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Characteristics of powdery mildew [*Sawadaea bicornis* (Wallr.) Miyabe] influence on the photosynthetic process in Norway maple (*Acer platanoides* L.) seedlings

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Abstract: The article presents the results of research on the impact of *Sawadaea bicornis* (Wallr.) Miyabe on the state of photosynthetic apparatus in *Acer platanoides* L. seedlings using a technique of chlorophyll fluorescence induction (ChlF) measurement, which at the present time can be implemented through the use of biosensors. The research was conducted in September 2022 in the territory of the Botanical Garden of Oles Honchar Dnipro National University. To diagnose a violation of the native chlorophyll photosynthesis in fresh leaves of *A. platanoides*, a portable fluorometer 'Floratest' was used (the selected spectral range for fluorescence intensity measurement was 670–800 nm). The research was carried out on fresh leaves of Norway maple seedlings both not unaffected and affected with powdery mildew. Analysis of the data obtained indicates a high sensitivity of the parameters of chlorophyll fluorescence induction to damage by the disease regardless of environmental conditions of local growth of *A. platanoides* seedlings. The high informativeness of induction changes in chlorophyll fluorescence in the structural organisation of chloroplasts in Norway maple leaves determined by the parameters F_o, F_m, F_v, F_v/F_o, F_v/F_m, $(F_m - F_{st})/F_{st}$, $(F_p - F_o)/F_v$ was revealed. This study demonstrated the effectiveness of using the studied chlorophyll fluorescence parameters to detect severe stress in Norway maple seedlings caused by powdery mildew exposure when the fungus affects more than 50% of the leaf blade area. It is further necessary to conduct dynamic studies throughout the growing season to determine the effectiveness of using these parameters to detect mild stress in the early stages of infection.

Keywords: biosensors; intensity of chlorophyll fluorescence induction; phytophagous insects; plant photosynthetic apparatus; woody plant species

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Continuous climate change towards its aridisation causes deterioration of environmental conditions influencing the growth of trees and the performance of their ecological and social functions. Qualitative assessment of the response of trees to extreme climatic conditions and associated changes in the tree habitats is an important part of the care of urban green spaces (Kunakh et al. 2022; Kvitko et al. 2022). The urban environment represents a wide range of stressors that have a serious negative effect on urban vegetation (Lovynska et al. 2022; Shupranova et al. 2022). Man-made contamination, long summer dry periods with high air temperatures and the presence of greenhouse gases effect significantly affect the physiological and biochemical characteristics and immunity of urban plants (Wang et al. 2019).

Norway maple (*Acer platanoides* Linnaeus, 1753) is one of the natural deciduous tree species the most common in forests and urban stands of Central Europe. It is a fast-growing tree that can grow in a wide range of soil and environmental conditions. Norway maple is intensively planted as an ornamental and shade tree valued for its large spreading dense crown and its autumn leaf colour (Kuzmin et al. 2020). In North America, *A. platanoides* is a common invasive species naturalised in various habitats. Norway maple trees are resistant to air pollution, but they do not long-live enough, especially in an urban environment where they are more vulnerable to pathogens (Korányi et al. 2022). Damage by phytopathogenic fungi reduces their decorative effect and also leads to disruption of photosynthetic and transpiration processes causing drying and death of both single branches and trees as a whole (Lu et al. 2022).

The powdery mildew disease caused by a parasitic fungus *Sawadaea bicornis* (Wallroth) Miyabe, 1937 is one of the most common diseases affecting both young seedlings and adult Norway maple plants. The negative effects of this phytopathogen are multiple and can be classified as direct (fungi take up nutrients from the host plant) and indirect (the epiphytic mycelium reduces assimilation by covering the leaf surface). At the leaf level, the effect of powdery mildew strongly depends on the infection time and severity since the susceptibility of leaves to phytopathogen depends on their age. Young leaves and stem tops are more vulnerable to damage by *S. bicornis*; so, powdery mould spots start off the tops of plants. In case of severe infection, all the leaves and stems are covered with powdery mould spots followed by turning yellow and drying up. Powdery mildew is one of the most damaging plant diseases, especially in the early stages of ontogenesis, as it can stop seedling growth, significantly worsen wintering, cause complete leaf fall, and deplete significantly the plant (Desprez-Loustau et al. 2019).

