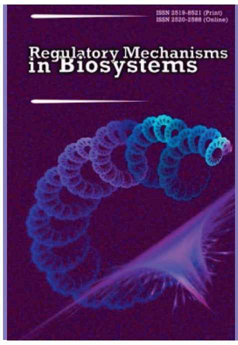

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Impact of invasive species *Parectopa robiniella* (Gracillariidae) on fluorescence parameters of *Robinia pseudoacacia* in the conditions of the steppe zone of Ukraine

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Robinia pseudoacacia L. is one of the most common and environmentally adaptable introduced tree species which has become an important element of artificial afforestation and landscaping in Ukraine over the past 150 years. Throughout the history of its introduction on the territory of Ukraine, this species was considered resistant because of the absence of dangerous phytophages. At the beginning of the XXI century, the phytosanitary situation changed as the result of the penetration and rapid spread of a number of North American invasive phytophages. The appearance and distribution of the miner *Parectopa robiniella* (Clemens, 1863) (Lepidoptera, Gracillariidae) feeding on *R. pseudoacacia* was recognized as the largest invasion in Ukraine. This paper considers the issues of studying the effect of *P. robiniella* caterpillars feeding on *R. pseudoacacia* in various forest-growing conditions in the steppe zone of Ukraine. The process of photosynthesis, as the most important physiological parameter, was chosen as indicator of condition. The study was conducted using biosensor technology which made it possible to measure the effect of caterpillar feeding on critical parameters of chlorophyll fluorescence (the Kautsky curve). The research has shown that the initial value of fluorescence induction was within the range of 196–284 RFU, and the maximum value of the background fluorescence parameter was recorded in undamaged leaves and under shading conditions. Both the effect of phytophages and the shading factor caused a significant decrease in the values of fluorescence induction of the "plateau" both in the conditions of an artificially washed sandbar, on the watershed area of a watershed-gully landscape, as well as on natural sandy-loam soil. The maximum values of photosynthetic fluorescence induction under the simultaneous influence of the studied factors had rather high variability. In contrast to the fluorescence induction parameter, the "plateau" of the highest maximum fluorescence induction was reached in the absence of pest damage under conditions of total shading. As revealed by dispersion and regression analyses, the maximum fluorescence index was most dependent on the amount of solar radiation and on the degree of the leaf surface damage by phytophages. Significantly higher values of the steady-state fluorescence induction parameter were determined in the absence of insect damage in both shading and lighting conditions. A statistically significant combined influence of abiotic and biotic factors on the "plateau" fluorescence induction parameter was determined in comparison with the mono-influence of individual factors. A highly significant dependence of the maximum efficiency indicator of primary photosynthesis processes on individual factors of exogenous influence was established, while the combined effect of these factors did not affect this parameter. The obtained data allow one to apply in practice the methods of analyzing chlorophyll fluorescence induction to establish the physiological state of tree flora in forest and garden farms.

Keywords: effect of invasive species; lepidopteran miners; the resistance of introducents; chlorophyll; chlorophyll fluorescence; plant photosynthetic apparatus.

Introduction

The North American species *Robinia pseudoacacia* L. (black locust) is an adventive tree species currently at its most common in Europe, and the total square of its secondary area in the world is estimated at approximately 2.3 × 10^6 ha (Nicolescu et al., 2020; Vítková et al., 2020). It is a drought-resistant, fast-growing tree species that has a wide ecological amplitude in relation to soil conditions (Vitkova et al., 2017); plantings from this species play an important role in the economics of many countries and perform a large number of necessary ecosystem resources: carbon sequestration, soil enrichment with nitrogen, soil protection from erosion, field-protective functions, microclimate optimization, bioenergy and wood production (Faly et al., 2017; Chaplygina et al., 2018; Zverkovsky et al., 2018; Gritsan et al., 2019; Nicolescu et al., 2020).

