



Impact of acute UV-B radiation on species specific metabolic responses in poplar and willow

V. Yatsiv*, S. Litvinov*, N. Kutsokon*, V. Sakada*, T. Isokov**, N. Rashydov*

*Institute of Cell Biology and Genetic Engineering of the National Academy of Sciences of Ukraine, Kyiv, Ukraine

**Institute of Physics of the National Academy of Sciences of Ukraine, Kyiv, Ukraine

Article info

Received 20.03.2026

Received in revised form

01.05.2026

Accepted 18.05.2026

Institute of Cell Biology
and Genetic Engineering,
National Academy
of Sciences of Ukraine,
Academician Zabolotnogo
st., 148, Kyiv, 03143,
Ukraine. E-mail:
scientist0612@gmail.com

Institute of Physics
of the National Academy
of Sciences of Ukraine,
Nauky av., 46, Kyiv, 03028,
Ukraine. E-mail:
isokovtd@gmail.com

Yatsiv, V., Litvinov, S., Kutsokon, N., Sakada, V., Isokov, T., & Rashydov, N. (2026). Impact of acute UV-B radiation on species specific metabolic responses in poplar and willow. *Regulatory Mechanisms in Biosystems*, 17(3), e26058. doi:10.15421/0226058

Increased levels of UV-B radiation represent an important environmental factor affecting the physiology of woody plants and determining their resilience under changing climatic conditions. This study investigated the biochemical and metabolic responses of microclonally propagated *Populus pyramidalis* × *P. laurifolia* cv. 'Novoberlinska-3' and *Salix* sp. cv. 'Zhytomyrska-1' following acute UV-B irradiation at a dose of 17 kJ/m². A broad set of metabolic parameters was assessed, including the content of nucleic acids, total proteins, total lipids, total carbohydrates, amide I and amide II protein domains, starch, cellulose, hemicellulose, lignin, phenylpropanoids, as well as biochemical markers of stress responses, using ATR-FTIR spectroscopy. The results revealed significant, species-specific differences in stress response pathways and dynamics. In poplar, an increase in the content of nucleic acids, lipids, starch, and aliphatic fatty acid esters was observed at an early stage, accompanied by an increase in the esterification index and activation of the phenylpropanoid pathway. An increase in the amide I / amide II ratio indicated the formation of misfolded proteins, which may represent an element of proteomic modification during stress. At a later stage, a decrease in cellulose, hemicellulose and phenylpropanoid content was observed, indicating a transition to a phase of long-term adaptation in poplar. In contrast, willow demonstrated a rapid intense response, characterised by a sharp increase in the content of lipids, carbohydrates, starch, cellulose, and hemicelluloses, accompanied by a decrease in the amide I / amide II ratio and inhibition of protein synthesis. A significant increase in the content and proportion of phenylpropanoids indicated intense activation of secondary metabolism as well as the induction of a potent antioxidant response. Therefore, willow implements a model of rapid resource mobilisation, whereas poplar employs a slower, more structurally oriented adaptation strategy. The obtained data demonstrate the high species-specificity of response mechanisms to UV-B radiation stress in Salicaceae tree species and highlight the potential of using a combination of spectroscopic methods to characterise clones based on their resistance to abiotic stress.

Keywords: UV-B radiation; *Salix*; *Populus*; ATR-FTIR spectroscopy; metabolomic profiling; stress physiology.

Introduction

Ultraviolet radiation at the Earth's surface is tightly linked to the condition of the stratospheric ozone layer, which experienced pronounced depletion in the latter half of the twentieth century, particularly at mid and high latitudes (McKenzie et al., 2011; Bernhard et al., 2023). Although the Montreal Protocol has slowed further ozone loss, recovery remains spatially uneven, and ongoing atmospheric pollution continues to influence UV transmission (Fang et al., 2019; Solomon et al., 2021). As a result, UV-B (280–320 nm) levels can be elevated and highly variable, with local patterns often diverging from model predictions due to differences in cloud cover and air quality (Bernhard et al., 2023).

UV radiation is readily absorbed by nucleic acids, proteins, and lipids, initiating photochemical reactions that alter cellular structure and function (Reisz et al., 2014). Increased UV exposure enhances the formation of reactive oxygen species (ROS) and activates signalling pathways associated with enzyme induction, gene regulation, and programmed cell death (Rai & Agrawal, 2017; Bomman et al., 2019). Excessive UV-B can damage DNA, proteins, and membrane lipids, disrupt the cell cycle, reduce pollen viability, and impair root and shoot development (Bomman et al., 2019). Numerous studies have shown that such stress affects plant morphology, reproduction, physiology, and metabolism across diverse taxa (Zlatev et al., 2012; Kataria et al., 2014; Rai & Agrawal, 2017).

Plants respond to UV-B by activating antioxidant systems and enhancing the activity of detoxification and DNA repair enzymes, including photolyases (Hui et al., 2013; Czégény et al., 2016). At the same time, UV exposure promotes the accumulation of secondary metabolites that absorb short wavelength radiation and protect cellular

structures (Yao et al., 2013; León-Chan et al., 2017). High UV-B doses can interfere with chlorophyll biosynthesis, modify pigment composition, and impair photochemical reactions and Calvin cycle enzymes, ultimately reducing photosynthetic efficiency (Wang et al., 2010; Hu et al., 2013; Hui et al., 2013). Structural and functional changes in photosystem II and altered stomatal behaviour further contribute to these declines (Lidon & Ramalho, 2011; Singh et al., 2012). UV-induced effects also extend to nitrogen metabolism, influencing pigment levels, enzyme activity, and nitrogen allocation among organs (Kataria et al., 2014; Klem et al., 2022).

The magnitude and direction of plant responses depend on wavelength, irradiance, genotype, and environmental context. Excessive UV-B typically suppresses growth, reduces leaf area, biomass, and yield, whereas UV-A can exert either stimulatory or inhibitory effects depending on species and exposure regime (Kataria et al., 2014; Verdager et al., 2017). In barley, UV combined with intense photosynthetically active radiation reduced leaf area, increased the root to shoot ratio, and stimulated flavonoid accumulation (Singh et al., 2015; Klem et al., 2022). Conversely, excluding UV components from sunlight enhanced root growth, nodule formation, nitrogenase activity, and leghemoglobin content in soybeans and alfalfa, indicating a limiting role of natural UV in symbiotic nitrogen fixation (Baroniya et al., 2014). Rice grown at high altitude, under increased UV-B levels, showed reduced biomass and disrupted nitrogen distribution, whereas elevated temperature partially compensated by promoting nitrogen redistribution to vegetative organs (Li et al., 2026).

Moderate UV exposure, however, can act as a regulatory signal rather than a purely damaging factor. Early work already suggested that low UV-B doses may stimulate plant development (Jansen et al., 1998), and subsequent studies have shown that activation of the UV-

B-specific photoreceptor UVR8 triggers signalling cascades that enhance DNA repair and antioxidant capacity (Nassour & Ayash, 2021). Under such conditions, plants often accumulate flavonoids, phenolics, anthocyanins, and carotenoids, which improve photoprotection and limit oxidative damage (Jadidi et al., 2023; Ali et al., 2024). UVR8 mediated signalling involves COP1, HY5, HYH, RUP1, and RUP2 proteins as well as integrates with hormonal pathways, including auxin, gibberellins, brassinosteroids, and salicylic acid, thereby linking light perception with growth and stress responses (Xie et al., 2019; Podolec et al., 2021).

In parallel with these physiological considerations, there is rising interest in fast growing woody species as renewable biomass sources. Bioenergy production from plant material is viewed as a more sustainable alternative to fossil fuels (Hangs et al., 2011; Khudolieieva et al., 2016; Dimitriou & Mola Yudego, 2017). Willows and poplars are particularly attractive in this context due to their high biomass productivity and suitability for bioenergy systems (Stolarski et al., 2013; Van Slycken et al., 2013). Willow wood can be used for solid fuel and methanol production (Dou et al., 2016; Volk et al., 2016). Members of the Salicaceae family also exhibit substantial functional and biochemical diversity, including secondary metabolites with ecological, pharmacological, and biotechnological relevance (Tawfeek et al., 2021; Roviello et al., 2025). Hybrids such as *Salix purpurea* × *S. daphnoides* combine high biomass yield with elevated salicin content, making them promising both as bioenergy feedstock and as sources of bioactive compounds (Warmański et al., 2021). Their phytoremediation potential is enhanced by rhizosphere microorganisms that promote heavy metal uptake and antioxidant activity (Guarino et al., 2018). Additional studies report species specific phenolic profiles with antibacterial, antioxidant, antihypertensive, and neuroprotective properties (Gligorić et al., 2019; Ramos et al., 2019; Jang et al., 2023). The aim of this study was to investigate the species specific metabolic and adaptive responses of poplar 'Novoberlinska 3' (*Populus pyramidalis* × *P. laurifolia*) and willow 'Zhytomyrska 1' (*Salix* sp.) plants obtained through *in vitro* microclonal propagation to acute UV-B irradiation using ATR-FTIR analysis.

Materials and methods

Plant material and microclonal propagation. The high-yielding poplar clone 'Novoberlinska-3' (*Populus pyramidalis* × *P. laurifolia*) and the willow clone 'Zhytomyrska-1' (*Salix* sp.) were used as the experimental material (Kutsokon et al., 2022). To obtain uniform, large-scale plant material, microclonal propagation *in vitro* was performed according to a protocol previously developed by Khoma et al. (2022). Seedlings were cultivated in sterile glass test tubes on a nutrient medium containing Murashige and Skoog (MS) salts and indole-3-butyric acid (IBA) at a concentration of 5 mg/L. The detailed composition of the medium is recently described by Yatsiv et al. (2025).

