## ORIGINAL PAPER

# Effect of *Parectopa robiniella* (Clemens, 1763) (Lepidoptera: Gracillariidae) on the photosynthetic efficiency of *Robinia pseudoacacia* L. trees in the forest strips of the Steppe zone, Ukraine

Kyrylo Holoborodko<sup>(1)</sup>, Svitlana Sytnyk<sup>(2)⊠</sup>, Viktoriia Lovynska<sup>(2,3)</sup>, Iryna Loza<sup>(4)</sup>, Yurii Grithan<sup>(5)</sup>, Olexandr Pakhomov<sup>(6)</sup>

<sup>(1)</sup> Research Laboratory of Terrestrial Ecology, Forest Soil Science and Land Reclamation, Research Institute of Biology, Oles Honchar Dnipro National University, Gagarin av. 72, 49010, Dnipro, Ukraine

<sup>(2)</sup> Laboratory of Forestry and Forest Management, Dnipro State and Economic University, Serhii Efremova str. 25, 49600, Dnipro, Ukraine

<sup>(3)</sup> Institute of Bio- and Geosciences: Agrosphere (IBG-3), Forschungszentrum Jülich GmbH, Wilhelm-Johnen-Straße, 52428, Jülich, Germany

<sup>(4)</sup> Research Laboratory of Biomonitoring, Research Institute of Biology, Oles Honchar Dnipro National University, Gagarin av. 72, 49010, Dnipro, Ukraine

<sup>(5)</sup> Department of Ecology, Faculty of Water supply Engineering and Ecology, Dnipro State Agrarian and Economic University, Serhii Efremov str. 25, 49600 Dnipro, Ukraine

<sup>(6)</sup> Department of Zoology and Ecology, Faculty of Biology and Ecology, Oles Honchar Dnipro National University, Gagarin av. 72, 49010 Dnipro, Ukraine

## ABSTRACT

The photosynthetic efficiency was studied in *Robinia pseudoacacia* (black locust) as one of the most common forest-forming species in artificially established stands of the northern Steppe of Ukraine. Plantings of this species in the region studied were established specifically to perform protective functions such as soil erosion control, phytoremediation of disrupted landscapes, and the protection of agricultural cenoses from wind erosion. The goal of this study was to investigate (I) how Parectopa robiniella caterpillars affect the photosynthesis system of black locust; (II) what age groups of black locust trees were most vulnerable to *P. robiniella* attacks. The study was conducted in September 2022; this period corresponded to the greatest activity of the second (more numerous) generation of *P. robiniella*. The artificially established forest strip of *R. pseudoacacia* of different ages was chosen as the object of research: I – young trees (up to 15 years old); II – middle--aged (15-25 years old), and III – old parent trees planted at the time of the forest belt creation (50-70 years old). The forest belt was situated near the Mayorka village on the right bank of the Dnieper River in the Dnipro District of the Dnipropetrovsk Oblast; it performs field-protective and anti-erosion functions. The effect of locust digitate leaf miner, P. robiniella, on the plant functioning was assessed by quantifying and comparing chlorophyll fluorescence parameters. The level of the miner exposure was evaluated in trees of three age groups (5-10, 15-25, and 50-70 years old). The study was performed with recording of background, maximum, stationary, and variable flu-

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<sup>⊠</sup>e-mail: sytnyk.s.a@dsau.dp.ua

orescence in live intact and damaged leaves using a 'Floratest' fluorometer. The level of photosynthetic activity inhibition in tree leaves damaged by the miner was determined. Data from the analysis of fluorescence indicators showed significant differences between the intact and miner-damaged leaves in trees of all age groups under conditions of field-protective forest planting. A decrease in background, stationary, maximum, and variable fluorescence under the influence of phytophagous insects was recorded. This trend was most pronounced in young trees under the age of 15 years. The results of the research may open up new approaches to an assessment of the black locust plantations in the Steppe zone of Ukraine the establishment of which is aimed at performing specific protective functions.

## **KEY WORDS**

black locust, chlorophyll fluorescence, field-protective forest strips, phytophagous, special-purpose forest stands

## Introduction

Black locust *Robinia pseudoacacia* L. is a medium-sized deciduous fast-growing woody species with wide-range environmental adaptations and native to North America; it has been introduced into South America, temperate Asia, Europe, North and South Africa, Australia, and New Zealand for obtaining economic benefits and performing ecosystem services (Lee *et al.*, 2004; Martin, 2019). The range of black locust is restricted mainly by temperature-related variables rather than precipitation-related ones (Li *et al.*, 2018). The future climate is conducive to the northward expansion of black locust with a speed of 21 km·decade<sup>-1</sup> (Li *et al.*, 2021).

Black locust has one of the widest distributions in Europe of any introduced plant, and it has increased its distribution into a number of Southern Hemisphere countries (Martin, 2019). European distribution of black locust appears to be limited mostly by low temperatures, but global warming can enhance its growth in colder areas. Nadal-Sala *et al.* (2019) indicated that increasing temperatures will prolong the vegetative period of black locust resulting in a substantially increased annual productivity especially when the phreatic groundwater level remains available.