The stress effect and adaptability of a tree to a changing environment are often assessed by measuring chlorophyll fluorescence (Holoborodko et al. 2022a). This method is reliable, rapid, non-destructive, and currently has widespread application in field conditions. The results are representative in studies of plants under the influence of abiotic stress.

Photosynthesis is a universal process of plant survival, and immune defence is a key process of plant adaptation to growing conditions. Various studies have found that these two processes are interrelated in a complex network. Photosynthesis can affect signalling pathways and provide materials and energy for the development of immune defence, while the immune defence process can also adversely affect photosynthesis (Lu et al. 2018). Changes in photosynthetic activity are known to be associated with the level of host resistance, the disease duration after infection, and the infection localisation (Bojović et al. 2017).

The main goal of the presented research was to investigate the impact of *S. bicornis* on the physiology of photosynthesis in Norway maple leaves using non-destructive fluorescence parameters. This goal is conditioned by the fact that the measurement of chlorophyll fluorescence can provide valuable additional information for understanding the primary processes of photosynthesis and the effect of stress on photochemistry. Accordingly, the results have to provide valuable information on what parameters of chlorophyll fluorescence exactly should be used in discovering, evaluating and monitoring powdery mildew infections.

MATERIAL AND METHODS

The research was conducted in Dnipro city (Northern Steppe subzone of Ukraine). The city is situated in a zone of temperate latitudes with a fairly active atmospheric circulation (the prevailing movement of air masses from East to West). The climate of the territory is temperate-continental. One of the climate features in the territory

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is significant fluctuations in weather conditions from one year to another. Moderately wet years alternate with sharply dry ones, and hot dry winds blow quite often. In general, the climate is characterised by rather cool winters and hot summers.

The Botanical Garden of Oles Honchar Dnipro National University was founded on the territory of Dnipro city in 1931 (48°26'N, 35°02'E; 127 m a.s.l.). Two test sites with the same environmental conditions were laid on its territory, within which 14 one- to two-year-old seedlings of Norway maple (*A. platanoides*) were selected by random selection (7 affected by *S. bicornis* and 7 unaffected); the seedlings have similar morphological features (10–15 cm in height; Figure 1A). All seedlings grew under the crown canopy with the same sunlight intensity. In general, the soils of the selected areas were represented by urban soils developed on the basis of zonal ordinary low-humus medium loamy chernozems on loess-like loams.

A portable fluorometer 'Floratest' (V.M. Glushkov Institute of Cybernetics of the National Academy of Sciences of Ukraine, Ukraine; Romanov et al. 2013) was used for the diagnosis of photosynthetic disorders of native chlorophyll in fresh leaves of *A. platanoides*. The 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 (Figure 1B). LED, as a component of the remote optoelectronic sensor, has a maximum radiation intensity at λ = 470 + 20 nm. Irradiation indicators in the sensor were the following: irradiation wavelength 470 + 15 nm; a spectral range of fluorescence intensity measurement 670–800 nm; receiving window area 9 mm^2; sensitivity of photodetector at λ = 650 nm: 0.45 A/W.

Measurements were carried out on fresh (live) leaves of *A. platanoides* (7 measurements per leaf) in September 2022, when the greatest degree of fungal cover on the leaves was observed. The measurements were carried out in plants incompletely damaged by the fungus and in plants with leaves

Figure 1. Experimental sprouts of (A) *A. platanoides* and (B) devices for measuring photosynthetic parameters: 1 – portable fluorometer 'Floratest' (V.M. Glushkov Institute of Cybernetics of the National Academy of Science of Ukraine, Ukraine); 2 – luxmeter RCE-174 (PCE Instruments, Germany); 3 – thermohygrometer NE-173 (Huato Electronic Co. Ltd., China)

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covered with the fungus at least of 50%. The percentage was determined visually. The biosensor (V.M. Glushkov Institute of Cybernetics of the National Academy of Sciences of Ukraine, Ukraine) was operated on the part of the leaf affected by the fungus. Since the start of light exposure, the chlorophyll fluorescence intensity [induction of fluorescence or light-induced (caused) fluorescence] begins 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; Stirbet et al. 2018). Alterations 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 is 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. 2022b).