Acclimatisation and cultivation in soil. The well-developed poplar seedlings were carefully removed from the glass test tubes and cleaned of any agar residue. They were then rinsed with distilled water and transplanted into Jiffy-7 peat pellets. The seedlings were placed in plastic bags to allow them to acclimatise gradually; the roots took two months to develop. The plants, along with the peat pellets, were then transplanted into one-litre pots containing a soil mixture of chernozem, peat and vermiculite at a ratio of 10:10:1.5 (by volume). After transplanting, the plants were grown in a greenhouse for one month at a constant temperature and humidity (Fig. 1). They were watered every two to three days to avoid moisture deficiency or excess.

UV-B irradiation treatment. The acclimatised poplar and willow plants were each divided into two groups (control and experimental), resulting in four groups in total. The experimental groups were irradiated with UV-B at a dose of 17 kJ/m², while the control groups were not exposed to ultraviolet radiation. The radiation source was a TL 20W/12 RS ultraviolet lamp in the B range (Philips, Heerlen, Netherlands, 2016). There were 7 poplar plants and 3 willow plants in each group. All the plants in the experimental and control groups were kept indoors under identical temperature and humidity conditions. The plants were watered every 2–3 days.

Sample collection and preparation. Leaf samples were collected on the 2nd and 34th days of the experiment, with 3 leaves taken from each plant. The properly labelled samples were dried at room temperature until they reached a constant weight over a period of 7 days. 50 mg-samples of the dried leaves were then placed in Eppendorf tubes and ground for 5 minutes using a Genie homogeniser (Scientific Industries, USA).



Fig. 1. Potted plants of the willow clone 'Zhytomyrska-1' (*Salix* sp.) (a) and the poplar clone 'Novoberlinska-3' (*Populus pyramidalis* × *P. laurifolia*) (b) obtained through *in vitro* microclonal propagation

Measurement of poplar and willow samples by ATR-FTIR spectroscopy. Samples of poplar and willow were analysed using Fourier transform infrared spectroscopy. The optical densities of aliphatic fatty acid esters, total lipids, triglycerides, amide bands (amide I and amide II), cellulose, total nucleic acids, hemicellulose, starch and lignin were determined by analysing the corresponding peaks in the FTIR spectra (Fig. 2). ATR-FTIR spectra in the mid-infrared range of 400–4000 cm⁻¹ were recorded using a Nicolet IS50 FTIR spectrometer (Thermo Fisher Scientific, USA). The spectra were processed using the OMNIC software package (Thermo Fisher Scientific, USA). Twenty measurements were performed for each sample (variant). Spectra were obtained by averaging 32 scans of the same field with background spectrum filtering. The spectra were baseline-aligned and smoothed using the Savitzky–Golay function to filter out spectral noise. The relative concentration of the corresponding components was estimated based on the peak area within the range of the peak centre ± 12 cm⁻¹ on the absorption spectrum. All spectra were recorded with a resolution of 4 cm⁻¹.

Statistical analysis of the data was performed using the method of relative change compared to the corresponding unirradiated control, where the error is calculated as the standard error of the mean (SEM). The results of measurements in samples of unirradiated leaves of the 'Novoberlinska 3' poplar clone (*Populus pyramidalis* × *P. laurifolia*) on 2nd day were used as the control for all variants. The statistical significance of differences between groups was assessed using the nonparametric Mann–Whitney U test, with results considered significant at $P < 0.05$.

To visualise the statistical differences between the experimental groups, the data points in the figures were assigned Latin letters (a, b, c, d, e). According to the Mann–Whitney U test, groups sharing the same letter did not differ significantly. The letters were assigned in alphabetical order, beginning with the group exhibiting the highest mean value for each parameter. Distinct letters indicate statistically significant differences between samples within a given biochemical parameter. All pairwise comparisons were performed exclusively within the same parameter.

Results

In the leaves of the *Populus pyramidalis* × *P. laurifolia* clone 'Novoberlinska-3', the nucleic acid content was 30.7% higher on the 2nd day of the experiment than on the 34th day, indicating a significant decrease in this parameter during the vegetative phase of development (Fig. 3). Following UV-B irradiation at a dose of 17 kJ/m², the nucleic acid level in the poplar leaves increased on the 2nd day, exceeding

control values by 17.3%. This indicates the activation of nucleic acid synthesis in the early period following UV-B irradiation. However, in poplar leaves, this increase was less pronounced than in the *Salix* sp.

willow clone 'Zhytomyska-1', where the nucleic acid content on the 2nd day after irradiation exceeded the control by 62.0% (Fig. 3).

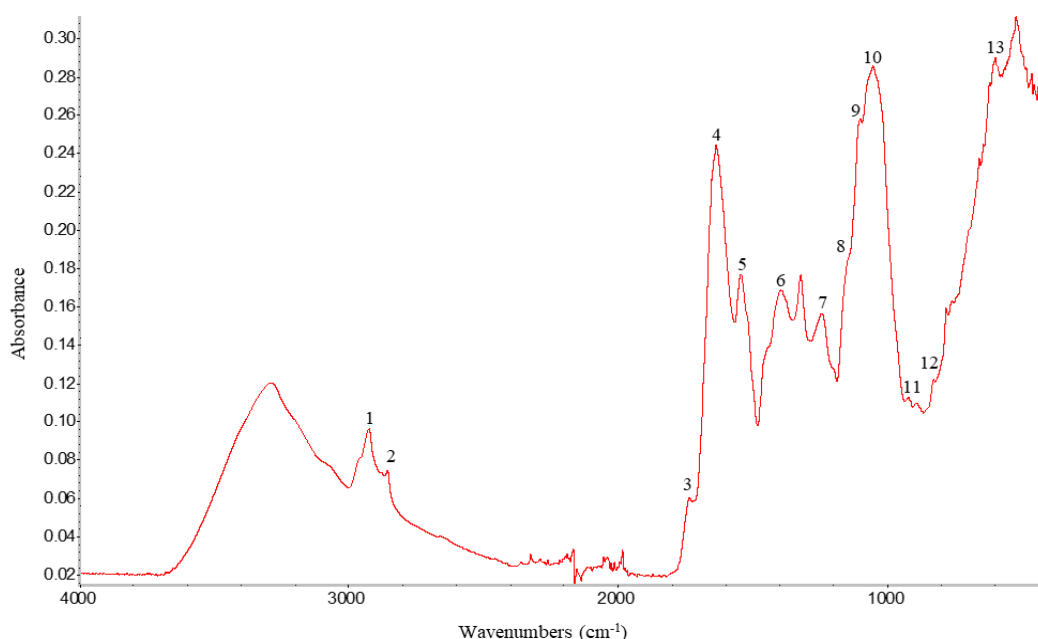


Fig. 2. Identification of peaks in a typical FTIR spectrogram of dried leaves of the studied poplar and willow plants: 1 – asymmetric CH₂ stretching of aliphatic fatty acid esters; 2 – symmetric CH₂ stretching of aliphatic fatty acid esters; 3 – triglycerides and fatty acids; 4 – amide I; 5 – amide II; 6 – cellulose; 7 – nucleic acids; 8 – hemicelluloses; 9 – C–O and C–C stretching of total polysaccharides; 10 – starch; 11 – skeletal vibrations of α -glycosidic linkages of total polysaccharides; 12 – lignin; 13 – phenylpropanoids

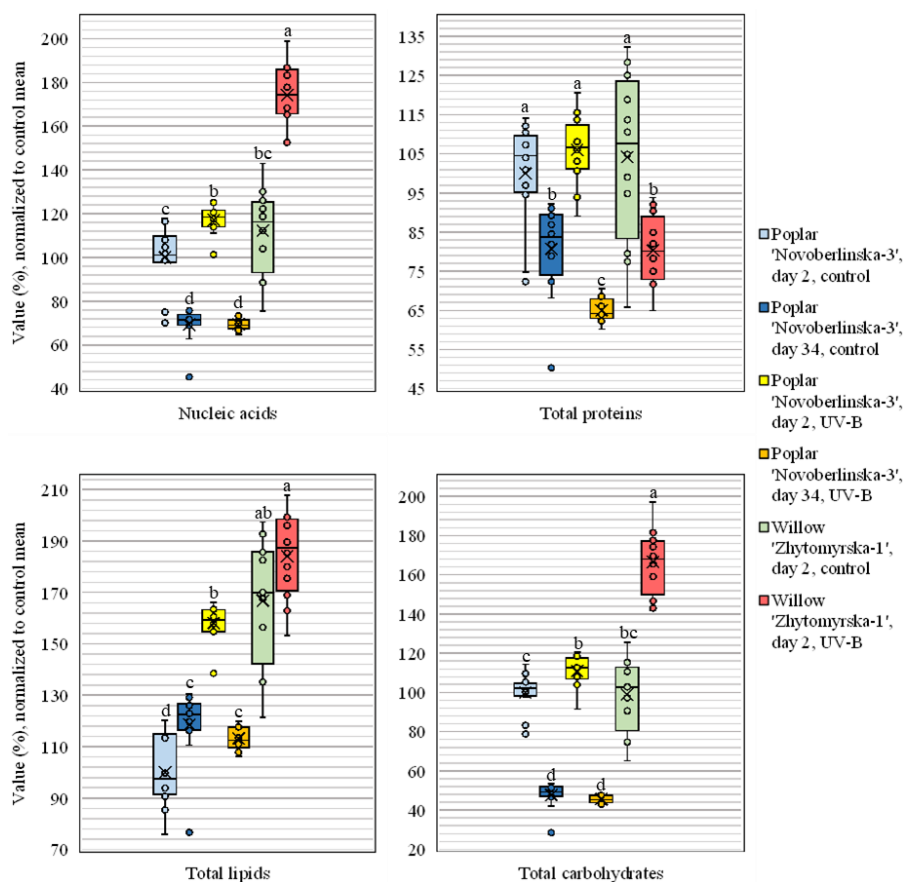


Fig. 3. Primary metabolic compounds in the leaves of the 'Novoberlinska-3' poplar clone on the 2nd and 34th days and the 'Zhytomyska-1' willow clone on the 2nd day after exposure to UV-B radiation at an intensity of 17 kJ/m²: all comparisons between groups were made within one biochemical parameter; on box and whisker plots, lines indicate the median; cross symbol is the mean; the box represents values within the 25–75% quartiles, and the whiskers show minimum and maximum values; values for unirradiated leaves of the 'Novoberlinska 3' poplar clone on 2nd day were set as 100%; different letters indicate values that are significantly different, as determined by the nonparametric Mann–Whitney U test ($P < 0.05$); $n = 12$ measurements

The total protein content on 2nd day in the 'Novoberlinska-3' poplar was 19.3% higher than on day 34, indicating the suppression of protein metabolism in mature leaves. UV-B irradiation at a dose of 17 kJ/m² did not affect the protein content of poplar leaves on 2nd day compared to the control. However, on day 34, the leaves of irradiated plants contained 15.7% less protein than the leaves of non-irradiated poplars. In irradiated willow leaves, protein content decreased by 23.9% below the control level by the 2nd day after irradiation (Fig. 3).

