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Parectopa robiniella (Lepidoptera, Gracillariidae) influence on key parameters of *Robinia pseudoacacia* photosynthetic function implementation in different environmental conditions

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Abstract. *Robinia pseudoacacia* L., a representative species of the North American dendroflora and introducent in the dendroflora of the steppe zone of Ukraine, is a part of the species composition of anti-erosion forests, systems of reclamation and field-protective plantings, landscaping of cities and natural objects having environmental status. The invaders of North American origin, Lepidoptera (Gracellariidae) species pose a main phytosanitary risk for the functioning of *R. pseudoacacia* in composition of cultured plantings in the steppe zone of Ukraine. The work considered characteristics of the photosynthetic function implementation, specifically, the chlorophyll content and estimated fluorescence coefficients (variable fluorescence and light-adapted steady-state fluorescence value), which can be used to evaluate the functioning of introducents in various landscapes under the condition of such biotic factor as the invasion of *Parectopa robiniella* (Clemens, 1863). The research was conducted in locations situated in the natural steppe zone of Ukraine within the Dnipropetrovsk Region. A trend towards lower concentrations of chlorophyll in damaged leaves both in shaded and lighted leaves was determined. A reduction in the variable fluorescence intensity was noted, which was greater at the shading of leaves, both in damaged leaves and in leaves without signs of damage from insects (intact leaves). The inhibition intensity of the light stage of photosynthesis was reduced in tree leaves damaged by insects. In the black locust plantations growing in the valley-terrace landscape, steady-state fluorescence values of shaded damaged leaves were significantly lower after light adaptation compared with intact leaves. Mathematical models were developed to calculate the ratio of variable to maximum chlorophyll fluorescence in black locust which comprised plantings in various steppe landscapes with and without damage by *P. robiniella*.

Keywords: invasive lepidopterans; trees adaptation in a new range; introduced dendroflora; leaf miner caterpillars; the chlorophyll fluorescence induction curve; biosensor research methods.

Introduction

Many tree species have been introduced outside their native ranges, but knowledge of their niche dynamics during afforestation in different regions is still insufficient. *Robinia pseudoacacia* L. (black locust) is a medium-sized deciduous nitrogen-fixing legume tree species native to the Southeastern United States. It is considered to be a valuable but problematic tree species due to its both positive and negative environmental effects. This species is widely spread outside its natural range; it grows in a wide range of edapho-climatic conditions and types of plant communities (Vitkova et al., 2017). The black locust has one of the largest distributions in Europe of any introduced plant and extends its range into a few Southern Hemisphere countries (Martin, 2019).

A comprehensive and mechanistic understanding of the effects of black locust afforestation on ecosystems and achieving a balance between ecosystem safety and functioning and naturalization of *R. pseudoacacia* represent an important modern challenge.

The significant remediation potential of the black locust and the effects provided during its introduction into natural ecosystems and agrocenoses were shown in numerous modern studies. The results obtained by Papaioannou et al. (2016) showed that restoration of degraded agricultural land using *R. pseudoacacia* (20 years after the establishment of these plantations) resulted in 1.3–3.0 times increase of soil organic matter, 1.2–2.5-fold increase in N content, and a significant increase in P and K contents, compared with the soil of degraded agricultural lands and the native forest areas, respectively, within Northern Greece.

Its ecological and economical importance is great due to fast growth and dinitrogen (N_2)-fixing ability of its rhizobia (Liu et al., 2020). This species has good reproductive potential. A study conducted by Masaka et al. (2010) examined the factors that influenced the size of a soil seed bank in black locust stands and determined that number of buried seeds is proportional to stand biomass rather than stand age.

