive (Kutsokon et al., 2022) micropropagated willow clone 'Zhytomyska-1' (*Salix* sp.). To ensure a sufficient amount of uniform material, microclonal propagation was conducted *in vitro*. The plants were cultivated in glass test tubes on the Murashige and Skoog (MS) medium supplemented with indole-3-butyric acid (IBA, 5 mg/L). The detailed composition of the growth medium is presented in Table 1.

Table 1

Composition of Murashige and Skoog-based nutrient medium used for the cultivation of willow clone 'Zhytomyska-1'

Component	Concentration, g/L
MS basal salts	2.18
Sucrose	20
L-glutamine	0.2
Myo-inositol	0.1
MES	0.26
500 FV vitamins	0.1
Agar	7.5
IBA	0.1*10 ⁻³

Well-developed plantlets were gently removed from the tubes, cleaned from agar residues, washed, transplanted into Jiffy-7 peat pellets, and placed in polyethylene bags for slow acclimatisation. Rooting continued for two months. Plants with well-developed roots were transferred, together with the peat pellets, into 1 L pots filled with a soil mixture containing black soil, peat and vermiculite, at a ratio of 10:10:1.5. These plants were grown under greenhouse conditions for one month (Fig. 1).

UV-B irradiation treatment. Acclimatised plants were divided into four groups: one control group consisting of 6 plants and three treated groups of 5 plants each, which were exposed to acute UV-B doses of 5, 10, and 15 kJ/m². UV-B radiation was provided using a TL 20W/12 RS ultraviolet-B lamp (Philips, Heerlen, Netherlands, 2016). All plants, both control and treated, were maintained in the laboratory under identical temperature and humidity conditions. Plants were watered every 2–3 days, with no over- or under-watering.

Measurement of physiological parameters and growth. Subsequent analyses were performed to determine the relative content of chlorophyll, anthocyanins, flavonols, and the nitrogen index in willow leaves using a portable multipigment meter "MPM-100" (Opti-Sciences, 2024. MPM-100 Multi-Pigment Meter brochure. Opti-Sciences, Inc. 8 Winn Avenue, Hudson, USA). For each plant, two widely expanded leaves located between the 3rd and 6th nodes from the apical bud were measured. The content of plant pigments may serve as significant indicators of the state of tree species (Holoborodko et al., 2022).

The MPM-100 fluorimeter uses two LEDs (720 nm and 850 nm) to measure light transmittance through the leaf. The relative chlorophyll content is assessed using the transmittance coefficient, which is calculated by dividing the transmittance value at 850 nm by the transmittance value at 720 nm.

For flavonols and anthocyanins, the device uses three LEDs (375, 525, and 660 nm) to induce chlorophyll fluorescence. Compounds in the leaf epidermis attenuate incident light before it reaches the mesophyll, and the attenuation intensity is wavelength-dependent, allowing

the estimation of the epidermal compounds content (Cerovic et al., 2008; Kameoka et al., 2017; Opti-Sciences, 2021). Flavonols, the key UV-absorbing compounds in dicots, absorb light at 375 nm. Consequently, chlorophyll fluorescence induced by this wavelength is inversely proportional to the flavonol concentration. Light at 660 nm, unaffected by flavonol absorption, serves as a reference. The flavonol index (F) is calculated based on the Beer-Lambert law: as the logarithm of the ratio of the intensities of fluorescence induced by 375 nm to that induced by 660 nm (Cerovic et al., 2008). Similarly, anthocyanin content is assessed using the 525 nm excitation wavelength in place of 375 nm (Cerovic et al., 2008).



Fig. 1. Potted plant of willow clone 'Zhytomyska-1' obtained by microclonal propagation

Measurements were performed within a two-month period following irradiation. Totally seven measurements were performed: the first one immediately after exposure (day 0), four within the first three weeks, to capture short- and medium-term effects (days 1, 4, 10, and 17), and two after two months, to capture long-term and seasonal changes (days 66 and 70). In addition to physiological parameters, plant stem height was measured at the end of the experiment for both control and treated groups.