To interpret the Kautsky curve, we used its known critical parameters: F_o 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 the calculated parameters: $F_v = F_m - F_o$ is variable chlorophyll fluorescence; F_v/F_m is the maximum efficiency of the primary processes of photosynthesis; F_v/F_o is the efficiency of the water-splitting complex on the donor side of photosystem II (PSII); $(F_m - F_{st})/F_{st}$ is the photochemical efficiency coefficient; $(F_p - F_o)/F_v$ is the share of the primary plastoquinone electron acceptors (QA) of non-renewable PSII reaction centres.

Descriptive statistics, analysis of variance (ANOVA), and relative variance components analysis were calculated using STATISTICA statistical software (Version 12.0, 2014).

RESULTS AND DISCUSSION

Photosynthesis is one of the processes most vulnerable to stress factors, so significant information on the state of photosynthetic apparatus in a host plant under the phytopathogen invasion can be obtained with fluorescence analysis (Baghbani et al. 2019). The rate of photosynthesis and electron transport are key physiological characteristics of plants that are able to respond quickly to sudden changes in solar radiation exposure. The light- and dark-dependent stages of photosynthesis play a significant role in the kinetics of induction transitions of chlorophyll fluorescence. To assess the state of the photosynthetic apparatus a set of parameters can be used, where F_o, F_m, F_v, F_v/F_o, F_v/F_m, $(F_m - F_{st})/F_{st}$, $(F_p - F_o)/F_v$ are among the key ones (Sancho-Knapik et al. 2018; Zhang et al. 2020).

The effect of the parasitic fungus *S. bicornis* in *A. platanoides* plants caused alterations in the induction of chlorophyll fluorescence (Table 1) quite different in their intensity and direction. Indicator F_o depends on the loss of excitation energy during its migration along the pigment matrix of light-harvesting complexes. In powdery mildew-affected Norway maple leaves sampled from Location 1 and Location 2, this indicator decreased by 16.3% and 19.3%, respectively, compared to unaffected ones, which indicates a decrease in energy loss during its migration to reaction centres (RC). As the number of antenna chlorophylls decreases, the initial level of fluorescence decreases, and vice versa (Zhang et al. 2018). The data obtained indicate a decrease in the efficiency of the use of absorbed light in affected Norway maple leaves.

The parameter F_m defines the highest chlorophyll fluorescence level. It looks like a maximum on the induction curve. It is characterised by the most variable behaviour due to adaptive changes in the pigment complex structure. A segment of the Kautsky curve within F_o and F_m reflects the rapid reduction of QA acceptors in PSII reaction centres not involved in the transport of electrons to the secondary plastoquinone electron acceptors (QB) of PSII and the slower reduction of QA in PSII complexes involved in the transport of electrons to the plastoquinone pool. The part of the Kautsky curve from background fluorescence to maximum is a fast fluorescence phase and lasts up to 1 s. The induction transitions that occur after reaching the fluorescence peak are combined into a slow fluorescence phase that depends on the redox state of QA (photochemical fluorescence quenching) and on the level of thermal dissipation (non-photochemical quenching; Shin et al. 2021). A de-

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Table 1. Descriptive statistics of fluorescence parameters (mean ± standard deviation, N = 7)

Trait	Unaffected		Affected	
	Location 1	Location 2	Location 1	Location 2
F_o	322.30 ± 22.30	413.40 ± 33.60	269.70 ± 61.10	333.70 ± 51.10
F_m	1 939.40 ± 187.70	2 534.60 ± 166.30	1 119.70 ± 287.90	1 382.60 ± 335.70
F_v	1 617.10 ± 169.60	2 090.30 ± 199.10	850.00 ± 241.70	1 106.00 ± 382.40
F_{st}	1 605.70 ± 123.80	2 114.60 ± 149.50	936.90 ± 236.90	1 230.90 ± 365.30
F_p	1 052.30 ± 117.10	1 856.00 ± 127.40	744.60 ± 227.50	1 118.30 ± 302.10
F_v/F_o	5.01 ± 0.35	5.07 ± 0.43	3.17 ± 0.64	3.28 ± 0.82
F_v/F_m	0.83 ± 0.01	0.82 ± 0.05	0.76 ± 0.04	0.78 ± 0.08
$(F_m - F_{st})/F_{st}$	0.21 ± 0.06	0.20 ± 0.05	0.19 ± 0.05	0.14 ± 0.07
$(F_p - F_o)/F_v$	0.45 ± 0.03	0.69 ± 0.04	0.55 ± 0.08	0.71 ± 0.07