However, despite its ecological, social and economic significance, *R. pseudoacacia* is recognized as an invasive species due to its active population strategy and introduction into various types of ecosystems in many countries of the world (Rumlerová et al., 2016; Wagner et al., 2017; Burda & Koniakin, 2019; Nicolescu et al., 2020; Vítková et al., 2020), and is included in the current list of the worst invasive alien species in Europe that cause the greatest negative ecological and socio-economic impact (Nentwig et al., 2018). The effect of *R. pseudoacacia* plantings on the reduction of species richness, unification and homogenization of forest vegetation has already been confirmed in Central Europe (Šibíková et al., 2019; Montecchiari et al., 2020). It is considered that Robinia has a high acclimatization potential in secondary areas. In the context of climate change, it is predicted that its potential climate niches in Europe will be spread eastwards, with their reduction in Southern Europe and expansion in Central and North-Eastern Europe (Klisz et al., 2021; Puchałka et al., 2021), where an expansion of its invasive activity is possible in the future.

The successful naturalization of *Robinia* in its secondary range and high potential for its invasiveness were largely determined by successful reproduction strategies of this species, among which the formation of root growth is a high-priority (Vítková et al., 2020). The rate and intensity of colonization of nearby biotopes by overgrowth largely depend on the type of their vegetation, the presence or absence of soil and vegetation disturbances, and the specifics of agricultural activities. Vegetative activity with the formation of a greater number of ramets increases in conditions of high light intensity in open areas and decreases in shading (Carl et al., 2019), which reduces the potential threat of colonization of natural broad-leaved forests with undisturbed canopy (Vitkova et al., 2017), but contributes to the active expansion of *Robinia* in illuminated areas of meadows, steppes, roadsides, etc. adjacent to parent *Robinia* plantings. It is known that root growth colonizes most often and intensively abandoned agricultural land (Sitzia et al., 2018; Carl et al., 2019; Vitkova et al., 2020).

Previously, it was believed that the absence of natural enemies outside the native area could be one of the main reasons for the long period of existence of spontaneous populations of *Robinia* in the secondary area (Cierjacks et al., 2013). But at the beginning of the 21st century, as with other massively introduced trees (Shupranova et al., 2019), phytophages mainly feeding on *R. pseudoacacia* began to be recorded on the territory of Ukraine; their invasions began to cause a phytosanitary threat to the normal existence of this plant species. Research Holoborodko et al. (2021) showed that primarily two species in the family of leaf blotch miners (Lepidoptera, Gracillariidae) are currently associated with the main phytosanitary risk to survival of *R. pseudoacacia* in the Ukrainian area. Among the complex of phytophages-invaders of *R. pseudoacacia*, *Parectopa robiniella* is characterized by the largest scale of invasion in Ukraine (Clemens, 1863) (Holoborodko et al., 2021; Shvydenko et al., 2021). Since its introduction in Europe, *P. robiniella* has been subjected to numerous environmental and biological studies (Guo et al., 2018; Kirichenko et al., 2018; Wilkaniec et al., 2021). The absence of natural enemies and diseases within the novel area and an almost unlimited food resource contribute to their rapid and wide spread. The objective of our research was to determine the impact of invasive *P. robiniella* on critical parameters of the Kautsky curve for *R. pseudoacacia* trees in the main types of forest-growing conditions in the steppe zone of Ukraine.

Materials and methods

The research was conducted in September 2021 in Dnipro city and its surroundings: Majorca village in the Dnipro district (northern subzone of the steppe zone of Ukraine, Table 1). The locations were situated in the zone of temperate latitudes with a relatively active atmospheric circulation (the predominant movement of air masses from East to West). The climate of the territory is temperate-continental. Significant fluctuations in weather conditions from one year to another are one of the features of the climate in the territory. Moderately wet years alternate with sharply dry ones, and hot dry winds occur quite often. In general, the climate regime is characterized by rather cool winters and hot summers.