This woody species is regarded to be a valuable but problematic plant due to its both beneficial and harmful environmental impact (Hu *et al.*, 2021). Within its introduced range, the species exhibits a number of invasive tendencies that result in harmful environmental impacts (Kleinbauer *et al.*, 2010; Radtke *et al.*, 2013; Miścicki and Wysocka-Fijorek, 2021). Colonization of river floodplains with black locust could exacerbate the problems associated with increasing nitrogen inputs into the riparian area and river ecosystem. Black locust affects the nitrogen cycle in the riparian ecosystem through the N-fixation, litterfall with high N content, and fast litter decomposition resulting in an increase in the nitrogen flow rate into the river and contaminating the water (Buzhdygan *et al.*, 2016). Riparian forest habitats and oak-dominated woodlands are among the most vulnerable to the invasion of black locust within the Alpine and Continental biogeographical regions of Europe (Campagnaro *et al.*, 2018).

Providing information to guide the decisions of forest managers involved in afforestation and restoration plays an essential role in research on invasive plant control. A possible solution is to use the biotic resistance of native vegetation to control biological invasions. The regenerative niches of black locust (germination, seedling growth, and adult height) were compared with those of native European species (Cruz *et al.*, 2021). Among the native species of Europe with characteristics in their regenerative niche suitable to compete successfully with black locust are tall shrub species such as *Adenocarpus lainzii* (Castrov.) Castrov., *Cytisus multiflorus* (L'Her.) or *Cytisus striatus* (Hill) Rothm. and some tree species such as *Corylus colurna* L., *Pinus sylvestris* L. and *Quercus ilex* L.

However, black locust plantations conduct economically valuable functions, such as land rehabilitation, soil erosion prevention, and energy crops at the local level (Hu et al., 2021; Wilkaniec et al., 2021). Forest plantations of R. pseudoacacia play an irreplaceable role in maintaining regional carbon balance and regulating climate (Jiao et al., 2016; Hao et al., 2022). Staska et al. (2014) found that the content of soil nitrogen, NO3, and carbon increased with the density of black locust trees and the stand age, respectively, while the total C/N ratio appeared to be less affected by riparian forests of the Donau-Auen National Park in Eastern Austria. Black locust has been widely used to restore degraded land in northern China for many decades, and the forest has become an important ecosystem in China (Li et al., 2021). Forest plantations of R. pseudoacacia in Loess Plateau Hilly Region were characterized by fast growth, drought tolerance, and nitrogen-fixing physiological adaptability (Mantovani et al., 2015); they are widely used in forest rehabilitation covering more than 70,000 km<sup>2</sup>. The results obtained by Papaioannou et al. (2016) showed that restoration of the degraded agricultural lands with *R. pseudoacacia* in Northern Greece (Chalkidiki, Macedonia; 20 years after the establishment of the plantations) led to an increase in organic matter content in 1.3-3.0 times, N content in 1.2-2.5 times, and in many cases to significantly higher P and K concentrations compared to the other two types of land use such as degraded agricultural lands and the native forest areas, respectively.

In the Northern Steppe, the total area of black locust stands is 17,683.7 ha accounting for 20.3% of the total forested area. All black locust stands are man-made forests only (Lovynska *et al.*, 2018). In this region, the black locust plantations are widely represented in protecting forest strips. Since the beginning of the XXI century, the complex of invasive species Gracillariidae which includes two phytophagous species with specialized feeding on *R. pseudoacacia: Parectopa robiniella* (Clemens) and *Macrosaccus robiniella* (Clemens), has occurred in the territory of Ukraine (Holoborodko *et al.*, 2022). *P. robiniella* is the species most widespread on the territory of the Steppe zone of Ukraine possibly due to the increase in average daily temperatures (Tytar *et al.*, 2022). The caterpillars of this miner feeds on the leaf mesophyll and forms light-colored complex-shaped mines. Massive bursts of reproduction have not yet been recorded whilst an increase in the number of this invasive species was observed (Holoborodko *et al.*, 2021; Wilkaniec *et al.*, 2021). Such trends cause reasonable concern (Kirichenko *et al.*, 2019), since the scale of *P. robiniella* impact on the physiological state of black locust remains unexplained (Shupranova *et al.*, 2022). Currently, one species from the family Gracillariidae, *P. robiniella*, has been recorded as feeding on *R. pseudoacacia.* 

A comprehensive understanding of the effects of *R. pseudoacacia* function on forest ecosystems and achieving a balance between ecosystem safety and black locust naturalization are crucially important. To achieve these aims, studying the features of the main physiological processes of black locust trees in the regions of its introduction is an essential prerequisite that remains understudied. Effective non-invasive evaluation of chlorophyll fluorescence is an important feature of the assessment of woody species damaged by phytophages and of the improvement of forest management programs. Alterations in chlorophyll fluorescence occurred during the induction of peaks have long been suitable for detection differences in photosynthetic performance between plants (Baker, 2004; Holoborodko *et al.*, 2022).