Statistical analysis. To establish statistical significance, the data were analysed by both one-way and two-way ANOVA with Tukey's post hoc tests and Bonferroni correction using the IBM SPSS for Windows, version 23 (SPSS Inc., Chicago, USA, 2015). The significance level was set at $P < 0.05$. The one-way ANOVA was performed separately for the non-irradiated control and plants treated with UV-B radiation at doses 5, 10, and 15 kJ/m² to establish the dependence of the measured physiological parameters on time. To evaluate the effects of UV-B treatment, one-way ANOVA was performed at the studied time points: 0, 1, 4, 10, 17, 66, and 70 days. Additionally, the two-way ANOVA was used to assess the combined effects of both independent variables – dose and time – on the physiological parameters of willow leaves (relative chlorophyll, and flavonol contents, and the nitrogen balance index). In this case, the time points were represented by 7 levels, and UV-B dose variants consisted of 4 levels.

Results

Changes in relative chlorophyll content showed a more pronounced dependence on time than on UV-B dose. In particular, comparisons with the control day (day 0) at different time points, within each dose, revealed a statistically significant increase of chlorophyll level in the late terms – days 66 and 70 (Fig. 2).

When comparing chlorophyll values to the dose controls, within the same day, the effects were observed only in plants exposed to 15 kJ/m² UV-B radiation immediately after exposure and in plants treated with 10 kJ/m² on day 70. In both cases chlorophyll levels increased comparing to un-irradiated controls. In all other experimental groups, no statistically significant differences from the control were detected throughout the measurement period. Similarly, relative flavonol content also increased at late time points, days 66 and 70, across all doses (Fig. 3). However, no statistically significant differences in flavonol content were found between irradiated and control plants.