Table 1
Description of the study location

Feature	L1: Taras Shevchenko Park Monastyrsky Island (Dnipro city)	L2: The landscape reserve of local importance "Levoberezhny" (Dnipro city)	L3: The forest planting surrounding Majorca village (Dnipro district)
GPS latitude, longitude (height above sea level)	48º27'34.02" N 35º04'58.01" E (height above sea level is 54 m)	48º30'36.50" N 34º58'54.89" E (height above sea level is 54 m)	48º15'49.97" N 35º09'47.90" E (height above sea level is 104 m)
Landscape type	valley-terrace landscape The Dnieper River valley (artificially washed sandbar)	valley-terrace landscape The Dnieper River valley	watershed-gully landscape Watershed
Soil, texture , granulometric composition of soils	arenosol	fluvic arenosol, sandy loam	calcic chernozem, loamy
Groundwater depth, m*	0.9–1.2	2.0–2.5	20–25
Dominant tree species	*Robinia pseudoacacia* L.	*Robinia pseudoacacia* L.	*Robinia pseudoacacia* L.
Other tree species	*Populus alba* L.	*Elaeagnus angustifolia* L., *Populus alba* L., *Ulmus pumila* L.	*Fraxinus pennsylvanica* Marshall., *Ulmus pumila* L., *U. minor* Mill., *Morus alba* L.
Canopy density	0.61 ± 0.04	0.74 ± 0.03	0.96 ± 0.07
Relevant vegetation	*Carex ligerica* J. Gay. (dominant), *Calamagrostis epigeios* (L.) Roth, *Anisantha tectorum* (L.) Nevski, *Secale sylvestre* Host, *Taraxacum officinale* Wigg., *Polygonum arenarium* Waldst. et Kit.	*Hordeum murinum* L. (dominant), *Calamagrostis epigeios* (L.) Roth, *Elytrigia repens* (L.) Nevski, *Coniza canadensis* (L.) Cronq, *Chenopodium album* L., *Ambrosia artemisifolia* L., *Berteroa incana* DC.	*Poa angustifolia* L. (dominant), *Gallium aparine* L., *Elytrigia repens* (L.) Nevski, *Ballota nigra* L., *Convolvulus arvensis* L.
The percentage grass cover	56.3 ± 0.11	84.7 ± 0.07	66.7 ± 0.09

Notes: soil classification was presented in accordance with the International Classification System IUSS Working Group WRB 2015 [IUSs Working Group WR. (2015). World Reference Base for Soil Resources 2014, update 2015 International soil classification system for naming soils and creating legends for soil maps. World Soil Resources Reports No. 106. FAO, Rome]; evaluation of soil granulometric composition was carried out according to the FAO method of field soil description [FAO 2006. Guidelines for soil description. 4th edition. Food and Agriculture Organization of the United Nations, Rome].

Black locust (*Robinia pseudoacacia* L.) was chosen as the research object because it is one of the tree species most commonly introduced within the research region (Svyrydchenko & Brygadyrenko, 2014; Brygadyrenko, 2015; Brygadyrenko & Nazimov, 2015; Baranovski et al., 2018). Trees of 10–14 years of age having similar morphological and taxational characteristics were studied. The studies were conducted on model *R. pseudoacacia* trees in local spontaneous plant communities dominated by black locust which were spontaneously formed near the parent artificial *Robinia* stands in different urban and suburban habitats characterized by different soil and hydrological conditions. In the studied plant communities, young trees of *R. pseudoacacia* were mainly of vegetative origin (root growth).

Location 1 (L1). Spontaneous planting in the Taras Shevchenko Park (Monastyrsky Island) was formed in a recreational area within an artificially washed sandbar on a site with a shallow groundwater depth (Table 1). In addition to the dominant black locust, the spontaneously formed community fragmentally includes the white poplar (*Populus alba* L.) undergrowth, which occupies up to 10% of the plantation composition. The grass cover under the canopy of the plant community was native and consisted mainly of mesophilic oligotrophic and eurytopic light-demanding species with complete dominance of *Carex ligerica* J. Gay.

Location 2 (L2). In the landscape reserve of local importance "Levoberezhny", a local spontaneous *Robinia* community was formed in a recreational zone within the valley-terraced landscape of the Dnipro River on natural soils characterized by sandy loam granulometric composition and fairly shallow groundwater. In addition to the dominant *Robinia*, the spontaneous ruderal community fragmentally includes young trees and undergrowth of *Elaeagnus angustifolia* L., *Populus alba* L. and *Ulmus pumila* L. The share of these species' participation reaches up to 30% of the plantation composition. Naturally formed vegetation cover within this plantation was mainly represented by eurytopic ruderal species with a predominance of adventive *Hordeum murinum* L.