The process of photosynthesis is considered to be a reliable indicator of the effect of various stress factors, including the impact of feeding by phytophagous insects (Velikova *et al.*, 2010;

Baghbanietal, 2019). The fluorescence analysis method can be applied to investigate the impact of phytophage feeding on the photosynthetic apparatus (Koski *et al.*, 2017). The evidence suggests that changes in chlorophyll fluorescence parameters indicate the effect of phytophagous insects on the photosynthetic apparatus of the plant (Carvalho de Almeida *et al.*, 2018). It was shown (Golanetal, 2015) the effect of the population density of *Coccus hesperidum* L. on the chlorophyll fluorescence parameters, namely the maximum quantum yield of photosystem II, Fv/Fm.

We hypothesize that the different aged black locust trees adapt differently to the life activity of the invasive *P. robiniella*.

The goal of this study was to investigate the following issues:

- (I) How *P. robiniella* affects the critical parameters of the chlorophyll fluorescence curve.
- (II) In which age groups the losses in photosynthesis due to *P. robiniella* attack were the highest.

# Materials and methods

STUDY AREA. The study was conducted in September 2022; this period corresponded to the greatest activity of the second (more numerous) generation of *P. robiniella*. The artificially established forest strip of *R. pseudoacacia* of different ages was chosen as the object of research: I – young trees (up to 15 years old); II – middle-aged trees (15-25 years old), and III – old (parent) trees planted at the time of the forest belt creation (50-70 years old). The forest belt was situated near the Mayorka village on the right bank of the Dnieper River in the Dnipro District of the Dnipropetrovsk Oblast (Fig. 1); it performs field-protective and anti-erosion functions. For the study, 60 trees of black locust were selected (20 trees per age group), in each age group 10 trees were damaged by the phytophage and 10 trees were intact. The chlorophyll fluorescence means for the age groups were found based on the values of 20 respective trees, while the mean values on the damaged and intact trees in the age groups were found based on the 10 respective trees.

Counting mines on the trees was carried out with the conventional 'model branch' method (Holoborodko *et al.*, 2022). A tree and branch with a length of at least 1 meter were selected by randomization. Branches to count mines on the trees were chosen from the same crown part in the same time. After that, we counted the number of leaves and the number of mines formed by invasive insect species and determined their position on the compound leaves of *R. pseudoacacia*.

CHLOROPHYLL FLUORESCENCE STUDY. To study the alterations in native chlorophyll fluorescence of fresh leaves, a portable fluorometer 'Floratest' (Ukraine) was used (Romanov *et al.*, 2013).





Portable fluorometer 'Floratest' comprises a base unit with a graphic liquid crystal display, control buttons, a remote optoelectronic sensor, connecting cable to the USB port of a personal computer and a network adapter. The remote optoelectronic sensor includes an LED that has a maximum radiation intensity of  $\lambda$  (470 ±20 nm). Irradiation indicators in the sensor were the following: irradiation wavelength 470 ±15 nm, irradiated spot area not less 15 mm<sup>2</sup>; illumination within the spot at least 2.4 W/m<sup>2</sup>. Signal reception indicators in an optoelectronic sensor the spectral range of fluorescence intensity measurement was 670-800 nm, receiving window area 9 mm<sup>2</sup>, photodetector sensitivity at  $\lambda$ =650 nm was 0.45A/W.

The operation of the device is based on the property of chlorophyll to fluoresce excess absorbed light depending on violations of individual links in the photosynthetic chain caused by the effects of the phytophage on plants.

Observations were made on black locust fresh leaves after their adaptation to darkness. Since the start of light exposure, the intensity of chlorophyll fluorescence induction of fluorescence/light-induced fluorescence begins to change significantly over time. The time dependence of the chlorophyll fluorescence intensity (ChlF) has the characteristic form of a curve with one or more maximums and is called the ChlF induction curve, or the Kautsky curve. The shape of this curve is quite sensitive to alterations that occur in the photosynthesis of the black locust trees damaged by phytophagous species.

To assess the state of photosynthesis in the black locust trees, both in reference (intact) and experimental (damaged by *P. robiniella*), the chlorophyll fluorescence parameters listed and explained in Table 1 were measured and calculated.

STATISTICS. The results of chlorophyll fluorescence content analyses were presented as the x value  $\pm$ SD (standard deviation). Mine-free leaves were used as a reference for each age group. The Tukey's honestly significant difference test was used to test differences between group means for significance. The differences were found to be statistically significant at *p*≤0.05. The data obtained were analyzed using the Statistica version 8 (StatSoft Inc., 2008). The generalized linear model (GLM) was used to test the significance of the dependence of chlorophyll fluorescence of black locust leaves on biotic predictors (*P. robiniella*, tree age). The adjusted coefficient of determinations (Radj2) was calculated as part of the GLM.