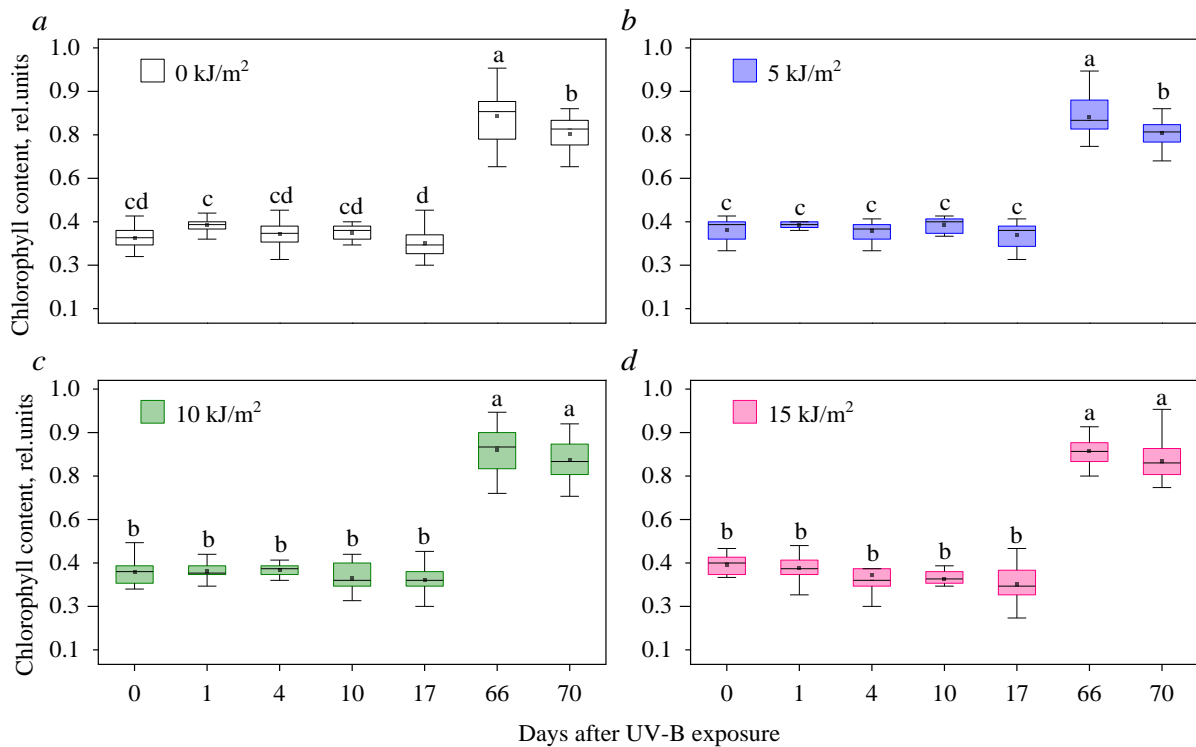


Fig. 2. Relative chlorophyll content in leaves of willow clone ‘Zhytomyrska-1’ in the non-irradiated control group (a), and plants treated with UV-B radiation at doses 5 kJ/m² (b), 10 kJ/m² (c) and 15 kJ/m² (d): on the box and whisker plots, the lines denote the median; the dot symbol is the mean; the box represents values within the 25–75% quartiles, and the whiskers show minimum and maximum values; different letters denote values that significantly differ within each treatment group according to the results of one-way ANOVA using the Tukey test with Bonferroni correction ($P < 0.05$); $n = 10\text{--}42$ measurements

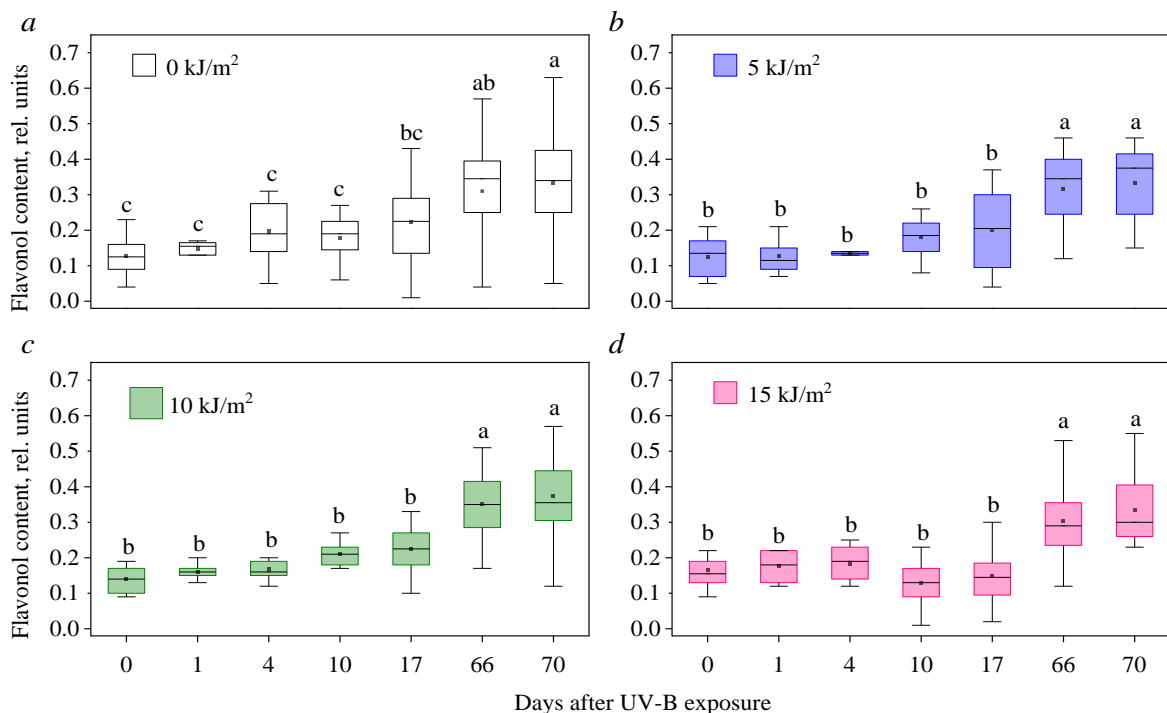


Fig. 3. Relative flavonol content in leaves of willow clone ‘Zhytomyrska-1’ in the control group (a), and plants treated with UV-B radiation in doses 5 kJ/m² (b), 10 kJ/m² (c) and 15 kJ/m² (d): see Figure 2 for symbol definitions and explanations