The lipid level in poplar leaves on 2nd day after irradiation had increased by over 50% compared to the control, likely reflecting the accumulation of lipids, a key component of the protective cuticle, in response to UV-B. On day 34, regardless of irradiation, the lipid content in poplar was lower than on 2nd day but higher than in the control, indicating accumulation of lipids in the cuticular layer of the leaves as they developed and grew (Fig. 3). Compared to willow on 2nd day, both poplar variants had lower lipid content values on 2nd day, while irradiated willow had the highest lipid level of all the variants. How-

ever, the difference between the control and irradiated willow plants was not statistically significant. The increase in total lipid content (Fig. 3) observed in the experiment was associated with the short-term accumulation of aliphatic fatty acid esters (which increased by 87.4% in poplar leaves) and triglycerides and fatty acids, which increased by 27.8% in willow leaves (Fig. 4).

The total carbohydrate content in the leaves of the 'Novoberlinska-3' poplar was twice as high on the 2nd day of the experiment in control plants compared to the 34th day, indicating a pronounced decline in this parameter during leaf growth and plant development (Fig. 3). Although irradiated poplar plants exhibited an 11% increase in total carbohydrate content on the 2nd day after irradiation compared to the control, these differences were smoothed out by the 34th day (Fig. 3). This suggests that ontogenetic changes exert a substantially stronger influence on carbohydrate content than UV-B radiation. In willow leaves, by contrast, the total carbohydrate content increased more sharply by 67.7% on the 2nd day after irradiation.

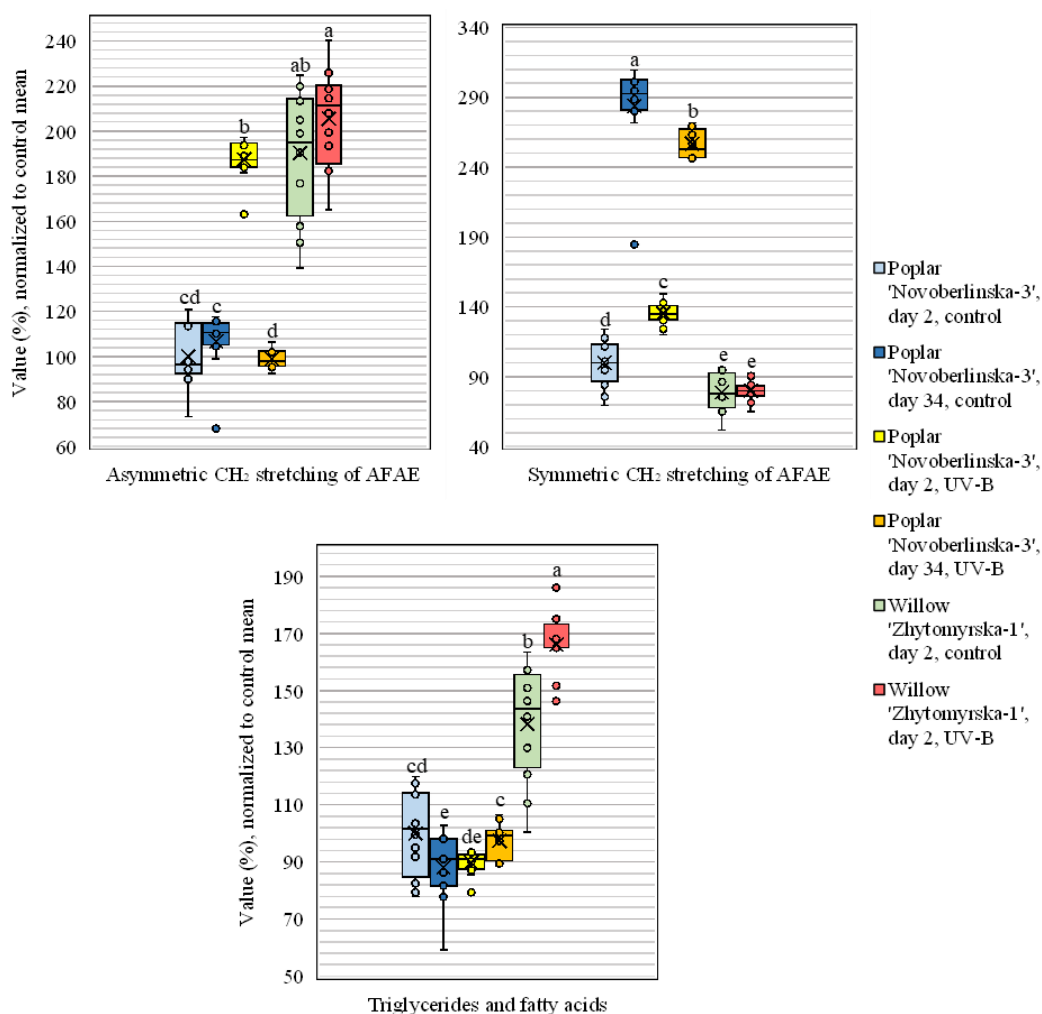


Fig. 4. The content of aliphatic fatty acid esters (AFAE), triglycerides and fatty acids in the leaves of the 'Novoberlinska-3' poplar clone on the 2nd and 34th days and the 'Zhytomyrska-1' willow clone on the 2nd day after exposure to UV-B radiation at an intensity of 17 kJ/m²: all comparisons between groups were made within one biochemical parameter; on box and whisker plots, lines indicate the median; cross symbol is the mean; the box represents values within the 25–75% quartiles, and the whiskers show minimum and maximum values; values for unirradiated leaves of the 'Novoberlinska 3' poplar clone on 2nd day were set as 100%; different letters indicate values that are significantly different, as determined by the nonparametric Mann–Whitney U test ($P < 0.05$); $n = 12$ measurements

On the 2nd day of the experiment, the leaves of the irradiated 'Novoberlinska-3' poplar plants showed a 13.6% increase in amide I protein content compared to the control values. In contrast, the amide I protein content in the leaves of the 'Zhytomyrska-1' willow decreased by 52.9% relative to the control (Fig. 5). By the 34th day, the amide I level in the irradiated poplar leaves was 25.2% lower than the control value. Meanwhile, the amide II content in the proteome did not change significantly in either poplar or willow leaves on the

2nd day after UV-B exposure. In both the control and irradiated 'Novoberlinska-3' poplar plants, the amide II domain content decreased by almost twofold on the 34th day compared to the 2nd day of the experiment, possibly due to age-related proteome remodelling (Fig. 5). The amide I / amide II ratio, considered a marker of the accumulation of amyloid, prion-like and misfolded proteins in plants, also changed accordingly (Fig. 6).

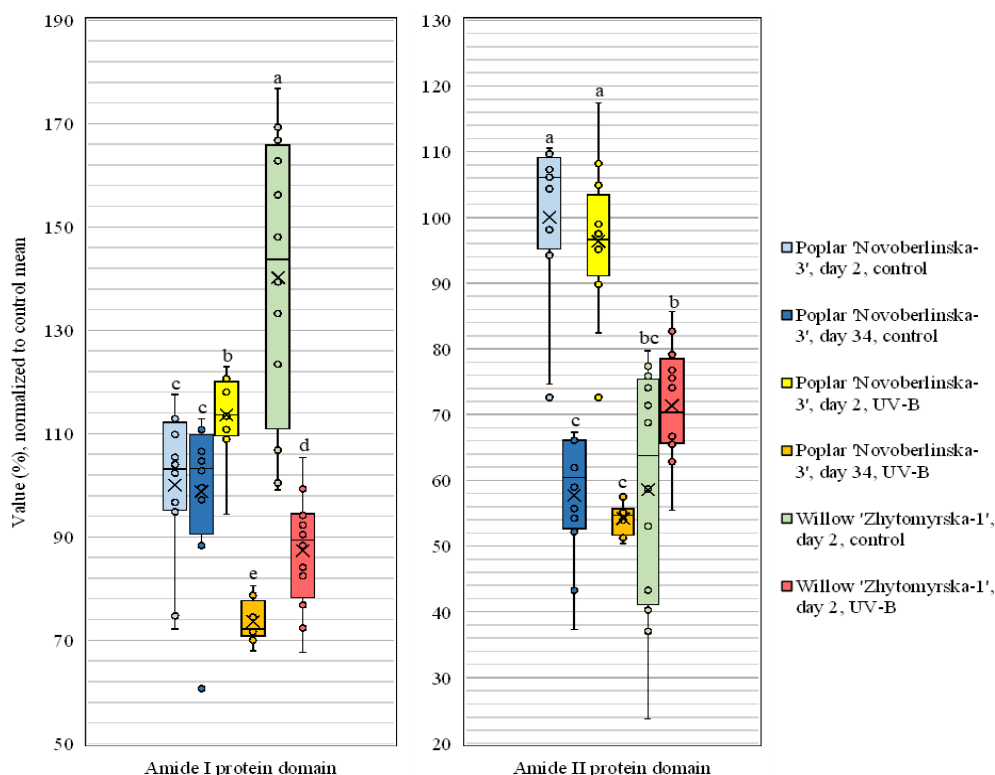


Fig. 5. Protein domains content in the leaves of the ‘Novoberlinska-3’ poplar clone on the 2nd and 34th days and the ‘Zhytomyrska-1’ willow clone on the 2nd day after exposure to UV-B radiation at an intensity of 17 kJ/m²; all comparisons between groups were made within one biochemical parameter; on box and whisker plots, lines indicate the median; cross symbol is the mean; the box represents values within the 25–75% quartiles, and the whiskers show minimum and maximum values; values for unirradiated leaves of the ‘Novoberlinska 3’ poplar clone on 2nd day were set as 100%; different letters indicate values that are significantly different, as determined by the nonparametric Mann–Whitney U test ($P < 0.05$); $n = 12$ measurements