Effects of *P. robiniella* and tree age on chlorophyll fluorescence of black locust are shown in Table 2; the results of normality testing in Table 3; and multivariate testing in Table 4.

# Results

Photosynthetic alterations in black locust trees of different ages caused by the influence of biotic factors, in particular, the damage by *P. robiniella* were manifested in changes in chlorophyll fluorescence induction (Table 5).

Considerable changes in chlorophyll fluorescence occurred at the induction of photosynthesis when a dark-adapted leaf was exposed to light. At immediate exposure to light, the fluorescence reduces to a minimal level. The values of the initial chlorophyll fluorescence induction ( $F_0$ ) in the studied forest planting were in the range 217.6 ±23.9-290.4 ±11.2 c.u. (Table 2). The smallest average value was recorded for miner-damaged black locust trees of the I age group, while the largest average background fluorescence was found in intact trees of the III age group (Fig. 2). Under the influence of the studied biotic factor, a significant decrease in  $F_0$  values was observed in plants of all age groups. The greatest difference in means was found in young plants under the age of 15 years. In phytophage-damaged plants, a significant increase in  $F_0$  value was recorded with the advancing age. However, there is no indication that the difference between miner-

damaged and reference trees increases, as the mean values for the respective age groups are inside the confidence intervals.

Under the study conditions, the parameter Fp reached a 'plateau' at 576.0 ±101.2-1414.4 ± 90.8 c.u. A significant difference was recorded in achieving saturation of reaction centers due to the effect of the phytophage. Insect damage caused a significant decrease in Fp values in the

The fluorescence	e parameters studied	
Fluorescence parameter	Definition	Physiological significance
F <sub>0</sub>	Initial value of fluorescence induction after the light was turned on.	The baseline fluorescence level depends on the loss of excitation energy during its migration along the pigment matrix, as well as on the content of chlorophyll molecules that do not have a functional connection with reaction centers.
Fp	A 'plateau' value of fluorescence induction means a short period of dark adaptation. It is the time when it temporarily slows down.	The process of electron transfer from PS II reaction centers through pheophytin to primary acceptors (quinones).
Fm	Maximum fluorescence induction value.	Level of fluorescence when QA is maximally reduced. PSII centers are closed.
Fst	Stationary value of fluorescence induction after light adaptation of the plant leaf.	Stabilization of reactions in the Calvin cycle and the flow of substances through the membranes and leaf vessels.Indicator of the number of chlorophylls not involved in the energy transfer to reaction centers.
Fv=(Fm-F <sub>0</sub> )	Variable fluorescence.	It demonstrates PS II ability to perform primary photochemistry. It characterizes the electron transport link (from $N_2O$ to ferredoxin and NADP; it is the so-called 'light phase' of photosynthesis. It serves as an indicator of photochemical redox reactions.
Fv/Fm	It is an indicator of quantum yield.	The efficiency of the light phase of photosynthesis. It demonstrates PS II capability to perform primary photochemistry. Maximum efficiency at which light absorbed by light-harvesting antennae of PS II is converted into chemical energy (QA reduction).
(Fm-Fst)/Fm	Coefficient of fluorescence induction.	It determines the fluorescence quantum yield.
Fm/Fst	It is an indicator of endogenous factors.	It demonstrates the effect of physiologically- biochemical processes.

## Table 2.

Effect of Parectopa robiniella and tree age on photosynthesis indicators of black locust (x ±SD)

Indi		Indices of chlorophyll fluorescence, RFU							
mui-	age group I		age gr	age group II		age group III			
cators	reference	damage	reference	damage	reference	damage			
F <sub>0</sub>	260.8 ±8.6	217.6 ±23.9	290.4 ±11.2	276.0 ±35.1	284.4 ±27.7	272.0 ±17.5			
Fp	1136.0 ±99.6	$576.0 \pm 101.2$	$1414.4 \pm 90.8$	819.2 ±199.9	$1251.2 \pm 156.2$	$1094.4 \pm 184.3$			
Fm	$1465.6 \pm 70.5$	716.8 ±115.9	$1861.2 \pm 103.1$	$996.0 \pm 218.4$	$1494.4 \pm 186.2$	$1382.4 \pm 236.4$			
Fst	1199.2 ±56.4	$566.4 \pm 101.9$	1516.8 ±86.7	723.2 ±156.7	$1270.4 \pm 160.5$	1145.2 ±265.4			
Fv	1204.8 ±66.3	499.2 ±95.7	1570.8 ±92.7	$720.0 \pm 202.6$	$1210.0 \pm 166.2$	$1110.4 \pm 230.4$			

Normality testing	
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Parameter	Kolmogor	ov-Smirnov test	Shapiro-Wilk test		
	statistic	significance	statistic	significance	
F <sub>0</sub>	0.290	0.195	0.869	0.263	
Fp	0.213	0.200*	0.935	0.634	
Fm	0.212	0.200*	0.949	0.732	
Fst	0.299	0.166	0.893	0.375	
Fv	0.190	0.200*	0.973	0.894	