Regarding the nitrogen balance index, significant deviations from day 0 were observed in the non-irradiated as well as in the 5 and 10 kJ/m² groups, during the mid-term period, particularly on days 10 and 17. However, no time-dependent changes were determined in the 15 kJ/m² group (Fig. 4). These results suggest that the highest UV-B dose may affect nitrogen metabolism in the willow clone. When comparing treated and untreated plants, only in the 5 kJ/m² group on day 0, did we observe an increase in the index of nitrogen balance. At all

other time points, no significant differences between UV-irradiated and non-irradiated plants were found.

A significantly lower level of relative anthocyanin content on day 10 was determined only after UV-B irradiation at a dose 5 kJ/m². By the end of the experiment, all groups showed anthocyanin levels below the detection limit of the device, likely due to seasonal metabolic changes in pigment concentrations. Therefore, the data from days 66 and 70 are not presented here. These results were also not subjected to two-way ANOVA.

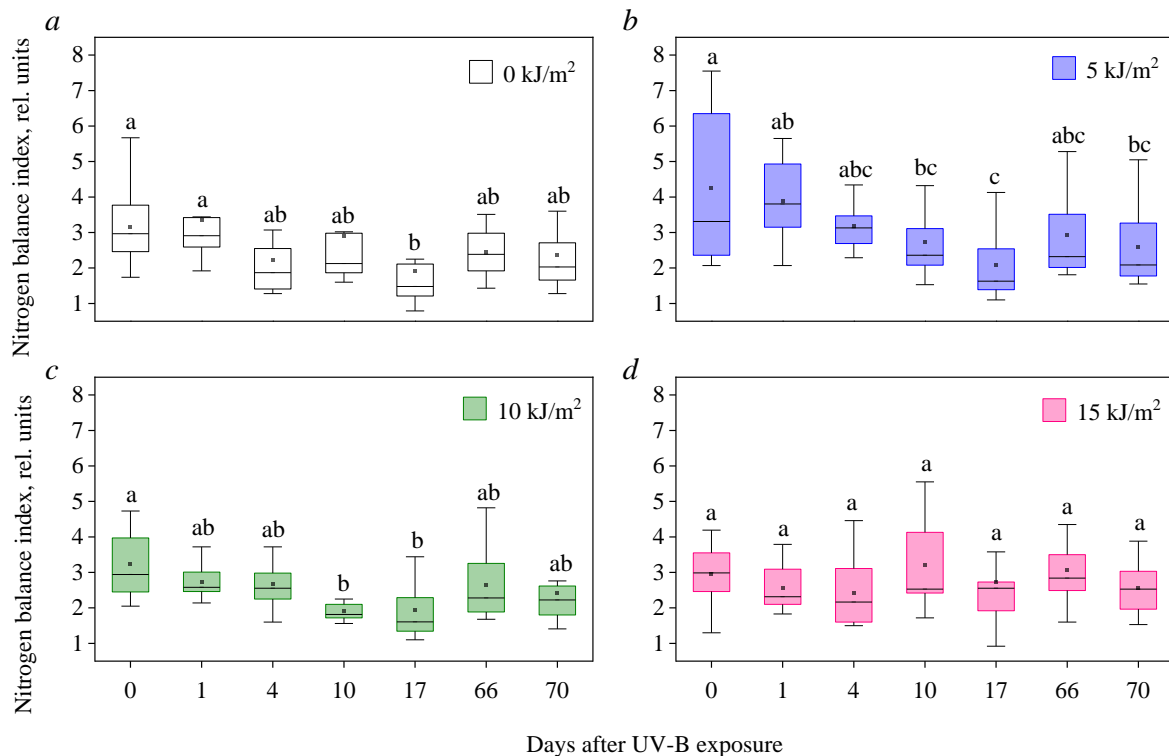


Fig. 4. Nitrogen balance index content in leaves of willow clone ‘Zhytomyrska-1’ in the control group (a), and plants treated with UV-B radiation in doses 5 kJ/m² (b), 10 kJ/m² (c) and 15 kJ/m² (d): see Figure 2 for symbol definitions and explanations; n = 9–38