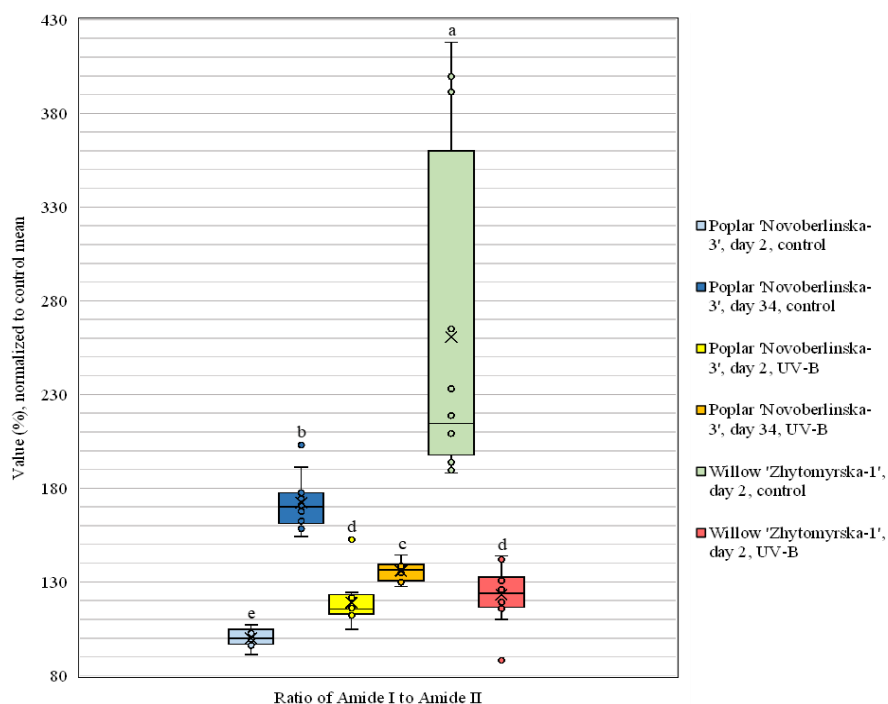


Fig. 6. Conformation of total proteins in the leaves of the ‘Novoberlinska-3’ poplar clone on the 2nd and 34th days and the ‘Zhytomyrska-1’ willow clone on the 2nd day after exposure to UV-B radiation at an intensity of 17 kJ/m²; on box and whisker plots, lines indicate the median; cross symbol is the mean; the box represents values within the 25–75% quartiles, and the whiskers show minimum and maximum values; different letters indicate values that are significantly different, as determined by the nonparametric Mann–Whitney U test ($P < 0.05$); $n = 12$ measurements; value for unirradiated leaves of the ‘Novoberlinska 3’ poplar clone on 2nd day was set as 100%

The starch content in both poplar and willow leaves increased by 27.3% and 81, respectively on 2nd day after UV-B irradiation, which is a typical stress response in plants (Fig. 7). On the 34th day of the experiment, the starch content of poplar leaves decreased significantly

in both control and irradiated plants. Similar trends were observed for the total content of carbohydrates (Fig. 3) detected by ATR-FTIR in poplar and willow leaves (starch, polysaccharides, cellulose and hemicelluloses).

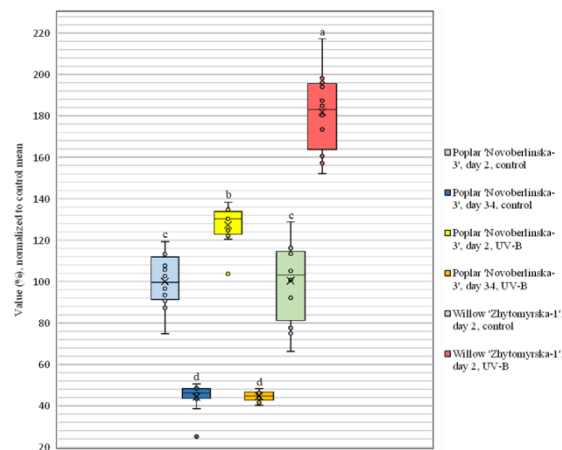


Fig. 7. Starch content in the leaves of the ‘Novoberlinska-3’ poplar clone on the 2nd and 34th days and the ‘Zhytomyrska-1’ willow clone on the 2nd day after exposure to UV-B radiation at an intensity of 17 kJ/m²: on box and whisker plots, lines indicate the median; cross symbol is the mean; the box represents values within the 25–75% quartiles, and the whiskers show minimum and maximum values; different letters indicate values that are significantly different, as determined by the nonparametric Mann–Whitney U test ($P < 0.05$); $n = 12$ measurements; value for unirradiated leaves of the ‘Novoberlinska 3’ poplar clone on 2nd day was set as 100%

The cellulose content, the main component of plant cell walls, decreased by 21.0% in poplar leaves following UV-B irradiation and by 56.5% with plant age. The content of another major component, hemicellulose, in poplar decreased with age by 13.9% in control and 43.4% in irradiated plants. Conversely, the cellulose content of willow leaves increased by 44.6% on the 2nd day after UV irradiation, while the hemicellulose content remained largely unchanged (Fig. 8).

The lignin content of the leaf tissues of irradiated poplars and willows did not differ significantly from that of the control group. However, a 32.3% and 95.2% higher accumulation of lignin was observed

in the leaves of both irradiated and non-irradiated poplars during development (on the 34th day compared to the 2nd day of the experiment). Additionally, on 2nd day of experiment irradiated poplars exhibited an increase by 26.8% in phenylpropanoid content, substances that protect plants from UV radiation and are also monomers of lignin. On the 34th day of the experiment, the level of phenylpropanoids in poplar leaves decreased below control values, confirming the hypothesis that these substances interact with stress-induced active radicals, breaking down in the process but preventing damage to biologically significant macromolecules (Fig. 8).

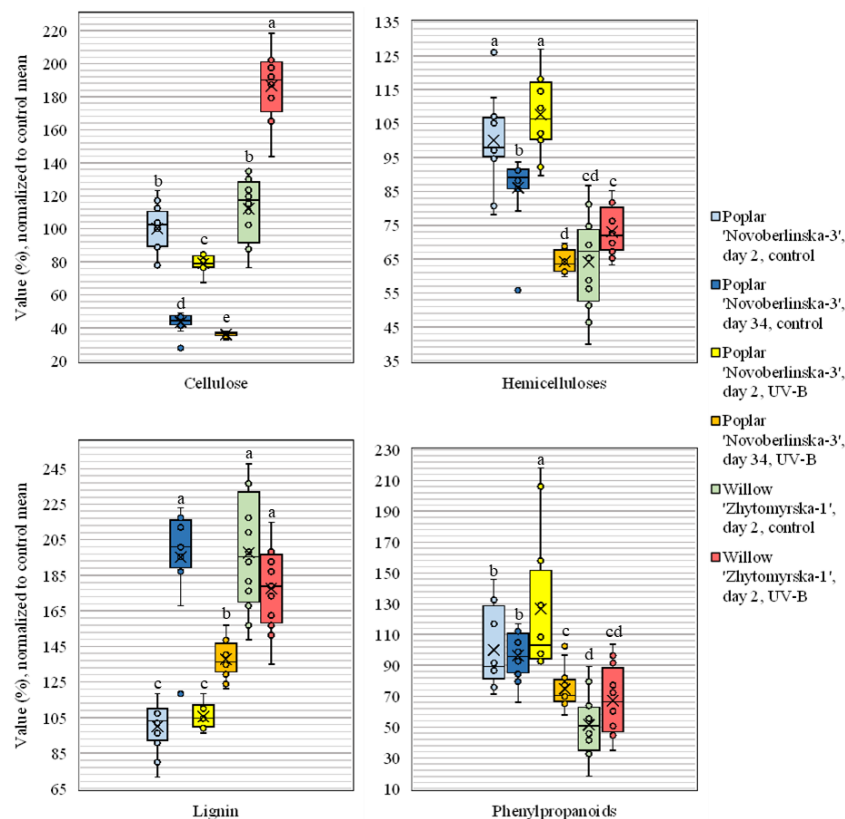


Fig. 8. Content of major cell wall components in the leaves of the ‘Novoberlinska-3’ poplar clone on the 2nd and 34th days and the ‘Zhytomyrska-1’ willow clone on the 2nd day after exposure to UV-B radiation at an intensity of 17 kJ/m²: all comparisons between groups were made within one biochemical parameter; on box and whisker plots, lines indicate the median; cross symbol is the mean; the box represents values within the 25–75% quartiles, and the whiskers show minimum and maximum values; values for unirradiated leaves of the ‘Novoberlinska 3’ poplar clone on 2nd day were set as 100%; different letters indicate values that are significantly different, as determined by the nonparametric Mann–Whitney U test ($P < 0.05$); $n = 12$ measurements

Following irradiation, the fatty acid esterification index increased twofold in poplar leaves, whereas it decreased by 13.9% in willow leaves. Furthermore, UV-B irradiation inhibited the age-related increase in the fatty acid esterification index in poplar by 19.6% (Fig. 9). Therefore, the cuticular lipid layer in the leaves of the 'Novoberlinska-3' poplar is more sensitive to a UV-B dose of 17 kJ/m² than that in the 'Zhytomyska-1' willow. We observed similar trends on 2nd day in irradiated poplar and willow leaves with an increased phenylpropanoids / lignin ratio of 18.7% and 11.8%, respectively. This reflects the

known plant response to reorganise the metabolism of phenolic compounds, converting them from macromolecular lignin to monomeric antioxidants that protect the photosynthetic apparatus from UV-B radiation. An increase in the ratio of nutritive to structural carbohydrates by 40.0% in poplar and 10.5% in willow also indicates the stress response of both plant species. The decrease in the ratio of two abiotic stress-sensitive parameters, total proteins to nucleic acids (Fig. 9) by 10.1% in poplar and 46.1% in willow, also indicates a stress response in irradiated plants of both species.