Location 3 (L3). Spontaneous *R. pseudoacacia* planting in the vicinity of the Majorca village was located on agricultural land abandoned more than 20 years ago near the parent artificial field-protective *Robinia* planting on the watershed area within a watershed-gully landscape. The habitat area is characterized by deep groundwater and the loamy granulometric composition of the soil. The young ruderal community was completely dominated by *R. pseudoacacia*, but there was also a sparse undergrowth of *Fraxinus pennsylvanica* Marshall., *Ulmus pumila* L., *U. minor* Mill. and *Morus alba* L. (no more than 10% of the plant composition), which was also present in the parent planting. Under the canopy of the spontaneous plant community, the vegetation is mainly represented by mesotrophic long-rhizome-forming cereals (with dominance of *Poa angustifolia* L.) and perennial dicotyledons (for example, *Ballota nigra* L.), *Gallium aparine* L. completely dominate in the spring period, drying up in the summer.

Leaves of the middle formation were examined on annual vegetative growth simultaneously sampled from the lower third of the crown in the illuminated (5 complex leaves) and shaded part (5 complex leaves) in dry clear weather in mid-September 2021 on five *Robinia* trees from each experimental site. The period of accounting for damaged leaves corresponds to the period of development of the most massive second generation of *Parectopa robiniella* Clemens, 1863. The degree of damage to *Robinia* leaf blades caused by *P. robiniella* was evaluated visually. Light intensity was measured using a Lux Meter RCE-174 (PCE Instruments, Germany, 2018). Temperature and relative humidity measurements were made using HE-173 thermohygrometer (Huato Electronic Co. LTD, China, 2018).

We used portable fluorometer "Floratest" for the diagnostics of photosynthetic disorders of native chlorophyll in living *R. pseudoacacia* leaves. The system of 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 (Fig. 1). The remote optoelectronic sensor includes an LED that has a maximum radiation intensity at λ = 470 ± 20 nm. Irradiation indicators in the sensor were the following: irradiation wavelength 470 ± 15 nm; spectral range of fluorescence intensity measurement 670–800 nm; receiving window area 9 mm^2; photodetector sensitivity at λ = 650 nm, 0.45 A/W.

The observations were made using fresh *R. pseudoacacia* leaves. After the start of light exposure, the intensity of chlorophyll fluorescence (fluorescence induction or fluorescence induced (caused) by light) begins to change significantly over time. A curve of the time dependence of the chlorophyll fluorescence intensity has the characteristic form with one or more maximum 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, based on the appearance of this curve, it was possible to diagnose the current state of the plant photosynthetic apparatus and to evaluate changes in the photosynthesis efficiency at changes in the light regime, temperature, humidity, and other factors (Holoborodko et al., 2022).

To interpret the Kautsky curve, we used its known critical parameters: 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. In addition to the critical parameters of the Kautsky curve, we used calculated parameters such as variable chlorophyll fluorescence ($F_v = F_m - F_0$); maximum efficiency of primary photosynthesis processes ($E_f = F_v/F_m$), and coefficient of photochemical processes efficiency ($E = (F_m - F_{St})/F_{St}$). The chlorophyll concentration was determined in the undamaged 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.

Fig. 1. Instrumental support for the field experiment: portable fluorometer "Floratest"

The data were processed using variational statistics and presented as mean and root-mean-square deviation (x ± SD). Comparison of samples in tables was carried out using ANOVA, and the differences between individual samples were considered reliable at $P < 0.05$ according to the results of the Tukey Test with Bonferroni adjustment. The influence of environmental factors on the parameters of the Kautsky curve and the chlorophyll content was assessed using three-way variance and regression analysis (Table 5).

Results

The values of the initial induction of chlorophyll fluorescence (F_0) were within the range of 196–284 RFU (Table 2). The minimum value was recorded in *Robinia* plantings at the L3 location in a damaged leaf under shading conditions, while the maximum background fluorescence was observed in an undamaged leaf, but also under shading conditions. A decrease in this indicator in damaged leaves in relation to undamaged ones was indicated in the planting of a local spontaneous *Robinia* community in the landscape reserve of local importance "Levoberezhny" (L2). An increase in the background concentration on the illuminated side of the leaf in relation to shading conditions was noted in the planting of the L3 location, and this trend was not significantly affected by caterpillar feeding.