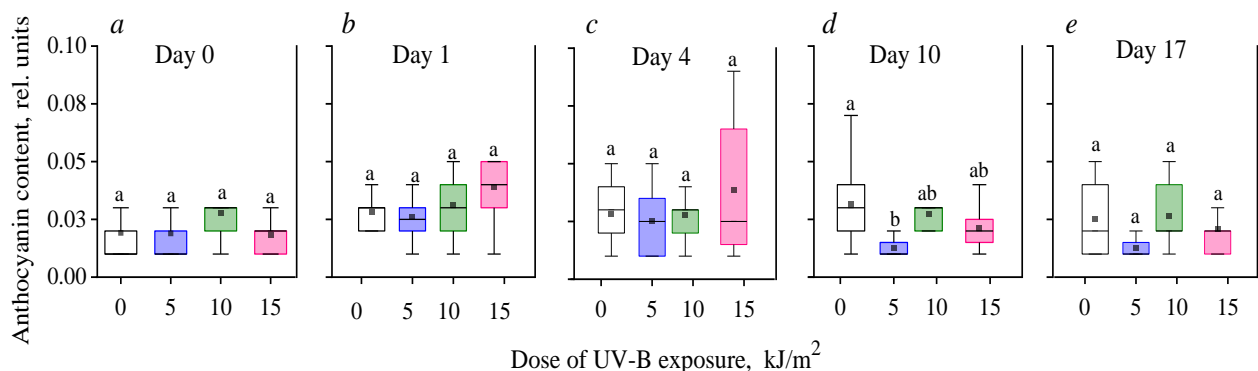


Fig. 5. Relative anthocyanin content in leaves of willow clone ‘Zhytomyrska-1’ measured at day 0 (a), day 1 (b), day 4 (c), day 10 (d), and day 17 (e) after UV-B treatment: see Figure 2 for symbol definitions and explanations; n = 8–35

No significant differences in stem height were observed between the treated and control plants by day 70 (Fig. 6), suggesting that UV-B had no substantial impact on plant height under the current experimental conditions. Two-way ANOVA revealed that time (i.e., measurement date) significantly affected relative contents of chlorophyll, flavonols, and the nitrogen balance index (Table 2), especially at later time points. In contrast, UV-B dose only significantly influenced the nitrogen balance index, and this effect was weaker than that of time. Dose-time interaction was also significant for the nitrogen balance index. Presumably, UV-B effects on willow leaf physiology were not always straightforward, with no dose-dependent impact on chlorophyll and flavonol content. However, seasonal changes in all parameters were statistically significant.

Discussion

Two-way ANOVA revealed that time significantly affected relative contents of chlorophyll, flavonols, and the nitrogen balance index, especially at later time points. Previously, we also observed seasonal changes of pigments in 17 *Brassica carinata* genotypes. In mustard, increased chlorophyll and reduced flavonol contents were determined within the period from bud formation to flowering, followed by decreased chlorophyll during fruiting (Rakhmetov et al., 2024).

The ambiguous effects of UV-B radiation on various physiological parameters observed in our experiment are partially consistent with previous findings reported for similar dose ranges. For instance, Ren et al. (2010) found that elevated UV-B exposure significantly increased the content of chlorophyll a, chlorophyll b, total chlorophyll (a + b), and carotenoids, and enhanced guaiacol peroxidase activity in two *Populus* species (*P. kangdingensis* and *P. cathayana*), while proline content remained unaffected.