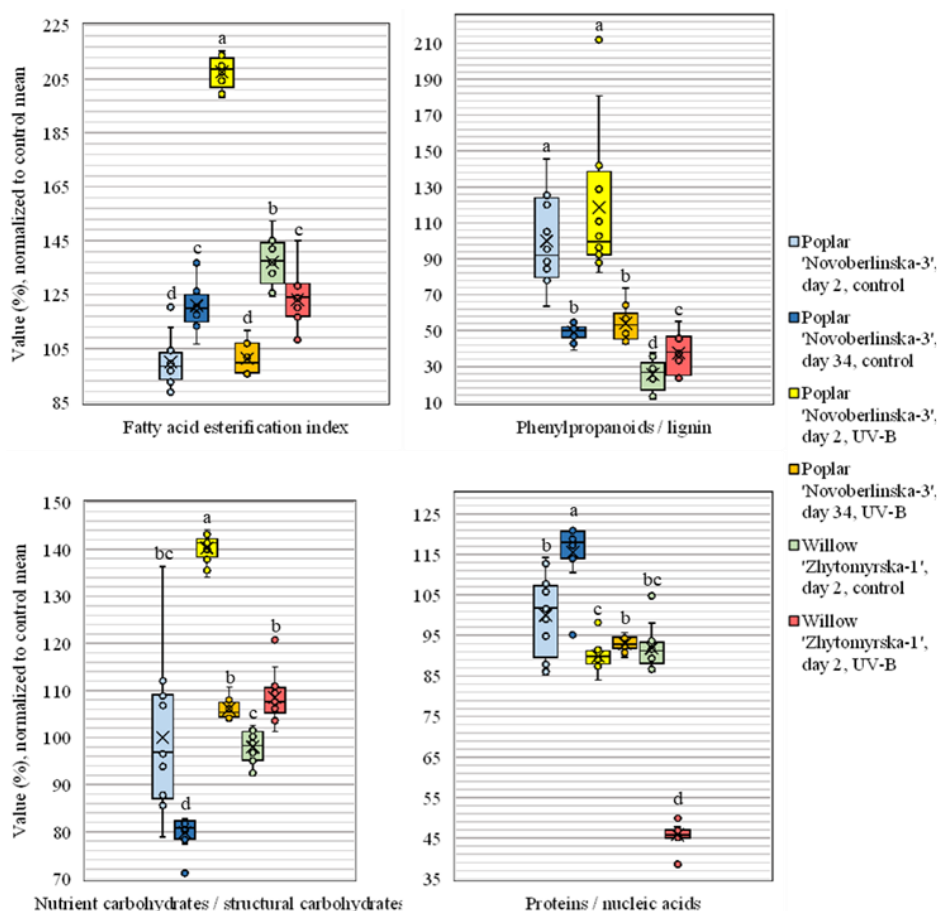


Fig. 9. Biochemical markers of stress responses in the leaves of the 'Novoberlinska-3' poplar clone on the 2nd and 34th days and the 'Zhytomyska-1' willow clone on the 2nd day after exposure to UV-B radiation at an intensity of 17 kJ/m²: all comparisons between groups were made within one biochemical parameter; on box and whisker plots, lines indicate the median; cross symbol is the mean; the box represents values within the 25–75% quartiles, and the whiskers show minimum and maximum values; values for unirradiated leaves of the 'Novoberlinska-3' poplar clone on 2nd day were set as 100%; different letters indicate values that are significantly different, as determined by the nonparametric Mann–Whitney U test ($P < 0.05$); $n = 12$ measurements

Discussion

Biochemical and metabolic changes in the 'Novoberlinska-3' poplar under the influence of UV-B. The results obtained indicate that the *Populus pyramidalis* × *P. laurifolia* cv. 'Novoberlinska-3' hybrid exhibits a distinct phasic pattern in response to acute UV-B exposure, combining early metabolic shifts with long-term adaptive changes. This organisation of the response over time is consistent with FTIR data from other species, in which short-term changes to the lipid and protein spectra precede stabilisation processes in the cell wall and secondary metabolism (Zhao et al., 2013; Sharma & Uttam, 2017a; Nikalje et al., 2019).

At the early stage (day 2), an increase in total lipid content, aliphatic fatty acid esters and the fatty acid esterification index was observed in poplar. As this index is a marker of lipid oxidation, which is directly linked to ROS-induced processes, its increase indicates the activation of the antioxidant response and the reorganisation of membrane structures. Similar patterns have been observed in plants exposed to salinity, heavy metals or drought, where FTIR spectra showed an increase in the intensity of the 2850–2860 cm⁻¹ and 2920–

2930 cm⁻¹ bands, which are associated with the CH₂ groups of lipids (Ogbaga et al., 2017; Willick et al., 2018; Nikalje et al., 2019). Furthermore, studies by Liu et al. (2018) and Willick et al. (2018) demonstrate that comparable alterations to the aliphatic chain bands are indicative of cuticular wax restructuring, which aligns with our observation of elevated aliphatic fatty acid ester content in poplar.

Concurrently, an increase in starch and nutritious carbohydrate content was observed in poplar, corresponding to a typical metabolic response to stress involving the mobilisation of energy resources to sustain recovery processes. Studies of other species have also demonstrated an increase in the intensity of the 1020–1080 cm⁻¹ bands associated with carbohydrates in response to stress factors (Sharma & Uttam, 2017b; Yu et al., 2020; Yun et al., 2024).

Compared to willow, the protein / nucleic acid ratio in poplar decreased by a smaller amount, indicating less inhibition of protein synthesis. The phenylpropanoids / lignin ratio in poplar increased on the 2nd day after UV irradiation, indicating a shift in phenolic metabolism and the activation of antioxidant synthesis – compounds that protect the photosynthetic apparatus from UV damage. Similar changes have been observed in studies of stressed plants, where a decrease in the

intensity of the 1510–1525 cm^{-1} band (lignin) has been accompanied by an increase in bands associated with phenolic groups (Osman et al., 2022; Shoaib et al., 2022). This reaction is typical for species of the genus *Populus*: UV-B stimulates the synthesis of flavonoids, condensed tannins and other antioxidants (Wong et al., 2022; Gourlay et al., 2022). Phenolic compounds play a key role in protecting against ROS.

On the 34th day of the experiment, a decrease in cellulose and hemicellulose content was observed in poplar, which corresponds to the 'structural economy' model during stress. FTIR spectroscopy often detects a decrease in the intensity of the 1030–1160 cm^{-1} bands, which are associated with polymeric polysaccharides in plant cell walls, when plants are exposed to stress factors (Sharma & Uttam, 2017a; Shoaib et al., 2022).

At the same time, an age-related increase in lignin content occurred on the 34th day in control plants, whereas this process was less pronounced in irradiated plants, indicating a prolonged reorganisation of the phenylpropanoid pathway.

One of the most significant findings was the increase in the amide I / amide II ratio in poplar two days after UV irradiation. An increase in this ratio is a recognised marker of amyloid-like and misfolded protein formation. This is consistent with the findings of Kryvolkhyzha et al. (2024) that ionising radiation stimulates the accumulation of amyloid aggregates in plant tissues. Therefore, poplar demonstrates early activation of the accumulation of protein structures that are resistant to proteolysis, which may be part of a universal plant stress response.

Thus, the response of the 'Novoberlinska-3' poplar to acute UV-B radiation at the selected intensity was characterised by a combination of early metabolic shifts and subsequent stabilisation processes forming an adaptive response. Initially, the plants activated lipid and carbohydrate metabolism and the phenylpropanoid metabolic pathway, showing signs of amyloid-like/misfolded proteins accumulation, consistent with existing data on early stress responses in tree species. At a later stage, a gradual change in biochemical indicators characterising the composition and structure of the cell wall was observed, alongside a decrease in the intensity of metabolic fluctuations relative to the non-irradiated control. However, a statistically significant modification of both primary metabolism (an increase in simple polysaccharide content and a decrease in cellulose and protein content) and secondary metabolism (a decrease in phenylpropanoid and lignin content) was maintained, indicating a transition to a phase of long-term adaptation. These changes demonstrate the poplar's high metabolic plasticity and its ability to maintain functional stability under conditions of acute ultraviolet irradiation.