Table 2

Influence of biotic and abiotic factors on photosynthesis indicators of *Robinia pseudoacacia* (x ± SD, n = 120)

Ecosystem	Side of the plant leaf and its damage by phytophage	Indicators of fluorescence, in relative fluorescence units (RFU)			
		F_0	F_p	F_m	F_{st}
L1	The light side of a leaf undamaged by phytophages	261 ± 12^{cd}	863 ± 46^{d}	1345 ± 75^{d}	1194 ± 64^{c}
	The shadow side of a leaf undamaged by phytophages	284 ± 16^{d}	908 ± 64^{d}	1704 ± 86^{e}	1451 ± 86^{d}
	The light side of a leaf damaged by phytophagse	266 ± 17^{cd}	760 ± 47^{c}	1225 ± 66^{cd}	1110 ± 61^{bc}
	The shadow side of a leaf damaged by phytophages	254 ± 7^{c}	637 ± 75^{ab}	1138 ± 141^{c}	930 ± 131^{b}
L2	The light side of a leaf undamaged by phytophages	223 ± 15^{b}	510 ± 59^{a}	656 ± 81^{a}	584 ± 75^{a}
	The shadow side of a leaf undamaged by phytophages	269 ± 8^{c}	1142 ± 42^{e}	1680 ± 86^{e}	1534 ± 92^{d}
	The light side of a leaf damaged by phytophages	214 ± 10^{ab}	549 ± 60^{a}	712 ± 91^{a}	649 ± 90^{a}
	The shadow side of a leaf damaged by phytophages	214 ± 11^{ab}	639 ± 40^{b}	926 ± 95^{b}	839 ± 82^{b}
L3	The light side of a leaf undamaged by phytophages	259 ± 16^{c}	1149 ± 29^{e}	1399 ± 49^{d}	1194 ± 58^{c}
	The shadow side of a leaf undamaged by phytophages	211 ± 11^{ab}	855 ± 51^{d}	1033 ± 68^{bc}	948 ± 62^{b}
	The light side of a leaf damaged by phytophage	266 ± 19^{c}	849 ± 38^{d}	1012 ± 74^{bc}	875 ± 32^{b}
	The shadow side of a leaf damaged by phytophages	196 ± 6^{a}	637 ± 35^{b}	776 ± 51^{a}	704 ± 46^{ab}

Notes: different letters within the column indicate datasets reliably ($P < 0.05$) differ from each other according to the results of the Tukey Test with Bonferroni adjustment; L1, L2, L3 – ecosystems which characteristics were shown in Table 1.

In the study conditions, the parameter F_p fluorescence reached a "plateau" at the level of 510-1149 RFU. A significant difference in achieving saturation of reaction centres is defined by the insect influence and the light intensity. The damage by insects, as well as shading, caused a significant decrease in F_p values, both in the conditions of the artificially washed sandbar (639 ± 40) and in the watershed area of the watershed-gully landscape (637 ± 35, while without damage these values were 1142 ± 42 and 1149 ± 29, respectively). The values of F_m as an indicator of photosynthesis under the simultaneous influence of the studied factors were fairly highly variable in the spontaneous planting within the valley-terrace landscape. A more than twofold excess of the maximum fluorescence level was recorded compared to the damaged leaves: 656 ± 81 to 1680 ± 86 (Table 2). Minimal fluorescence values were observed at all locations when the leaf mesophyll was damaged by insects under both intense lighting and shading conditions. The maximum fluorescence reached the highest values in the absence of insect damage under shading conditions.

Stationary fluorescence level (F_{St}) was provided by chlorophyll molecules that are not involved in energy transfer to the reaction centres of photosystem II. An increase in the values of this indicator evidences an inhibition of the outflow of reduced photoproducts from the reaction centres as a result of various factors. The steady-state fluorescence level was significantly higher in the absence of insect damage, both under shading (1534 ± 92) and lighting (1194 ± 58) conditions. As can be seen from the data shown in Table 3, the initial induction of photochemical processes depends on the action of exogenous factors. Each of them in its separate action did not have a statistically significant effect on the fluorescence index. Further, the statistically significant influence of factors of forest-growing conditions, as well as phytophages, on the F_p indicator was determined (Table 3). The complex effect of all three factors of exogenous nature was revealed as statistically significant in comparison with the mono-influence of individual factors.