Estimating the effects of high doses of UV-B radiation (43.2 and 86.4 KJ/m²), with the same method for leaf measurements, Ali et al. (2023) determined that only the higher dose 86.4 KJ/m² caused a significant decrease in the chlorophyll index in spearmint (*Mentha spicata* L.). No changes in the chlorophyll index from dose 43.2 KJ/m² and in flavonol index under both doses were found. Plant growth was depressed under the higher dose of 86.4 KJ/m². Similar results were obtained by the same authors on wild rocket *Diplotaxis tenuifolia* (Ali et al., 2024) where a decrease in total content of chlorophyll was observed in UV-B dose range 21.6–172.8 KJ/m². Flavonol and anthocyanin indices were increased under UV irradiation, but similarly to our results, no dose-dependent effects were observed. Therefore, these two studies demonstrate that the loss of chlorophyll after high doses of UV-B irradiation may be explained by the destruction of UV-B damage to the chloroplast followed by the degeneration of photosystem

II (Ali et al., 2023). However, the doses used in mentioned studies were substantially higher than the doses we employed in our research.

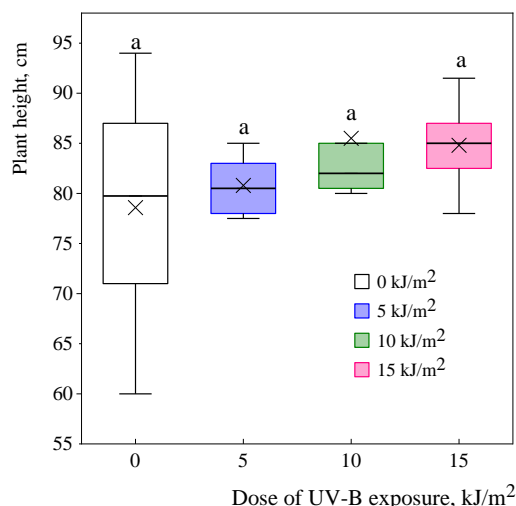


Fig. 6. Average stem height (cm) of willow clone ‘Zhytomyrskia-1’ on day 70 after UV-B exposure: letter a indicates no differences between variants according to the results of comparison using the Tukey test with Bonferroni correction; n = 5 for irradiated, n = 6 for non-irradiated (0 kJ/m²) plants

Table 2

Results of two-way ANOVA for relative contents of chlorophyll, flavonols, and the nitrogen balance index in leaves of willow clone ‘Zhytomyrskia-1’ under UV-B radiation

Parameter	Factor	df	P
Chlorophyll	Dose	3	0.129
	Time	6	1.63*10 ⁻²²⁹
	Dose × Time	18	0.151
Flavonols	Dose	3	0.121
	Time	6	6.69*10 ⁻⁵¹
	Dose × Time	18	0.500
Nitrogen balance index	Dose	3	0.002
	Time	6	1.13*10 ⁻⁸
	Dose × Time	18	0.039

Notes: df – degrees of freedom; P – significance level.

Kaling et al. (2014) demonstrated that UV-B radiation at 2.8 W/m² for 13 days triggered extensive reprogramming of metabolic pathways in transgenic grey poplar (*Populus × canescens*, syn. *P. alba × P. tremula*), including elevated levels of flavonoids, anthocyanins, and polyphenols, along with decreased levels of their precursors: phenylpyruvate, 4-hydroxyphenylpyruvate, coumaric acid derivative, phenylalanine, tyrosine, p-coumaroyl CoA, coniferin, syringin, catechin and galocatechin. These changes occurred within the first 36 hours, indicating short-term metabolic responses. Similarly, Randriamanana et al. (2015) reported that UV-B exposure led to the accumulation of flavonoids, condensed tannins, and salicylates in *Salix myrsinifolia*. Interestingly, in that study, the concentration of metabolites depended on plant sex, suggesting that gender-related physiological responses may modulate UV-B tolerance.