Biochemical patterns and metabolic changes in the 'Zhytomyrska-1' willow under the influence of UV-B. The response of the willow 'Zhytomyrska-1' to acute UV-B exposure differed significantly from that of the poplar, characterised by a rapid, metabolically intense response within the first two days after acute irradiation. Unlike the more balanced, structured adaptation of the poplar, the willow exhibits a 'rapid resource mobilisation' model involving a sharp increase in primary and secondary metabolic activity, aimed at immediately compensating for the effects of stress. Similar rapid responses have been observed in studies of stressed plants, where initial alterations in lipid and carbohydrate profiles indicate the activation of energy metabolism and ROS-dependent processes (Ogbaga et al., 2017; Sharma & Uttam, 2017a; Nikalje et al., 2019).

In particular, a significant increase in total lipid content, aliphatic fatty acid ester content and the fatty acid esterification index was observed in willow on the 2nd day after irradiation. As this index is a marker of lipid oxidation and is directly linked to the formation of lipid peroxidation products, the increase indicates an intense ROS-induced response. Similar trends have been reported in studies where the FTIR spectra of stressed plants showed an increase in the intensity of the 2850–2930 cm^{-1} bands, which are associated with the lipid CH_2 groups. This reflects a restructuring of membrane and leaf cuticle structures (Zhao et al., 2013; Willick et al., 2018; Liu et al., 2018; Yu et al., 2020). At the same time, the total carbohydrate and starch content of the willow increased sharply. The increase in the ratio of nutri-

tive to structural carbohydrates indicates the active accumulation of energy reserves, which is caused by a reduction in the synthesis of structural cell wall polysaccharides. This response is common in plants experiencing acute stress and has been extensively studied in salt- and metal-tolerant species (Sharma & Uttam, 2017a; Nikalje et al., 2019; Yun et al., 2024).

A more significant decrease in the protein / nucleic acid ratio was observed in willow leaves than in poplar leaves, indicating the suppression of protein synthesis alongside RNA accumulation. This mechanism is characteristic of plants that switch to a 'resource-saving' mode, in which energy expenditure on translation decreases while transcriptional activity increases in order to maintain stress signalling pathways. Similar patterns have been observed in studies of plants exposed to heavy metals or drought (Ogbaga et al., 2017; Osman et al., 2022). On the 2nd day of the experiment, the phenylpropanoid / lignin ratio in willow increased significantly. This could be explained by a shift in secondary metabolic pathways, such as the shikimate and polyketide pathways, towards synthesising protective phenylpropanoids. This is a typical response in woody plants to UV-B radiation, whereby phenylpropanoids act as antioxidants and stabilisers of chloroplast membranes, thereby protecting photosystems I and II. Studies of stressed plants often show that an increase in the intensity of bands associated with phenolic groups (1510–1600 cm^{-1}) is accompanied by a decrease in lignin signals (Shoaib et al., 2022; Yun et al., 2024). This reaction is particularly characteristic of willows, as members of the genus *Salix* have a high capacity for the rapid synthesis of phenolic compounds, including salicylates, flavonoids and condensed tannins. This is consistent with data on the high phenolic plasticity of willows in response to stress factors.

Unlike the poplar, the willow showed an increase in the content of structural polysaccharides (cellulose and hemicellulose) on the 2nd day of the experiment, accompanied by a simultaneous increase in nutritive carbohydrate content. This indicates the activation of carbohydrate metabolism. Similar changes have been observed in studies on plants exposed to salinity or heavy metals, where a reduction in the intensity of the 1030–1160 cm^{-1} bands indicates a weakening of the cell wall's structural component (Sharma & Uttam, 2017a; Shoaib et al., 2022).

In the context of protein metabolism, the response of the 'Zhytomyrska-1' willow to UV-B radiation was found to differ fundamentally from that of the poplar, reflecting the species-specific regulation of protein structure in *Salix* species. The decrease in the amide I / amide II ratio observed on the 2nd day after irradiation indicates a reduction in the formation of β -structural/amyloid proteins and an increase in processes associated with the inhibition of protein synthesis. Similar changes to FTIR spectra have been observed in plants exposed to intense oxidative stress, particularly that associated with heavy metal exposure. In these cases, a decrease in amide I is accompanied by reduced protein domain stability and cells entering an energy-saving mode (Zhao et al., 2013; Yu et al., 2020). In this case, such dynamics may reflect a temporary restriction of translational activity and a redistribution of resources in favour of rapid signalling and metabolic responses aimed at neutralising the effect of stress. The absence of signs of an amyloidogenic response, which is characteristic of poplar, highlights that willow employs a distinct strategy for adapting proteins, prioritising the rapid reorganisation of metabolic fluxes and maintaining cellular metabolic flexibility over stabilising protein structures.

Thus, the 'Zhytomyrska-1' willow exhibits a rapid and energy-intensive model of adaptation to UV-B. This includes a sharp increase in lipid and carbohydrate metabolism, activation of the phenylpropanoid pathway and suppression of protein synthesis. Unlike poplar, willow does not develop an amyloidogenic response. This strategy indicates a high metabolic response rate, but less pronounced structural stabilisation than poplar.

Comparison of the biochemical responses of two species of the Salicaceae family to UV-B radiation. A comparative analysis of the responses of 'Novoberlinska-3' poplar and 'Zhytomyrska-1' willow to acute UV-B exposure revealed significant differences in the structure and dynamics of metabolic responses between the two species. Despite belonging to the same family (Salicaceae) and being charac-

terised by high plasticity of adaptive processes, the two species exhibited different biochemical adaptation strategies (Lahlali et al., 2014; Sharma & Uttam, 2017a; Nikalje et al., 2019). These differences encompass primary and secondary metabolism, as well as the structural components of cell walls and conformational changes in proteins. This is consistent with data from studies of other tree species, in which stress responses exhibit distinct species specificity (Ren et al., 2010; Kutsokon & Khoma, 2025).

Poplar demonstrated a balanced adaptation model, combining an early increase in lipid, starch and aliphatic fatty acid ester content with the maintenance of protein synthesis, despite a decrease in cellulose and hemicellulose content. This indicates the maintenance of metabolic stability, even under conditions of acute stress. In contrast, willow exhibited a model of rapid resource mobilisation, characterised by a sharp increase in available carbohydrates, lipids, the fatty acid esterification index and cellulose and hemicellulose content, accompanied by the suppression of protein synthesis. This strategy is typical of plants that direct resources towards immediate compensation for the effects of stress (Zhao et al., 2013; Ogbaga et al., 2017; Sharma & Uttam, 2018).

An increase in the phenylpropanoids / lignin ratio was observed in both species, indicating the activation of phenolic compound synthesis. However, this process was significantly more intense in willow, consistent with its ability to rapidly accumulate phenolic metabolites, including salicylates and condensed tannins. In poplar, this process was less pronounced, stabilising gradually in the late stage of adaptation at a level close to the control. This is consistent with previous studies, which have shown that *Populus* exhibits a longer-lasting but less pronounced phenolic response to UV-B, whereas *Salix* reacts rapidly and intensely (Gourlay et al., 2022; Wong et al., 2022).

In *Populus*, gradual stabilisation of the content of cellulose, hemicellulose and lignin was observed in the late stage of the stress response (day 34 of the experiment), indicating a transition to the phase of structural stabilisation. In contrast, *Salix* demonstrated an accumulation of structural polysaccharides as early as day 2 after irradiation.

One of the most significant differences observed between the studied species relates to the dynamics of the amide I / amide II ratio. In poplar, this ratio increased, indicating the formation of β -structural proteins and the possible accumulation of amyloid-like proteins. This is consistent with the proteomic stress response described by Kryvokhyzha et al. (2024). Conversely, in willow, the amide I / amide II index decreased, indicating the suppression of protein synthesis and the absence of an amyloidogenic response. These results demonstrate the different strategies employed by the two species to adapt their proteins: poplar stabilises protein structures, while willow maintains metabolic flexibility by reducing translational activity.

In summary, the ‘Novoberlinska-3’ poplar and the ‘Zhytomyrska-1’ willow implement two distinct yet effective biochemical adaptation strategies in response to acute UV-B exposure. The poplar exhibits a more prolonged response, involving moderate activation of primary metabolism alongside the formation of amyloid-like protein structures and the gradual stabilisation of cell wall components. In contrast, willow is characterised by a rapid response involving probable cell wall renewal/thickening, as well as a sharp increase in lipid and carbohydrate metabolism, intense activation of the phenylpropanoid pathway and inhibition of protein synthesis. These findings highlight the high species-specificity of metabolic strategies within the Salicaceae family, demonstrating that even closely related species can follow fundamentally different biochemical adaptation trajectories in response to elevated UV-B radiation levels.

Conclusions

A study investigating the impact of elevated UV-B levels (17 kJ/m²) on microclonally propagated *Populus pyramidalis* × *P. laurifolia* ‘Novoberlinska-3’ poplar and *Salix* sp. ‘Zhytomyrska-1’ willow plants revealed significant variations in primary and secondary metabolic processes, as well as protein conformational changes. The results suggest that two distinct adaptation strategies are employ-

ed in response to acute UV-B stress, reflecting species-specific metabolic plasticity in *Salix* and *Populus* species.

In the poplar ‘Novoberlinska-3,’ exposure to UV-B radiation at an early stage triggered the activation of several metabolic processes, including an increase in the levels of nucleic acids, total lipids, starch and aliphatic fatty acid esters. The increase in the fatty acid esterification index within the species indicates enhanced lipid oxidation and the formation of a ROS-dependent response, consistent with FTIR data from studies of stressed plants. An early increase in the amide I / amide II ratio in poplar suggests the accumulation of amyloid-like proteins may be a mechanism of stress adaptation through proteome stabilisation. Concurrently, an increase in the phenylpropanoids / lignin ratio was observed, suggesting a shift in the phenylpropanoid pathway towards synthesising UV-B protective compounds. At the late stage, the poplars exhibited decreased starch, cellulose, hemicellulose and phenylpropanoid content, indicating a transition from an acute metabolic response to a stabilisation phase involving the suppression of primary and secondary metabolism. An increase in lignin content in control plants on the 34th day of the experiment confirms an age-related increase in cell wall stiffness; however, this process was less pronounced in irradiated plants.