Black locust occurs from the bases to summits of mountains in the urban centers, whereas its range is restricted to mountain bases in urban outskirts and rural areas in South Korea (Lee et al, 2004). On Mount Tai, afforestation with black locust trees is helpful in restoring ecosystems and improving soil quality, especially by increasing the clay and silt contents and reducing the sand content (Li et al., 2022). *Robinia pseudoacacia* also had a homogenization effect on understory functional composition and divergence (Hu et al., 2021). Buzhdygan et al. (2016) showed that black locust affects the nitrogen cycle in the riparian ecosystem through N-fixation, high N content in leaf litter, and rapid litter decomposition that results in the

increase of nitrogen flow. Black locust has been widely used to restore degraded land in northern China for many decades (Li et al., 2021). This study replies to the question of in what way the range shift of black locust can be changed in response to future climate change, which is the first step for adaptive management of black locust. The global niche model was proposed to show that the range of black locust is mainly controlled by temperature-related variables rather than precipitation-related ones. Li et al. (2018) studied the climatic niche dynamics of *R. pseudoacacia* planted worldwide between its native range (southeastern parts of the United States) and four introduced ranges (North America, Europe, East Asia, and Australia). According to Nadal-Sala et al. (2019), the black locust's European distribution appears to be mostly limited by low temperatures, but global warming might enhance its spread in areas with a relatively cold climate.

In the steppe zone of Ukraine, black locust occurs in anti-erosion forests, systems of reclamation plantings, landscaping of cities and natural objects with environmental status. The paper (Lovynska & Sytnyk, 2016) focused on the peculiarities of the distribution and taxation structure of the black locust plantings.

An expansion of invasive species of North American origin, primarily from the family of the leaf blotch miner moths (Lepidoptera, Gracellariidae), is currently posing the main phytosanitary risk to *R. pseudoacacia* existence in the European range. *Parectopa robiniella* (Clemens, 1863) is characterized by the largest-scale invasion among the complex of invasive phytophages in Ukraine (Holoborodko et al., 2021). Since its introduction to Europe, *P. robiniella* has been the subject of numerous environmental and biological studies (Guo et al., 2018; Kirichenko et al., 2018; Wilkaniec et al., 2021).

However, the impact of *P. robiniella* on the photosynthesis processes in *R. pseudoacacia* remains unclear. Significant information on the state of photosynthetic apparatus in the plant influenced by various abiotic and biotic stress factors can be studied by the method of fluorescence analysis (Kargar et al., 2019; Pérez-Bueno et al., 2019).

Chlorophyll fluorescence is an indicator system that allows studying the way by which the photochemical reactions associated with the operation of photosystem II (FSII) occur in living objects, because this photosystem is the most sensitive to environmental factors. The results of studies on chlorophyll fluorescence intensity make it possible to find out the specifics of the regulatory mechanisms that ensure efficient energy conversion in the primary and subsequent stages of photosynthesis (Kalaji et al., 2017; Chen et al., 2019; da Silva et al., 2020). Analysis of indicators of critical parameters of chlorophyll fluorescence curves allows (Holoborodko et al., 2022) determining the adaptive capacity of the tree to various stressors.

The objective of this study was to analyze the photosynthesis indicators of *R. pseudoacacia* in different environmental conditions under the influence of entomophages and to determine the dependence of the intensity of the light stage of photosynthesis on the chlorophyll content. A study of the dependence between chlorophyll content and fluorescence indexes may provide new prospects for development of management practices of black locust plantations and a robust background to maintain safe, stable, and well-functional plantings in different types of ecosystems.

Material and methods

The research was conducted in September 2021 in the territory of the Dnipropetrovsk Region, within three sites (Dnipro city and its surroundings, the Mayorka village in the Dnipro district). These locations are in the northern subzone of the steppe zone of Ukraine located in the zone of temperate latitudes with quite active atmospheric circulation. The climate of the territory is temperate continental.

The *R. pseudoacacia* trees were chosen as the object of research because it is the most common introduced tree species in the researched region. Trees aged 10–15 years with similar morphological and taxational characteristics were studied.

Location 1 (L1) was situated within the Taras Shevchenko Park (Monastyrsky Island). A plant community comprising *R. pseudoacacia* was developed spontaneously within a recreational area on alluvium sandy soils. In addition to *R. pseudoacacia*, the plant community included *Populus alba* L. (up to 10% of the total planting composition). Herbaceous vegetation cover on the site was mainly represented by mesophilic vegetation with dominance of *Carex ligerica* J. Gay.