In another study, Wong et al. (2022) showed that UV-B doses ranging from 10 to 35 kJ/m² promoted the synthesis of anthocyanins, flavonoids, and lignin precursors in the leaves of *Populus trichocarpa* and *P. deltoides*. Compared to their study, the doses applied in our experiment were moderate and may not have been high enough to elicit similarly robust biochemical responses (Zhao et al., 2023).

Molecular analyses of UV-B perception through the UV resistance locus 8 photoreceptor signalling pathway clarify how brief acute exposures can produce rapid transcriptional and metabolic shifts that cause slower changes in pigments and nitrogen status. Recent reviews show that UV resistance locus 8 photoreceptor activation and its interactions with COP1 domain and downstream regulators rapidly induce phenylpropanoid and flavonoid biosynthesis (Liu & Jenkins, 2024),

providing an explanatory framework for the changes in NBI we observed in our experimental data.

Controlled experiments on herbs and ornamentals further illustrate the dual effect of reduced growth combined with accumulation of secondary metabolites under UV regimes. In *Pelargonium graveolens*, combined UV-A/UV-B treatment increased phenolic and flavonoid content and reduced biomass, while combined increased photosynthetically active radiation and UV-A/UV-B treatment caused an increase in phenolic and flavonoid content without significant biomass loss (Jadidi et al., 2023). In our case, no significant effect of UV-B on plant growth and flavonol content was observed.

Our results align with the notion that UV-B radiation induces both protective and stress-related physiological changes in woody plants, with effects that depend on timing, species, and experimental conditions. The UV-B intensity, exposure time as well as proximity of the UV-B source should be taken into account when investigating the secondary metabolite production from UV-B irradiation (Ali et al., 2024).

Conclusions

According to our data, the timing of measurements significantly influenced all analysed parameters in apical leaves of *Salix* clone ‘Zhytomyrskia-1’. The contents of chlorophyll and flavonol increased at later stages of the vegetation, on days 66 and 70. Meanwhile, the nitrogen balance index tended to decrease at time points 10–17 days, however, this effect was absent after UV-B irradiation at 15 kJ/m², where the nitrogen balance index remained relatively stable during all the studied period.

By anthocyanin content, no clear seasonal or dose-dependent patterns were identified. We can not exclude the possibility that this may be related to technical limitations in the measurements, since anthocyanin spectra can partially overlap in the presence of high concentrations of other pigments (chlorophyll and flavonol), especially in the later stages of plant seasonal development, which can mask the actual anthocyanin level.

The effect of UV-B radiation at the tested doses (5–15 kJ/m²) was neither unambiguous nor consistent across all variants. According to ANOVA results, radiation affected only the nitrogen balance index – a composite indicator derived from chlorophyll and flavonol levels. In both control plants and those exposed to lower doses of UV-B, the nitrogen balance index decreased within 10–17 days, whereas at the highest dose (15 kJ/m²), such seasonal changes were absent, suggesting that higher UV-B doses may stimulate nitrogen balance.

The obtained results indicate the tolerance of the willow clone ‘Zhytomyrskia-1’ to UV-B radiation in the range of applied doses (5–15 kJ/m²), which corresponds to the average annual dose (10 kJ/m²) in the environment of the Polissia region in Ukraine. Obviously, at higher acute doses UV-B irradiation would be more effective, especially in a shorter time after irradiation.

In brief, the changes in chlorophyll and flavonol content, and the nitrogen balance index in the leaves of willow clone ‘Zhytomyrskia-1’ were primarily determined by the plant’s vegetative development stage. However, UV-B radiation elicited measurable, though unsystematic, shifts in these parameters, in some cases increasing the levels of chlorophyll and the nitrogen balance index, while decreasing the level of anthocyanins. In our work, we did not establish dose-related dependences, and clearly demonstrated a number of age-related effects. The findings suggest that the willow clone is resilient to UV-B radiation within the tested dose range. Nevertheless, the possibility of early, transient UV-B-induced effects remains and warrants further investigation.

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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