Indicators of the maximum fluorescence value showed a different trend (Table 3). This indicator depends to the greatest extent on the intake of solar radiation and on the degree of damage to the leaf surface by phytophages, which cannot be noted in the case of the edaphic factor exposure on the plants. In the case of intensification of solar energy supply, the F_m indicator is expected to increase. In contrast, leaf surface damage by phytophages resulted in inhibition of the reactions of maximum fluorescence.

Statistical analysis of F_v values showed that, like Fm, the most significant effect on this indicator was achieved in the event of solar radiation effect on plants and in the case of plant damage by phytophages. Statistical processing of data on the effect of environmental factors and phytophages on the E value separately and with their combined effect did not reveal statistically significant results (Table 4). The results of statistical analysis obtained for the maximum efficiency index of primary photosynthesis processes revealed its highly significant dependence on individual factors of exogenous influence, while the complex effect of these factors did not have a significant effect on E_f. No statistically significant results were found for the efficiency coefficient of dark photochemical reactions.

Studies of changes in the level of chlorophyll components (Table 5) revealed statistically significant dependences of chlorophylls *a* and *b* on the factors of plant localization and the amount of incoming solar radiation, while the effect of phytophages on the studied parameter was insignificant. No statistically significant effect on chlorophyll levels was observed *a*, as well as amounts of *a* + *b* chlorophylls in the case of a combination of environmental factors.

Table 3

Results of three-way dispersion and regression analysis of the influence of location, light intensity,
and influence of phytophages on the fluorescence in the leaves of *Robinia pseudoacacia* model trees (N = 120)

Fluorescence parameters	Factor of influence	Beta	Standard error	B	Standard error	t_{116}	P	R^2	F	P
F_0	Location	–0.025	0.091	–1.475	5.348	–0.276	0.783	0.039	1.562	0.20230
	Light intensity	–0.106	0.091	–10.200	8.733	–1.168	0.245			
	Influence of phytophages	–0.164	0.091	–15.733	8.733	–1.802	0.074			
	Intercept	–	–	2904.183	1265.930	2.294	0.024			
F_p	Location	–0.246	0.081	–81.29	26.827	–3.030	0.003	0.237	12.041	<0.00001
	Light intensity	0.043	0.081	23.02	43.808	0.525	0.600			
	Influence of phytophages	–0.419	0.081	–226.22	43.808	–5.164	<0.001			
	Intercept	–	–	21781.88	6350.582	3.429	<0.001			
F_m	Location	–0.059	0.084	–30.82	43.89	–0.702	0.484	0.190	9.046	0.00010
	Light intensity	0.176	0.084	151.27	71.68	2.110	0.037			
	Influence of phytophages	–0.394	0.084	–337.67	71.68	–4.711	<0.001			
	Intercept	–	–	20301.52	10390.80	1.954	0.053			
F_{st}	Location	–0.031	0.084	–14.43	39.316	–0.367	0.714	0.163	8.743	0.00030
	Light intensity	0.174	0.084	133.50	64.203	2.079	0.039			
	Influence of phytophages	–0.391	0.084	–299.57	64.203	–4.665	<0.001			
	Intercept	–	–	18051.70	9307.026	1.939	0.054			
F_v	Location	–0.060	0.082	–29.35	40.361	–0.727	0.468	0.234	10.130	0.00001
	Light intensity	0.202	0.082	161.47	65.909	2.449	0.016			
	Influence of phytophages	–0.404	0.083	–321.93	65.909	–4.884	<0.001			
	Intercept	–	–	17397.33	9554.376	1.820	0.071			

Table 4

Results of three-way dispersion and regression analysis of the effect of location, light intensity,
and influence of phytophages on the calculated fluorescence parameters in the leaves of *Robinia pseudoacacia* model trees (N = 120)

Fluorescence parameters	Factor of influence	Beta	Standard error	B	Standard error	t_{116}	P	R^2	F	P
E_f	Location	–0.229	0.082	–0.024	0.008	–2.766	0.006	0.205	9.940	0.00001
	Light intensity	0.274	0.082	0.046	0.014	3.303	0.001			
	Influence of phytophages	–0.278	0.082	–0.047	0.014	–3.355	0.001			
	Intercept	–	–	0.882	2.044	0.431	0.666			
E	Location	–0.175	0.091	–0.014	0.007	–1.918	0.057	0.031	1.233	0.30087
	Light intensity	0.009	0.091	0.001	0.012	0.109	0.913			
	Influence of phytophages	0.007	0.091	0.001	0.012	0.079	0.937			
	Intercept	–	–	–0.069	1.746	–0.040	0.968			