Location 2 (L2) was situated in the landscape reserve "Levoberezhny" It was formed spontaneously, in the recreation area within the valley-terraced landscape of the Dnipro River valley, on native sandy loam soils. In addition to *R. pseudoacacia*, the dendroflora in the location included *Elaeagnus angustifolia* L., *Populus alba* L. and *Ulmus pumila* L. Herbaceous vegetation was mainly represented by ruderals dominated by adventitious *Hordeum murinum* L.

Location 3 (L3) is in the vicinity of the Mayorka village in the Dnipro district, Dnipropetrovsk Region). Spontaneous planting was located on arable land abandoned 20 years ago near the "parent" cultivated forest belt in the watershed area. The dendroflora composition was dominated by *R. pseudoacacia*, also *Fraxinus pennsylvanica* Marshall., *Ulmus pumila* L., *U. minor* Mill. and *Morus alba* L. occurred sporadically (up to 10% of the total planting composition). Herbaceous vegetation was mainly representted by mesotrophic cereals with a dominance of *Poa angustifolia* L.

Leaves of *R. pseudoacacia* of the middle formation were examined on plants during their annual vegetative growth, simultaneously sampled from the lower-third crown in the lighted (5 complex leaves) and shaded parts (5 complex leaves) in dry clear weather in mid-September 2021 from five *Robinia* trees from each experimental site. The period for accounting of damaged leaves corresponds to the period for the development of the most massive second generation of *P. robiniella*.

The portable Floratest fluorometer was used for the diagnostics of photosynthetic disorders of native chlorophyll in living *R. pseudoacacia* leaves. The portable fluorometer Floratest comprises a base unit with a graphic liquid crystal display, control buttons, a remote optoelectronic sensor, wire connecting it to the USB port of a personal computer, and a network adapter. LED, as a component of the remote optoelectronic sensor, has a maximum radiation intensity at $\lambda = 470 \pm 20$ nm. Irradiation indicators in the sensor were the following: irradiation wavelength 470 ± 15 nm; a spectral range of fluorescence intensity measuring 670–800 nm; receiving window area of 9 mm^2; sensitivity of photodetector at $\lambda = 650$ nm: 0.45 A/W. Light intensity was measured using the PCE-174 Lux Meter (PCE Instruments, Germany, 2018).

Fig. 1. Instrumental support of the experiment: Floratest, Thermo-hygrometer NE-173 and PCE-174 Lux Meter

The observations were performed using fresh *R. pseudoacacia* leaves. After the start of light exposure, the chlorophyll fluorescence intensity (induction of fluorescence or light-induced (caused) fluorescence) began to change significantly over time. The time-dependent curve of the chlorophyll fluorescence intensity has the characteristic form with one or more maximums and is called the chlorophyll fluorescence induction curve (the Kautsky curve) (Kautsky & Hirsch, 1931). Changes in any link of the photosynthetic chain cause a change in the appearance of the chlorophyll fluorescence induction curve. Therefore, by the appearance of this curve, it

is possible to determine the current state of the plant's photosynthetic apparatus and to evaluate changes in the photosynthesis efficiency on changes in the light regime, temperature, humidity, and other factors (Holoborodko et al., 2022).

In addition to the critical parameters of the Kautsky curve (F_0 is the initial value of fluorescence induction after irradiation is turned on; F_p is the value of "plateau" fluorescence induction; F_m is the maximum value of fluorescence induction; F_{St} is the stationary value of fluorescence induction after light adaptation of a plant leaf), we used calculated parameters, such as variable fluorescence calculated as the difference between the maximum fluorescence at closed reaction centers, and the chlorophyll fluorescence intensity at open reaction centers of photosystem II ($F_v = F_m - F_0$), and light-adapted steady-state fluorescence value ($K_{pl} = K_{pl}–F_0/F_m–F_0$). Adapted ($K_{pl}$) fluorescence value reflects the saturation rate of inactive reaction centers of photosystem II responsible for water decomposition and oxygen release. This system is most sensitive to environmental conditions such as extremely high and low temperatures, excessive light intensity, overmoistening, drying, and increased salt content in the nutrient medium (Kerneev et al., 2000).