\*This is a lower bound of the true significance

Table	4.
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Multivariate testing

Effect	Test	Value	F-ratio	<i>p</i> -value
	Pillari's Trace	0.993	761.973a	< 0.001
Intercept	Wilks' lambda	0.007	761.973a	< 0.001
Intercept	Hotelling's Trace	145.138	761.973a	< 0.001
	Roy's Largest	145.138	761.973a	< 0.001
	Pillari's Trace	0.992	5.414	< 0.001
Ago group	Wilks' lambda	0.252	5.204a	< 0.001
Age group	Hotelling's Trace	1.997	4/992	< 0.001
	Roy's Largest	1.166	6.412	< 0.001
	Pillari's Trace	0.769	17.513a	< 0.001
Damaga	Wilks' lambda	0.231	17.513a	< 0.001
Damage	Hotelling's Trace	3.336	17.513a	< 0.001
	Roy's Largest	3.336	17.513a	< 0.001
Age group × damage	Pillari's Trace	0.748	3.288	< 0.001
	Wilks' lambda	0.336	3.811a	< 0.001
	Hotelling's Trace	1.729	4.321	< 0.001
	Roy's Largest	1.569	8.631b	< 0.001

a – exact statistic

b – the statistic is an upper bound on F that yields a lower bound on the significance level

trees of I and II age groups (Fig. 3). In damaged plants, a trend of increase in the indicator with the advanced age within the studied range.

The maximum level of fluorescence is caused by an intense pulse of light which resulted in the closure of all photosynthetic reaction centers. The values of maximum fluorescence (Fm) indicators under the influence of biotic factor in trees of the studied age groups had a fairly high variability (Fig. 4). In the insect-damaged young trees under 15 years of age, a two-fold decrease in the maximum fluorescence level (in relation to reference trees) was recorded from 716.8  $\pm$ 115.9 to 1465.6  $\pm$ 70.5 (Table 2). The maximum fluorescence reached the highest values in trees of the II age group free from insect damage. A trend of increasing Fm with the advanced tree age was observed in trees with mining insect-damaged leaf mesophyll. It should be noted that in trees of the III age group, the values of maximum fluorescence were quite similar both in damaged and reference (intact) leaves.

An increase in the values of this indicator evidences an inhibition of the outflow of reduced photoproducts from the reaction centers is a result of various factors, particularly due to the effect of phytophage. This indicator was significantly higher in damage-free trees of the I and II age groups; it was equal to  $1199.2 \pm 66.3$ ;  $1516.8 \pm 92.7$  (Table 2).

,	Tal	ble 5	
Multi	ple	com	parison

Danandant	Age	Age	Mean	St d	Cianifi	95% confidence	
variable	group	group	difference	error	cant	lower	upper
variable	(I)	(J)	(I-J)	enor	eane	bound	bound
	T	II	-44.00*	11.325	0.002	-72.28	-15.20
	1	III	-39.00*	11.325	0.006	-67.28	-10.72
Г	TT	Ι	44/00*	11.325	0.002	15.72	72.28
F <sub>0</sub>	11	III	5.00	11.325	0.899	-23.28	33.28
	TTT	Ι	39.00*	11.325	0.006	10.72	67.28
	111	II	-5.00	11.325	0.899	-33.28	23.28
	т	II	-260.80*	72.678	0.004	-442.30	-79.30
	1	III	-316.80*	72.678	< 0.001	-498.30	-135.30
Fn	П	Ι	260.80*	72.678	0.004	79.30	442.30
rp	11	III	-56.00	72.678	0.724	-237.50	125.50
	ш	Ι	316.80*	72.678	< 0.001	135.30	498.30
	111	II	56.00	72.678	0.724	-125.50	237.50
	Ι	II	-337.40*	83.495	0.001	-545.91	-128.89
		III	-347.20*	83.495	< 0.001	-555.71	-138.69
Fm	II	Ι	337.40*	83.495	0/001	128.89	545.91
1,111		III	-9.80	83.495	0.992	-218.31	198.71
	Ш	Ι	347.20*	83.495	< 0.001	138.69	555.71
	111	II	9.80	83.495	0.992	-198.71	218.31
	T	II	-237.20*	76.871	0.014	-429.17	-45.23
	1	III	-325.00*	76.871	< 0.001	-516.97	-133.03
Fet	τī	Ι	237.20*	76.871	0.014	45.23	429.17
I'st	11	III	-87.80*	76.871	0.498	-279.77	104.17
	ш	Ι	325.00*	76.871	< 0.001	133.03	516.97
	111	II	87/80	76.871	0.498	-104.17	279.77
	T	II	-293.40*	77.438	0/002	-486.79	-100.01
	1	III	-308.20*	77.438	0/002	-501.59	-114.81
Ev	п	Ι	293.40*	77.438	0/002	100/01	486.79
T. A.	11	III	14/80	77.438	0.980	-208/19	178.59
	ш	Ι	308.20*	77.438	0.002	114.81	501.59
	111	II	14.80	77.438	0.980	-178.59	208.19