Discussion

The process of photosynthesis begins with primary photochemical reactions being the initial link in the light energy conversion chain. In low light intensity under optimal plant growth conditions, primary reactions proceed with high intensity (Zhou et al., 2012; Antal et al., 2018; Guidi et al., 2019). These reactions include several stages: absorption of light energy by pigments, energy migration to the reaction centres of photosystems, and charge separation, after which the process of electron transfer along the electron transport chain is activated (Stirbet et al., 2018). For efficient absorption and migration of light energy, pigment molecules are assembled in antennas and stay in the form of pigment-protein complexes. As a result of interaction with proteins, chlorophyll changes its optical properties, which makes it possible to obtain a set of spectral forms in the antenna, in which the absorption spectra overlap with each other. This ensures efficient energy migration from antenna chlorophylls to reaction centres. Pigments in the reaction centers are functionally closely related to the electron acceptor and donor, which ensures the continuous electron outflow along the electron transport chain and reduction of pigment in the reaction center (Strasser et al., 2004).

Table 5

Results of three-way dispersion and regression analysis of the effect of location, light intensity, and influence of phytophages on the content of chlorophyll components in the leaves of *Robinia pseudoacacia* model trees (N = 120)

Chlorophyll components	Factor of influence	Beta	Standard error	B	Standard error	t_{116}	P	R^2	F	P
Chlorophyll a	Location	–0.186	0.086	–0.144	0.067	–2.150	0.033	0.130	5.763	0.00104
	Light intensity	–0.298	0.086	–0.377	0.109	–3.441	0.000			
	Influence of phytophages	0.078	0.086	0.099	0.109	0.906	0.366			
	Intercept	–	–	29.872	15.882	1.880	0.062			
Chlorophyll b	Location	–0.309	0.084	–0.106	0.029	–3.654	0.000	0.169	7.867	0.00008
	Light intensity	–0.268	0.084	–0.150	0.047	–3.174	0.001			
	Influence of phytophages	0.034	0.084	0.019	0.047	0.411	0.681			
	Intercept	–	–	14.139	6.867	2.059	0.041			
Chlorophyll a+b	Location	–0.301	0.083	–0.141	0.039	–3.615	0.000	0.191	9.119	0.00002
	Light intensity	–0.303	0.083	–0.233	0.064	–3.637	0.000			
	Influence of phytophages	0.085	0.083	0.065	0.064	1.027	0.306			
	Intercept	–	–	18.158	9.295	1.953	0.053			

Taking into account the research of a number of scientists (Flexas et al., 2002; Sáez et al., 2018; Petrova et al., 2019), it can be assumed that the chlorophyll content serves as a significant short-term indicator of the state of tree species due to its direct role in the photosynthetic reactions. The chlorophyll content is closely related to the plant photosynthetic functioning and this ability varies within the range of soil-environmental factors (Hari & Luukkanen, 2006; He et al., 2018; Lichtenthaler & Babani, 2022). Based on the results obtained by us, taking into account the influence of various factors on the photosynthetic apparatus, the effect on the concentration of chlorophylls under the influence of solar radiation and soil conditions was revealed, which is consistent with the data obtained by many authors (Huang et al., 2017). At the same time, there was no clear response of plants to the action of phytophages, but according to information available in the literature (Cardenas & Gallardo, 2016), this type of response will vary depending on the type of plant, as well as the type of harmful stress-causing agent.

The output level of induction of background fluorescence corresponds to the minimum fluorescence quantum yield (Zhang et al., 2020). The background fluorescence level is determined by chlorophyll fluorescence under conditions when all reaction centers stay in an open working state and all molecules of the primary quinone acceptor coenzyme are ready to accept an electron from P_{680}. It is likely that of the analyzed factors, insect damage affects the activation of reaction centers the most (Cardenas & Gallardo, 2016). Fluorescence index at the F_p level is caused by rapid saturation of energy through reaction centers that do not transfer energy to the electron transport circuit. Thus, the reaction centers do not restore the primary coenzyme acceptor and therefore act as reaction centers that do not restore the electron transport chain. The maximum fluorescence value characterizes the potential productivity of plant photosynthesis. When the acceptor molecules accept coenzyme electrons (i.e., under conditions of the complete reduction occurring at bright light exposure), the reaction centers are closed, since the transfer of electrons from P_{680} to pheophytin is impossible because of electrostatic repulsion. In this case, the electron excitation energy is realized mainly in the process of fluorescence emission; its absolute value and quantum yield reach the maximum values, corresponding to F_m in the experiment. With insufficient light intensity, the number of light-absorbing and antenna chlorophylls increases causing increase in this indicator.