The chlorophyll concentration was determined in the intact parts of the leaves in acetone extraction using SF-46 spectrophotometer at wavelengths of 662 and 641 nm. Then the obtained results were recalculated to mg/g of raw mass of plant tissues with the use of Wettstein's formula.

The data were analyzed using variational statistics and presented as mean and standard error (x ± SE). Comparison of samples in tables was carried out using ANOVA, and the differences between individual samples were considered significant at $P < 0.05$ according to the results of the Tukey Test with Bonferroni correction.

Result

The value of variable chlorophyll fluorescence in the experimental trees at all locations was in the wide range of 433–1420 c.u. (Table 1).

Table 1
Effect of lighting and invasion of damage-causing pests on black locust fluorescence indicators (x ± SE, n = 120)

Side	Fluorescence indicators		
	F_v	F_v/F_m	K_{pl}
	L1		
Lighted, intact	1084 ± 77	0.807 ± 0.022	0.862 ± 0.016
Shaded, intact	1420 ± 78	0.834 ± 0.013	0.831 ± 0.025
Lighted, damaged	959 ± 82	0.772 ± 0.011	0.874 ± 0.022
Shaded, damaged	884 ± 95	0.763 ± 0.024	0.761 ± 0.012
	L2		
Lighted, intact	433 ± 72	0.623 ± 0.043	0.843 ± 0.024
Shaded, intact	1411 ± 82	0.842 ± 0.012	0.894 ± 0.022
Lighted, damaged	498 ± 57	0.695 ± 0.024	0.876 ± 0.014
Shaded, damaged	712 ± 138	0.732 ± 0.038	0.622 ± 0.021
	L3		
Lighted, intact	1140 ± 48	0.813 ± 0.012	0.823 ± 0.032
Shaded, intact	822 ± 60	0.792 ± 0.015	0.793 ± 0.014
Lighted, damaged	747 ± 108	0.722 ± 0.024	0.812 ± 0.032
Shaded, damaged	580 ± 46	0.745 ± 0.017	0.881 ± 0.021

The minimum value (433 ± 72 c.u.) was recorded in the lighted intact leaves sampled from the trees of the black locust plantation in the Livoberezhny Landscape Reserve of Local Importance, but this indicator differed slightly at the corresponding location under the influence of damage-causing pests, accounting for 498 ± 56.9 c.u. In general, there was a tendency to decrease in variable fluorescence, both in the case of pest-damaged and undamaged trees that form plantings on an man-made sandbar, on the watershed near the water-divided and valley-terraced landscapes. The intensity of the decrease in variable fluorescence was greater with shading. In trees that formed a local spontaneous community in a valley-terraced landscape under shading conditions, the variable fluorescence values were two times less than the corresponding indicators in the leaves sampled from the lighted side of the tree (Table 1).

It should be noted that higher absolute values of variable fluorescence were found in black locusts grown on the man-made sandbar, reaching1420 ± 79 in a shaded intact leaf and 1084 ± 77 in a lighted intact leaf.

Relationship F_v/F_m characterized the inhibition intensity of the light phase of photosynthesis which could be caused by abiotic and biotic factors of various etiologies. In two locations (under the conditions of the sandbar of Monastyrsky Island and the forest strip of the Mayorka village), decrease in this ratio in leaves sampled from pest-damaged trees was recorded on the watershed near the water-divided landscape (Table 2). An exception was the type of planting in the Livoberezhny Landscape Reserve, where F_v/F_m ratio in the lighted damaged leaves was 0.695, while in the undamaged leaves it was 0.623.