\* The mean difference is significant at the 0.05 level

In damaged plants within the I and II age groups, a significant decrease in the indicator was observed compared to reference plants. In the course of tree growth, the stationary fluorescence level increases in both intact and insect-damaged plants (Fig. 5). However, this indicator decreases in intact trees upon attaining the age of maturity, while in miner-damaged trees the value of stationary fluorescence continued to increase. According to Figure 6 we can observe a trend in the dynamics of ratio Fv/Fm.

Additionally, fluorescence coefficients were calculated to detect the phytophage effect; the values were given in Table 6. It is important to note the tendency of increase in the values of the coefficients (Fm-Fst)/Fm and Fm/Fst in phytophage-damaged trees. The difference in these indicators between reference and damaged trees significantly decreased with the advanced plant age. In our study, with phytophage invasion in the black locust trees, a significant decrease in this indicator was observed most pronounced in young trees under the age of 15 years.





Estimated marginal means of  $F_0$  in *R. pseudoacacia* trees of different age groups affected by the phytophagous insects



## Fig. 3.

Estimated marginal means of Fp in *R. pseudoacacia* trees of different age groups affected by the phytophagous insects

# Discussion

Photosynthesis is a crucial process for the plant surviving; it provides essential elements for growth and reproduction. The excitation of chlorophyll by photons initiates an electron transport resulted in the generation of NADPH and ATP subsequently consumed by the plant to maintain their growth and development. The balance can be upset relatively easily when plants are exposed





Estimated marginal means of Fm in *R. pseudoacacia* trees of different age groups affected by the phytophagous insects





Estimated marginal means of Fst in *R. pseudoacacia* trees of different age groups affected by the phytophagous insects

to unfavorable environmental conditions, including biotic stresses. Unfavorable insect effects on photosynthesis can be explained by a theoretical framework based on the argument that the resource-rich photosynthetic apparatus can be sacrificed to provide the metabolic precursors and energy needed for the proper deployment of the resource (Frier *et al.*, 2012).

Since photosynthesis is the basis for the formation of the energetic potential in plants, its response to the intensity of any impact can be considered the most important characteristic of



#### Fig. 6.

Estimated marginal means of Fv/Fm in *R. pseudoacacia* trees of different age groups affected by the phytophagous insects

#### Table 6.

Effect of *P. robiniella* and tree age on photosynthesis indicators in black locust (x ±SD)

Indicators	Age group I		Age group II		Age group III	
	reference	damage	reference	damage	reference	damage
Fv/Fm	$0.822 \pm 0.007$	$0.696 \pm 0.025$	$0.844 \pm 0.004$	$0.723 \pm 0.047$	$0.810 \pm 0.015$	$0.803 \pm 0.042$
(Fm-Fst)/Fm	$0.182 \pm 0.006$	$0.210 \pm 0.032$	$0.185 \pm 0.010$	$0.274 \pm 0.027$	$0.150 \pm 0.034$	$0.172 \pm 0.073$
Fm/Fst	$1.222 \pm 0.009$	$1.266 \pm 0.050$	$1.227 \pm 0.014$	$1.377 \pm 0.052$	$1.176 \pm 0.048$	$1.207 \pm 0.123$

the plant resistance to this factor. Disruption in the primary photosynthetis processes causes alterations in the chlorophyll fluorescence which appear long-lasting before the visible deterioration of the plant's physiological state manifests itself. At physiologically optimal temperatures, fluorescence is emitted mainly by the photosystem II reaction centers of chlorophyll 'a' in the wavelength range 670-750 nm (Kalaji *et al.*, 2017, Lin *et al.*, 2022). The fluorescence level depends inversely on the intensity of photochemical reactions; so, the less photochemical work, the higher the fluorescence. Poor fluorescence is typical for viable photosystem II, and strong one is typical for weakened or inhibited photosystem II.

Photosynthesis is one of the processes most vulnerable to biotic stressors, so valuable information on the state of the photosynthetic apparatus in a plant under the impact of phytophage feeding can be obtained by fluorescence analysis (Koski *et al.*, 2017). The rapid measurement of chlorophyll fluorescence photoinduction is one of the most effective techniques intended to detect the effect of phytophagous insects on the physiological conditions of woody plants (Golan *et al.*, 2015; Moustaka *et al.*, 2017; Ullah *et al.*, 2020; Holoborodko *et al.*, 2022).

Studies of chlorophyll fluorescence indicators allow obtaining information about alterations in photosynthetic processes both associated with the development of adaptation syndrome and with irreversible damage in the photosynthetic apparatus in plants. This, therefore, allows us to obtain an objective characterization of the stability of the plant species studied (Gottardini *et al.*,

2014). Research on chlorophyll fluorescence intensity is a contemporary informative method applicable to biomonitoring (Zhang *et al.*, 2020).