F_v/F_m ratio is widely used as an indicator of the functional state of the photosynthetic system in intact green plant tissues. It was found (Duysens, 1961) that a coenzyme A reduction represents the cause of the increase in fluorescence from the F_0 level up to F_m level. Reducing the values of the F_v/F_m ratio is caused by inhibition of photosystem II (Van Rensburg & Kruger, 1993) and a decrease in the proportion of reaction centers of photosystem II that are unable to reduce coenzyme B (Ouzounidou, 1993). Sensitivity F_v/F_m to the inhibition of the light stage of photosynthesis makes this indicator an effective means to monitor the stressful effects of the environment on the plant. F_v/F_m value can be easily measured. Due to the reaction's high sensitivity, rate and non-invasiveness, the determination of the F_v/F_m parameter was often preferred in studies of a wide variety of light photosynthesis reactions (Van Rensburg & Kruger, 1993).

Photosystem II makes the main contribution to chlorophyll fluorescence at room temperature (as F_m, so and F_0). F_0 is a component generated in low actinic light or as a rapid response to any actinic light that develops prior to the triggering of primary photochemical reactions (Stirbet et al., 2018). In both cases, the primary electron acceptor plastoquinone cannot be recovered. Actually, F_0 reflects a constant fluorescence component independent of photochemical reactions (Khan et al., 2021). Background fluorescence F_0 is emitted by chlorophyll molecules that are part of the photosystem II antenna complex (Longoni & Goldschmidt-Clermont, 2021; Pashayeva et al., 2021). Technically, it is measured before the initiation of primary photochemical reactions associated with coenzyme reduction. The fluorescence yield increases immediately after starting of coenzyme A reduction. Since variable fluorescence F_v is determined by the redox status of coenzyme A, its level serves as an indicator of photochemical redox reactions (Tsai et al., 2019). When electron transport from coenzyme A to the following components of the photosynthetic electron transport chain is blocked or the intensity of actinic illumination exceeds the saturation level, F_v quickly reaches the maximum possible values. Therefore, any external influences affecting the electron transport process in the electron transport chain of the thylakoid will also affect the F_v value. This circumstance allows the use of F_v as a physiological indicator that reflects the influence of environmental and experimental factors on plants. Chlorophyll fluorescence has been shown to be potentially used in environmental and forestry research due to the relationship demonstrated with a set of leaf economic characteristics indicators of the photosynthetic metabolism (Bucher et al., 2018; Bussotti et al., 2020; Cetner et al., 2020; Guimarães et al., 2022).

Conclusion

Feeding of *P. robiniella* caterpillars causes a decrease in the activity of the photosynthetic apparatus in *R. pseudoacacia*. It is reflected in almost all values of critical chlorophyll fluorescence parameters. The maximum value of the background fluorescence parameter was recorded in undamaged leaves and under shading conditions. Both phytophage exposure and shading factor caused a significant decrease in fluorescence induction values (F_p), which was confirmed by us in all variants of *R. pseudoacacia* habitats. Under simultaneous exposure of the studied factors, values of the maximum fluorescence index (F_m) of photosynthesis were fairly highly variable. Unlike the F_p parameter, the highest F_m values were achieved in the absence of phytophage damage under conditions of total shading. As revealed by dispersion and regression analyses, the maximum fluorescence index was most dependent on the amount of solar radiation and on the degree of the leaf surface damage by phytophages. Significantly higher values of the steady-state fluorescence induction parameter (F_{St}) were determined in the absence of insect damage in both shading and lighting conditions. A highly significant dependence of the maximum efficiency values of primary photosynthesis processes (E_f) on individual factors of exogenous influence was established, while the complex effect of these factors did not affect this parameter.

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