The indicator of photosynthesis occurring, K_{pl}, which characterizes the proportion of reaction centers that do not restore the primary electron acceptor, for black locust plantings ranged 0.622 to 0.894. There were no significant differences in the variants of the experiment. However, it should be noted that the shaded damaged black locust leaves had a significantly lower coefficient K_{pl} 0.622 ± 0.021 compared to intact leaves 0.894 ± 0.022 in the planting in the valley-terraced landscape of the reserve.

The average value of the total chlorophyll content in the black locust leaves varied, both by location and by the experiment variant (Table 2).

Table 2
Chlorophyll content of *R. pseudoacacia* (mg/g, x ± SE, n = 120)

Side	Location		
	L1	L2	L3
Lighted, intact	1.258 ± 0.145	0.480 ± 0.084	0.580 ± 0.045
Shaded, intact	0.950 ± 0.073	0.405 ± 0.055	0.448 ± 0.027
Lighted, damaged	1.618 ± 0.086	0.314 ± 0.013	0.769 ± 0.066
Shaded, damaged	0.522 ± 0.032	0.378 ± 0.012	0.916 ± 0.082

The maximum value was recorded in the lighted damaged leaves of black locust trees of the sandbar plantation, equaling1.618 ± 0.08. Tendency towards decrease in the chlorophyll concentration was characteristic of damaged leaves, both in leaves under shaded and lighted conditions. However, there we observed increase in the chlorophyll content against the background of insect invasion in the lighted leaves of trees planted in 1st location compared with the chlorophyll content in intact leaves, which was 1.258 ± 0.14 in similar conditions.

According to absolute values, the lower chlorophyll content in all experiment variants was recorded in the black locust plantation in the Livoberezhny Landscape Reserve; the minimum value was recorded in the damaged leaves under lighted conditions: 0.314 ± 0.013. It was found (Table 3) that F_v/F_m ratio depended on the total chlorophyll content. When developing the dependencies, second-degree polynomial function ($Y = ax^2 + bx + c$) was chosen; its equations were characterized by the coefficient of determination (R^2) equaling 0.11 to 0.64.

Discussion

The risk of invasion of non-native species has recently increased exponentially (Chapman et al., 2017; Seebens et al., 2017). It is now known that insect species have colonized European forests, and their number increases by an average of 6 per year (Harvey et al., 2020; Roques et al., 2020). The greatest harmful effect on plants is caused by the direct action of invasive harmful pests and fungal pathogens (Lapin et al., 2021). The rate of photosynthesis and electron transport are key physiological characteristics of plants that can respond quickly to sudden changes in solar radiation exposure.

Photosynthesis regulation is associated with the functioning of two photosystems (PSI and PSII), and their efficiency can be estimated by the maximum quantum yield of photosystem II (F_v/F_m) (Pollastrini et al., 2022). The indicator is very stable and varies in undamaged plants within a narrow range of values (0.75–0.84) (Murchie & Lawson, 2013). So, F_v/F_m relation is an effective tool for monitoring plant stressors, as it is sensitive to inhibition of the light phase of photosynthesis (Pfündel, 1998; Guidi et al., 2019).

Due to the high photochemical efficiency of F_v/F_m, more electrons are released, whereby PSII is added to the electron transport chain (Pfündel, 1998). Thus, there may be a limitation of PSI due to

the limitation of end acceptors or substrate to be regenerated (CO_2). A number of authors associated this reduced FSI ability with the nitrogen content in leaves (Kitao et al., 2018), which plays a fundamental role in the formation of photosynthetic systems. Increase K_{pl} indicates impairment in both energy migration and electron transport, and decrease indicates a possible acceleration of electron transport processes.

The influence of stress factors on plants at later stages of development caused decrease in the chlorophyll content. Decrease in the rate of photosynthesis, increased content of phenol, peroxide, and ascorbic acid were noted for plants that have a protective reaction against oxidative stress (Tang et al., 2006). At the same time, Bown et al. (2002), according to the results they obtained, interpreted the increase in chlorophyll, considering this response a rapid local mechanism of plant resistance to the influence of herbivorous insects. In their opinion, the presence of insects on the leaves stimulates the synthesis of certain substances (such as 4-aminobutyrate), which increases chlorophyll-containing pigment.