It is known that the activity of phytophagous insects also can change the development of plant tissues. Petanovic and Kielkiewicz (2010) showed that early mite gall development caused the intense proliferation of epidermal cells and dedifferentiation of cells from parenchyma to meristematic cells; the proliferation decreased with gall maturation, and lignification occurred (Chetverikov et al., 2015). However, leaf galls induced by multiple organisms often stay green, chlorophyll-containing, and could possibly contribute to leaf photosynthesis (Dorchin et al., 2006). It has even been suggested that the green galls can be self-sustainable and not necessarily have an impact on the leaf photosynthesis of the host plant (Fernandes et al., 2010; Oliveira et al., 2011; Haiden et al., 2012). Maintenance of active photosynthesis under physiological stress is usually associated with developing plant resistance to unfavorable environmental biotic factors such as the activities of insect species. Significant reductions in photosynthesis and stomatal conductance were reported in Tilia cordata Mill. leaves infested with gall- and erineum-forming mites (Jiang et al., 2020). Spindle gall mite-induced photosynthesis inhibition is observed in the sugar maple Acer saccharum Marsh. trees already at very low (1% of leaf area) galling levels (Patankar et al., 2011). This is consistent with the results of our studies, which show a statistically significant decrease in all types of chlorophyll fluorescence under the influence of the phytophagous insect *P. robiniella*.

The ratio Fv/Fm is a dimensionless energetic characteristic of photosynthesis that determines the maximum quantum fluorescence yield of photosystem II. It can be used for estimating the fraction of adsorbed quantum energy required for photosystem II to perform photochemical processes. Measurement of the ratio of chlorophyll fluorescence intensity at photosynthesis-saturating excitation light (Fm) and conditions that do not cause alterations in the photosynthetic apparatus (F<sub>0</sub>) allows determining the maximum efficiency of the primary processes of photosystem II with the use of the ratio (Fm – Fo)/Fm = Fv/Fm. A quantum yield shows the proportion of light energy consumed by plants to perform photosynthetic reactions. Accordingly, the higher the quantum yield value, the greater the percentage of energy captured by plants for photosynthesis. The optimal Fv/Fm value is about 0.83 for most plants (Suchocka *et al.*, 2021).

In older trees, the difference in this coefficient between the reference and damaged tree groups was less pronounced. A similar trend was demonstrated in some papers (Uhrin and Supuka, 2016; Sonti *et al.*, 2020) where a decrease in this coefficient under the influence of environmental factors was shown.

As a result of studies on the effects of *Cameraria ohridella* Desch. & Dim. on the photosynthesis in *Aesculus hippocastanum* L. (Holoborodko *et al.*, 2021), the data were obtained that confirm a decrease in the quantum efficiency of PS II in the leaves of different parts of the tree crown, which indicates the destructive effect of caterpillar feeding on the photosynthetic apparatus.

In condition when all reaction centers of photosystem II perform photochemical processes photosynthetic electron transfer channels are open, the maximum energy of excited electrons is consumed for the photosynthetic process, and chlorophyll fluorescence is minimal. The transition from  $F_0$  to Fp is caused by the transfer of electrons from PS II reaction centers through pheophytin to primary acceptors represented by quinones (Zhang *et al.*, 2020).

Sperdouli *et al.* (2022) assessed the effect of feeding of the sap-sucking insect *Halyomorpha halys* (Stål) on the photosynthesis efficiency in potato leaves. A decrease in the proportion of absorbed light used in photochemistry (FPSII)) was noted due to a decrease in the number of open PSII reaction centers.

# Conclusions

The obtained results showed a single-vector alteration in photosynthetic activity of *R. pseudoacacia* trees of different ages that respond to the harmful effects of phytophagous insect *Parectopa robiniella*; it indicated the physiological adaptability of this tree species to the damaging effects of the insect in artificially established forest planting in the Northern steppe. Detection of a decrease in the indicators of background, stationary, maximum, and variable chlorophyll fluorescence in trees of different ages (especially under the age of 15 years) revealed the high vulnerability of the black locust trees to the effects of phytophagous insects.

Providing new insight into the general mechanisms of plant response to the phytophage activity would have significant implications in agriculture and forestry, considering that many economically important plant species are acting as hosts of different insects. In addition, the host specificity of biotic agents can potentially be used in the biocontrol of weeds and invasive species.

This study may provide new prospects for forest management practices of plantations and a robust scaffold to maintain safe and resilient artificial stands of *R. pseudoacacia* with safe function within the steppe zone in Ukraine.

# Authors' contributions

K.H. – conceptualization, data curation; S.S. – methodology, formal analysis, writing original draft, editing, software, visualization; V.L. – methodology, validation; I.L. – validation, editing; Y.G. – resources, data curation; O.P. – project administration, resources, editing.