The willow ‘Zhytomyrska-1’ demonstrated a different response pattern, characterised by a rapid response to UV-B irradiation. In irradiated plants, significant increases were observed in the content of nucleic acids, total lipids, aliphatic fatty acid esters, total carbohydrates, starch, cellulose and hemicellulose. Unlike poplar, the amide I / amide II ratio in willow decreased, alongside a reduction in the protein / nucleic acid ratio. This may be associated with the inhibition of protein synthesis, consistent with known mechanisms of stress-induced plant responses. An increase in the phenylpropanoid / lignin ratio in irradiated willow indicates the activation of secondary metabolism and the synthesis of defensive phenolic compounds.

A comparison of the two species revealed that poplar exhibits a less intense adaptation model, involving early metabolic shifts followed by moderate metabolic suppression. In contrast, willow demonstrates a rapid and intense metabolic response aimed at mobilising energy and defence resources. Overall, both species exhibited signs of stress tolerance. Combining FTIR spectroscopy with primary and secondary metabolic analysis enabled species-specific adaptation mechanisms to be identified, which is important for further selecting Salicaceae clones with optimal stress tolerance characteristics.

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.

This work was supported by the National Research Foundation of Ukraine (2020–2023, grant number 2020.02/0316, ‘The influence of stress factors on the synthesis of proteins with prion properties in plants’).

References

- Ali, A., Santoro, P., Mori, J., Ferrante, A., & Cocetta, G. (2024). Effect of UV-B elicitation on spearmint's (*Mentha spicata* L.) morpho-physiological traits and secondary metabolites production. *Plant Growth Regulation*, 104, 63–76.
- Baroniya, S. S., Kataria, S., Pandey, G. P., & Guruprasad, K. N. (2014). Growth, photosynthesis and nitrogen metabolism in soybean varieties after exclusion of the UV-B and UV-A/B components of solar radiation. *The Crop Journal*, 2(6), 388–397.
- Bernhard, G. H., Bais, A. F., Aucamp, P. J., Klekociuk, A. R., Liley, J. B., & McKenzie, R. L. (2023). Stratospheric ozone, UV radiation, and climate interactions. In: Aucamp, P. J., & Bais, A. F. (Eds.). *Environmental effects of stratospheric ozone depletion, UV radiation, and interactions with climate change: UNEP Environmental Effects Assessment Panel, Quadrennial Assessment 2022*. Springer Nature, Cham. Vol. 22. Pp. 937–989.
- Bormann, J. F., Barnes, P. W., Robson, T. M., Robinson, S. A., Jansen, M. A. K., Ballaré, C. L., & Flint, S. D. (2019). Linkages between stratospheric ozone, UV radiation and climate change and their implications for terrestrial ecosystems. In: Aucamp, P. J., & Bais, A. F. (Eds.). *Environmental effects of ozone depletion and its interactions with climate change: 2018 Assessment*. Royal Society of Chemistry, Cambridge. Vol. 18(3). Pp. 681–716.

- Czégény, G., Máta, A., & Hideg, É. (2016). UV-B effects on leaves – oxidative stress and acclimation in controlled environments. *Plant Science*, 248, 57–63.
- Dimitriou, I., & Mola-Yudego, B. (2017). Poplar and willow plantations on agricultural land in Sweden: Area, yield, groundwater quality and soil organic carbon. *Forest Ecology and Management*, 383, 99–107.
- Dou, J., Galvis, L., Holopainen-Mantila, U., Reza, M., Tamminen, T., & Vuorinen, T. (2016). Morphology and overall chemical characterization of willow (*Salix* sp.) inner bark and wood: Toward controlled deconstruction of willow biomass. *ACS Sustainable Chemistry and Engineering*, 4(7), 3871–3876.
- Fang, X., Pyle, J. A., Chipperfield, M. P., Daniel, J. S., Park, S., & Prinn, R. G. (2019). Challenges for the recovery of the ozone layer. *Nature Geoscience*, 12, 592–596.
- Glgorić, E., Igić, R., Suvajdžić, L., & Grujić-Letić, N. (2019). Species of the genus *Salix* L.: Biochemical screening and molecular docking approach to potential acetylcholinesterase inhibitors. *Applied Sciences*, 9(9), 1842.
- Gourlay, G., Hawkins, B. J., Albert, A., Schnitzler, J. P., & Constabel, C. P. (2022). Condensed tannins as antioxidants that protect poplar against oxidative stress from drought and UV-B. *Plant, Cell and Environment*, 45(2), 362–377.
- Guarino, C., Paura, B., & Sciarillo, R. (2018). Enhancing phytoextraction of heavy metals at real scale by combining Salicaceae trees with microbial consortia. *Frontiers in Environmental Science*, 6, 137.
- Hangs, R. D., Schoenau, J. J., Van Rees, K. C. J., & Steppuhn, H. (2011). Examining the salt tolerance of willow (*Salix* spp.) bioenergy species for use on salt-affected agricultural lands. *Canadian Journal of Plant Science*, 91(3), 509–517.
- Hu, Z., Li, H., Chen, S., & Yang, Y. (2013). Chlorophyll content and photosystem II efficiency in soybean exposed to supplemental ultraviolet-B radiation. *Photosynthetica*, 51(1), 151–157.
- Hui, R., Li, X., Chen, C., Zhao, X., Jia, R., Liu, L., & Wei, Y. (2013). Responses of photosynthetic properties and chloroplast ultrastructure of *Bryum argenteum* from a desert biological soil crust to elevated ultraviolet-B radiation. *Physiologia Plantarum*, 147(4), 489–501.
- Jadidi, M., Mumivand, H., Ehteshami Nia, A., Shayganfar, A., & Maggi, F. (2023). UV-A and UV-B combined with photosynthetically active radiation change plant growth, antioxidant capacity and essential oil composition of *Pelargonium graveolens*. *BMC Plant Biology*, 23, 555.
- Jang, Y. S., Lee, D. E., Hong, J.-H., Kim, K. A., Kim, B., Cho, Y. R., Ra, M.-J., Jung, S.-M., Yu, J.-N., An, S., & Kim, K. H. (2023). Phytochemical investigation of marker compounds from indigenous Korean *Salix* species and their antimicrobial effects. *Plants*, 12(1), 104.
- Jansen, M. A. K., Gaba, V., & Greenberg, B. M. (1998). Higher plants and UV-B radiation: Balancing damage, repair and acclimation. *Trends in Plant Science*, 3(4), 131–135.
- Kataria, S., Sajoo, A., & Guruprasad, K. N. (2014). Impact of increasing ultraviolet-B (UV-B) radiation on photosynthetic processes. *Journal of Photochemistry and Photobiology B: Biology*, 137, 55–66.
- Khoma, Y., Khudolieieva, L., Rashydov, N., & Kutsokon, N. (2022). *In vitro* culture initiation and regeneration of two highly productive clones of poplar. *Nova Biotechnologica et Chimica*, 21(1), e1089.
- Khudolieieva, L., Kutsokon, N., Rashydov, N., & Dugan, O. (2016). Quantitative and qualitative evaluations of environmentally dangerous wastes emission from burning wood comparing to natural gas and coal. *Studia Biologica*, 10(3), 61–70 (in Ukrainian).
- Klem, K., Oravec, M., Holub, P., Šimor, J., Findurová, H., Surá, K., Veselá, B., Hodaňová, P., Jansen, M. A. K., & Urban, O. (2022). Interactive effects of nitrogen, UV and PAR on barley morphology and biochemistry are associated with the leaf C:N balance. *Plant Physiology and Biochemistry*, 172, 111–124.
- Kryvokhyzha, M., Litvinov, S., Danchenko, M., Khudolieieva, L., Kutsokon, N., Baráth, P., & Rashydov, N. (2024). How does ionizing radiation affect amyloidogenesis in plants? *International Journal of Radiation Biology*, 100(6), 922–933.
- Kutsokon, N., & Khoma, Y. (2025). Effects of drought stress on spring bud development in poplar and willow clones. *Dendrobiology*, 93, 86–97.
- Kutsokon, N., Rakhmetov, D., Rakhmetova, S., Khudolieieva, L., & Rashydov, N. (2022). Nursery screening of poplar and willow clones for biofuel application in Ukraine. *iForest: Biogeosciences and Forestry*, 15(5), 401–410.
- Lahlali, R., Jiang, Y., Kumar, S., Karunakaran, C., Liu, X., Borondics, F., Hallin, E., & Bueckert, R. (2014). ATR-FTIR spectroscopy reveals involvement of lipids and proteins of intact pea pollen grains in heat stress tolerance. *Frontiers in Plant Science*, 5, 747.
- León-Chan, R. G., López-Meyer, M., Osuna-Enciso, T., Sañudo-Barajas, J. A., Heredia, J. B., & León-Félix, J. (2017). Low temperature and ultraviolet-B radiation affect chlorophyll content and induce the accumulation of UV-B-absorbing and antioxidant compounds in bell pepper (*Capsicum annuum*) plants. *Environmental and Experimental Botany*, 139, 143–151.
- Li, H., Meng, W., Xiao, H., Li, M., Yan, K., Li, Y., & He, Y. (2026). Elevated temperature and enhanced UV-B radiation alter soil nitrogen supply and allocation within rice plants in high-altitude paddy fields. *BMC Plant Biology*, 26, 91.
- Lidon, F. C., & Ramalho, J. C. (2011). Impact of UV-B irradiation on photosynthetic performance and chloroplast membrane components in *Oryza sativa* L. *Journal of Photochemistry and Photobiology B: Biology*, 104(3), 457–466.
- Liu, N., Karunakaran, C., Lahlali, R., Warkentin, T., & Bueckert, R. A. (2018). Genotypic and heat stress effects on leaf cuticles of field pea using ATR-FTIR spectroscopy. *Planta*, 248, 539–552.
- McKenzie, R. L., Aucamp, P. J., Bais, A. F., Björn, L. O., Ilyas, M., & Madronich, S. (2011). Ozone depletion and climate change: Impacts on UV radiation. In: Aucamp, P. J., & Björn, L. O. (Eds.). *Environmental effects of ozone depletion and its interactions with climate change: 2010 Assessment*. Royal Society of Chemistry, Cambridge. Vol. 10(2). Pp. 182–198.
- Nassour, R., & Ayash, A. (2021). Effects of ultraviolet-B radiation in plant physiology. *Agriculture (Pol'nohospodárstvo)*, 67(1), 1–15.
- Nikalje, G. C., Kumar, J., Nikam, T. D., & Suprasanna, P. (2019). FT-IR profiling reveals differential response of roots and leaves to salt stress in a halophyte *Sesuvium portulacastrum* (L.) L. *Biotechnology Reports*, 23, e00352.
- Ogbaga, C. C., Miller, M. A. E., Athar, H., & Johnson, G. N. (2017). Fourier transform infrared spectroscopic analysis of maize (*Zea mays*) subjected to progressive drought reveals involvement of lipids, amides and carbohydrates. *African Journal of Biotechnology*, 16(18), 1034–1042.
- Osman, S. O. M., Saad, A. S. I., Tadano, S., Takeda, Y., Konaka, T., Yamasaki, Y., Tahir, I. S. A., Tsujimoto, H., & Akashi, K. (2022). Chemical fingerprinting of heat stress responses in the leaves of common wheat by Fourier transform infrared spectroscopy. *International Journal of Molecular Sciences*, 23(5), 2842.
- Podolec, R., Demarsy, E., & Ulm, R. (2021). Perception and signaling of ultraviolet-B radiation in plants. *Annual Review of Plant Biology*, 72, 793–822.
- Rai, K., & Agrawal, S. B. (2017). Effects of UV-B radiation on morphological, physiological and biochemical aspects of plants: An overview. *Journal of Scientific Research*, 61, 87–113.
- Ramos, P. A. B., Moreirinha, C., Silva, S., Costa, E. M., Veiga, M., Coscueta, E., Santos, S. A. O., Almeida, A., Pintado, M. M., Freire, C. S. R., Silva, A. M. S., & Silvestre, A. J. D. (2019). The health-promoting potential of *Salix* spp. bark polar extracts: Key insights on phenolic composition and in vitro bioactivity and biocompatibility. *Antioxidants*, 8(12), 609.
- Reisz, J. A., Bansal, N., Qian, J., Zhao, W., & Furdul, C. M. (2014). Effects of ionizing radiation on biological molecules – mechanisms of damage and emerging methods of detection. *Antioxidants and Redox Signaling*, 21(2), 260–292.
- Ren, J., Duan, B., Zhang, X., Korpelainen, H., & Li, C. (2010). Differences in growth and physiological traits of two poplars originating from different altitudes as affected by UV-B radiation and nutrient availability. *Physiologia Plantarum*, 138(3), 278–288.
- Roviello, G. N. (2025). The multifunctional role of *Salix* spp.: Linking phytoremediation, forest therapy and phytomedicine for environmental and human benefits. *Forests*, 16(12), 1808.
- Sharma, S., & Guruprasad, K. N. (2012). Enhancement of root growth and nitrogen fixation in *Trigonella* by UV-exclusion from solar radiation. *Plant Physiology and Biochemistry*, 61, 97–102.
- Sharma, S., & Uttam, K. N. (2016). Investigation of the manganese stress on wheat plant by attenuated total reflectance Fourier transform infrared spectroscopy. *Spectroscopy Letters*, 49(8), 566–574.
- Sharma, S., & Uttam, K. N. (2017a). Early diagnosis of mercury stress of wheat seedlings using attenuated total reflection Fourier transform infrared spectroscopy. *Analytical Letters*, 50(18), 2924–2937.
- Sharma, S., & Uttam, K. N. (2017b). Rapid analyses of stress of copper oxide nanoparticles on wheat plants at an early stage by laser-induced fluorescence and attenuated total reflectance Fourier transform infrared spectroscopy. *Vibrational Spectroscopy*, 92, 135–150.
- Sharma, S., & Uttam, K. N. (2018). Early stage detection of stress due to copper on maize (*Zea mays* L.) by laser-induced fluorescence and infrared spectroscopy. *Journal of Applied Spectroscopy*, 85(4), 771–780.
- Shoib, A., Nafisa, Riaz, G., Fatima, Q., Fatima, U., & Iqbal, N. (2022). Fourier-transform infrared spectroscopy identified changes in the cell wall components associated with the simultaneous trafficking of white mold fungus and copper. *Pakistan Journal of Phytopathology*, 34(2), 241–254.
- Singh, S., Agrawal, S. B., & Agrawal, M. (2015). Responses of pea plants to elevated UV-B radiation at varying nutrient levels: N metabolism, carbohydrate pool, total phenolics and yield. *Functional Plant Biology*, 42(11), 1045–1056.
- Singh, S., Kumari, R., Agrawal, M., & Agrawal, S. B. (2012). Differential response of radish plants to supplemental ultraviolet-B radiation under varying NPK levels: Chlorophyll fluorescence, gas exchange and antioxidants. *Physiologia Plantarum*, 145(3), 474–484.