Table 3
Mathematical models of the fluorescence coefficient dependence on the chlorophyll content

Variant	2th degree polynomial	R^2	Linear	R^2
		L1		
Lighted, intact	$F_v/F_m = 188.2Cl^2 - 470.5Cl + 294.7$	0.51	$F_v/F_m = 2.5212Cl - 2.3696$	0.44
Shaded, intact	$F_v/F_m = 127.2Cl^2 - 241.7Cl + 115.5$	0.34	$F_v/F_m = 0.2326Cl + 0.6099$	0.21
Lighted, damaged	$F_v/F_m = -209.4Cl^2 + 678.1Cl - 547.5$	0.31	$F_v/F_m = 0.366Cl + 0.1816$	0.20
Shaded, damaged	$F_v/F_m = 37.01Cl^2 - 36.726Cl + 9.85$	0.28	$F_v/F_m = 2.072Cl + 1.3167$	0.03
		L2		
Lighted, intact	$F_v/F_m = 2272.9Cl^2 - 2184.5Cl + 525.4$	0.23	$F_v/F_m = -6.1795Cl + 3.6054$	0.07
Shaded, intact	$F_v/F_m = -7790.5Cl^2 + 6314.4Cl - 1278.7$	0.19	$F_v/F_m = 6.5632Cl - 1.8209$	0.04
Lighted, damaged	$F_v/F_m = 2147.7Cl^2 - 1346.0Cl + 211.2$	0.11	$F_v/F_m = 1.1127Cl + 0.3371$	0.01
Shaded, damaged	$F_v/F_m = -32.721Cl^2 + 13.085Cl + 329.9$	0.23	$F_v/F_m = -32.721Cl + 13.085$	0.22
		L3		
Lighted, intact	$F_v/F_m = -258.1Cl^2 + 294.2Cl - 82.9$	0.66	$F_v/F_m = -4.944Cl + 3.6795$	0.64
Shaded, intact	$F_v/F_m = -54.43Cl^2 + 49.1Cl - 10.2$	0.62	$F_v/F_m = 0.3665Cl + 0.629$	0.01
Lighted, damaged	$F_v/F_m = -326.3Cl^2 + 501.8Cl - 191.65$	0.40	$F_v/F_m = 0.0951Cl + 0.6461$	0.01
Shaded, damaged	$F_v/F_m = 59.4Cl^2 + 108.9Cl + 50.71$	0.17	$F_v/F_m = -0.2886Cl + 1.005$	0.03

In our studies, the results on the change of chlorophyll content variability towards its increase were observed in specimens of the black locust exposed to the invasive effects of *P. robiniella*. At the same time, predominant decrease in F_v/F_m ratio was recorded under the impact of harmful insects, which in both cases demonstrated the similarity of data obtained by researchers during studying of the effects of other stressors on the black locus plants (Dezhban et al., 2015).

Ultimately, because of the abiotic stress caused by an invasive species, we may assume that *R. pseudoacacia* trees spend less energy on their growth and reproduction, and spent more resources on the synthesis of protective metabolites and other anti-stress reactions that ensure the survival of *R. pseudoacacia* under unfavorable conditions.

Conclusion

Invasion by *P. robiniella* caused decrease in the chlorophyll concentration and estimated indicators of fluorescence intensity. Tendency to decrease the chlorophyll concentration was typical in damaged leaves, both in leaves under shaded and lighted conditions. The intensity of the decrease in variable fluorescence was greater when the leaves were shaded, both in the damaged and intact leaves. The invader influence and the shading factor caused a significant decrease in the values of F_v/F_m ratio, which characterizes the intensity of inhibition of the light phase of photosynthesis. The developed mathematical dependencies could be used to calculate F_v/F_m in *R. pseudoacacia*, which forms plantings in various steppe landscapes under damage by *P. robiniella*.

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