# Competing interests

Authors declare no competing interests.

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#### STRESZCZENIE

## Wpływ *Parectopa robiniella* (Clemens, 1763) (Lepidoptera: Gracillariidae) na efektywność fotosyntezy drzew *Robinia pseudoacacia* L. rosnących w pasach leśnych na obszarze stepów Ukrainy

Spośród roślin introdukowanych do Europy robinia akacjowa Robinia pseudoacacia L. charakteryzuje sie jednym z najszerszych zasiegów występowania. Ze względu na wpływ na środowisko drzewa tego gatunku są uważane zarówno za cenne, jak i szkodliwe. Na obszarze Stepu Północnego łączna powierzchnia zajmowana przez robinię akacjową wynosi 17 683,7 ha, co stanowi 20,3% całkowitej powierzchni leśnej. Pasy leśne występujące na tym obszarze, pełniące funkcje ochronne, są porośnięte głównie plantacjami robinii akacjowej. Obecnie na R. pseudoacacia obserwuje się żerowanie jednego owada reprezentującego rodzinę Gracillariidae: Parectopa robiniella Clemens. Celem badań było zbadanie: (I) w jaki sposób larwy P. robiniella wpływają na aparat fotosyntetyczny robinii akacjowej oraz (II) drzewa jakich klas wieku robinii akacjowej były najbardziej podatne na żerowanie tego owada. Badanie przeprowadzono we wrześniu 2022 r., w okresie największej aktywności drugiej (liczniejszej) generacji P. robiniella. Drzewostan akacjowy, w którym prowadzono badania, znajdował się w pobliżu wsi Mayorka, na prawym brzegu rzeki Dniepr w rejonie Dniepropietrowska (obwód dniepropetrowski) (ryc. 1), gdzie pełnił funkcje ochronne i przeciwerozyjne. Obszar badań stanowiły sztucznie założone pasy drzewostanów porośnięte R. pseudoacacia, wśród których wyróżniono 3 klasy wieku: I – drzewa młode (do 15 lat), II – drzewa średniej klasy wieku (15-25 lat) i III – drzewa stare (rodzicielskie) posadzone w czasie zakładania pasów drzewostanu (50-70 lat). Wpływ żerowania gasienic *P. robiniella* na fotosyntezę robinii akacjowej oceniano przez ilościowe i porównawcze wskaźniki fluorescencji chlorofilu (tab. 1). Wpływ żerowania P. robiniella i wieku drzew na wskaźniki fluorescencji chlorofilu robinii akacjowej przedstawiono w tabeli 2, wyniki testów normalności w tabeli 3, a testy analizy wielowymiarowej w tabeli 4. Zmiany w procesie fotosyntezy drzew robinii akacjowej różnych klas wieku spowodowane wpływem czynników biotycznych, w szczególności uszkodzeniami wywołanymi przez P. robiniella, objawiały się zmianami wskaźników fluorescencji chlorofilu (tab. 5). W roślinach uszkodzonych przez owady zaobserwowano istotny wraz z wiekiem drzew wzrost wartości F<sub>0</sub>. W roślinach referencyjnych wzrost tego wskaźnika wraz z wiekiem drzew nie był tak istotny, zwłaszcza w przypadku drzew starszych niż 25 lat (ryc. 2). Uszkodzenia spowodowane przez owady wpłynęły istotnie na spadek wartości Fp w drzewach I i II klasy wieku. W roślinach uszkodzonych przez owady obserwowano tendencję wzrostu tego wskaźnika w miarę starzenia się drzew (ryc. 3). Pod wpływem działania czynnika biotycznego wartości wskaźników maksymalnej fluorescencji (Fm) w wyróżnionych klasach wieku drzew charakteryzowały się dość dużą zmiennością (ryc. 4). W uszkodzonych roślinach w I i II klasie wieku odnotowano istotny spadek maksymalnej fluorescencji w porównaniu do drzew referencyjnych. W trakcie wzrostu drzewa poziom fluorescencji stacjonarnej (Fst) wzrastał zarówno w roślinach nieuszkodzonych, jak i uszkodzonych przez owady (ryc. 5). Dodatkowo w celu oceny wpływu fitofagów na aparat fotosyntetyczny drzew obliczono wartości współczynnika fluorescencji (tab. 6). U drzew robinii akacjowej, na których żerowały fitofagi, zaobserwowano istotny spadek tego wskaźnika, co było najbardziej wyraźne wśród młodych robinii akacjowych, tj. w wieku poniżej 15 lat. W starszych drzewach różnica tego współczynnika między grupą referencyjną a uszkodzonymi *R. pseudoacacia* była mniej wyraźna. Przytoczone badania mogą otworzyć nowe perspektywy dla praktyki zarządzania plantacjami, mogą również stanowić podstawę do utrzymywania stabilnych i odpornych, sztucznie odnawianych drzewostanów *R. pseudoacacia*, pełniących funkcje ochronne stepów w Ukrainie.