- Solomon, S. (2021). Risks to the stratospheric ozone shield in the Anthropocene. *Ambio*, 50(1), 44–48.
- Stolarski, M. J., Szczukowski, S., Tworowski, J., & Klasa, A. (2013). Yield, energy parameters and chemical composition of short-rotation willow biomass. *Industrial Crops and Products*, 46, 60–65.
- Tawfeek, N., Mahmoud, M. F., Hamdan, D. I., Sobeh, M., Farrag, N., Wink, M., & El-Shazly, A. M. (2021). Phytochemistry, pharmacology and medicinal uses of plants of the genus *Salix*: An updated review. *Frontiers in Pharmacology*, 12, 593856.
- Van Slycken, S., Witters, N., Meiresonne, L., Meers, E., Ruttens, A., Van Peteghem, P., Weyens, N., Tack, F. M. G., & Vangronsveld, J. (2013). Field evaluation of willow under short rotation coppice for phytomanagement of metal-polluted agricultural soils. *International Journal of Phytoremediation*, 15(7), 677–689.
- Verdaguer, D., Jansen, M. A. K., Llorens, L., Morales, L. O., & Neugart, S. (2017). UV-A radiation effects on higher plants: Exploring the known unknown. *Plant Science*, 255, 72–81.
- Volk, T. A., Heavey, J. P., & Eisenbies, M. H. (2016). Advances in shrub-willow crops for bioenergy, renewable products, and environmental benefits. *Food and Energy Security*, 5(2), 97–106.
- Wang, G., Hao, Z., Anken, R. H., Lu, J., & Liu, Y. (2010). Effects of UV-B radiation on photosynthesis activity of *Wolffia arrhiza* as probed by chlorophyll fluorescence transients. *Advances in Space Research*, 45(7), 839–845.
- Warminski, K., Stolarski, M. J., Gil, L., & Krzyżaniak, M. (2021). Willow bark and wood as a source of bioactive compounds and bioenergy feedstock. *Industrial Crops and Products*, 171, 113976.
- Willick, I. R., Lahlali, R., Vijayan, P., Muir, D., Karunakaran, C., & Tanino, K. K. (2018). Wheat flag leaf epicuticular wax morphology and composition in response to moderate drought stress are revealed by SEM, FTIR-ATR and synchrotron X-ray spectroscopy. *Physiologia Plantarum*, 162(3), 316–332.
- Wong, T. M., Sullivan, J. H., & Eisenstein, E. (2022). Acclimation and compensating metabolite responses to UV-B radiation in natural and transgenic *Populus* spp. defective in lignin biosynthesis. *Metabolites*, 12(8), 767.
- Xie, X., He, Z., Chen, N., Tang, Z., Wang, Q., & Cai, Y. (2019). The roles of environmental factors in regulation of oxidative stress in plant. *BioMed Research International*, 2019, 9732325.
- Yao, X., Chu, J., He, X., Liu, B., Li, J., & Yue, Z. (2013). Effects of selenium on agronomical characters of winter wheat exposed to enhanced ultraviolet-B. *Ecotoxicology and Environmental Safety*, 92, 320–326.
- Yatsiv, V., Kutsokon, N., & Rasydov, N. (2025). Physiological responses of microclonally propagated willow to excessive levels of UV-B radiation. *Regulatory Mechanisms in Biosystems*, 16(4), e25185.
- Yu, S., Sheng, L., Mao, H., Huang, X., Luo, L., & Li, Y. (2020). Physiological response of *Conyza canadensis* to cadmium stress monitored by Fourier transform infrared spectroscopy and cadmium accumulation. *Spectrochimica Acta Part A: Molecular and Biomolecular Spectroscopy*, 229, 118007.
- Yun, S. M., Kim, C. S., Lee, J. J., & Chung, J. S. (2024). Application of ATR-FTIR spectroscopy for analysis of salt stress in Brussels sprouts. *Metabolites*, 14(9), 470.
- Zhao, X., Yang, X., Shi, Y., Chen, G., & Li, X. (2013). Protein and lipid characterization of wheat roots plasma membrane damaged by Fe and H₂O₂ using ATR-FTIR method. *Journal of Biophysical Chemistry*, 4(1), 28–35.
- Zlatev, Z. S., Lidon, F. C., & Kaimakanova, M. (2012). Plant physiological responses to UV-B radiation. *Emirates Journal of Food and Agriculture*, 24(6), 529–540.