F_o – the initial value of fluorescence induction after irradiation is turned on; F_m – the maximum value of fluorescence induction; F_v – variable chlorophyll fluorescence; F_{st} – the stationary value of fluorescence induction after light adaptation of a plant leaf; F_p – the value of 'plateau' fluorescence induction; F_v/F_o – the efficiency of the water-splitting complex on the donor side of PSII; F_v/F_m – the maximum efficiency of the primary processes of photosynthesis; $(F_m - F_{st})/F_{st}$ – the photochemical efficiency coefficient; $(F_p - F_o)/F_v$ – the share of QA acceptors of non-renewable PSII reaction centres

crease in the F_m value by 42.3–45.5% was detected in the pigment complex structure of powdery mildew-affected *A. platanoides* leaves, regardless of germination conditions. It should be explained by the blocking of chlorophyll resynthesis, degradation, destruction of the structure of chloroplasts, and a decrease in their number under the influence of *S. bicornis*.

The value of variable chlorophyll fluorescence in experimental plants at both locations was within the wide range of 850–2 900 conventional units. The minimum value (850.0 ± 241.7 conventional units) was recorded in powdery mildew-affected Norway maple leaves sampled from Location 1. At the same time, the highest value of F_v (2 090.3 ± 199.1 conventional units) was recorded in unaffected maple leaves from Location 2. Since variable fluorescence F_v is determined by the redox status of QA, its level serves as an indicator of photochemical redox reactions (Liang et al. 2020). When electron transport from QA to subsequent components of the electron transport chain (ETC) is blocked or the light intensity is higher than the maximum level, saturation F_v quickly reaches possible values. Therefore, any factors affecting the process of electron transport in the thylakoid ETC will also affect F_v values. This fact allows using the parameter F_v as a physiological indicator reflecting the influences of *S. bicornis* on *A. platanoides* plants.

The quantum yield of PSII is estimated by the F_v/F_m ratio. The value of F_v/F_m at the level of 0.81–0.83 is assumed to be typical for a fully functioning PSII under optimal conditions for vegetation, and the indicator F_v/F_m decreased under stress (Matlok et al. 2020). In *A. platanoides* under the influence of *S. bicornis*, the indicators F_v/F_m were below the optimal level, indicating a decrease in PSII efficiency in affected leaves. Lowering the F_v/F_m values indicates a gradual reduction in the PSII light-harvesting antenna due to the degradation of pigment-protein complexes in its composition (Zhu et al. 2021). Therefore, the relation F_v/F_m is an effective means of monitoring plant stressors, as it is sensitive to inhibition of the light stage of photosynthesis.

Another index demonstrating PSII efficiency is F_v/F_o, the maximum quantum yield of a water-photolysis system. This parameter is a more sensitive detector of plant stress since it is normalised by measurements of minimum fluorescence (F_o), and not by maximum fluorescence (F_m) as in the ratio F_v/F_m. Decreasing the value F_m and increasing the value F_o led to significant changes in the F_v/F_o index. Whereas changing the parameter F_v/F_m was not so noticeable (Skórska, Murkowski 2018) under the influence of a parasitic fungus *S. bicornis* on *A. platanoides* plants sampled from Location 1 and Location 2, the parameter F_v/F_m decreased by 4.9–8.4% and parameter F_v/F_o as much

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as 35.3–36.7%, which confirms its sensitivity and detects the presence of stress.

Another index important in assessing the functional state of leaves is the efficiency coefficient of dark-dependent photochemical processes, $(F_m - F_{st})/F_{st}$. This parameter demonstrates the amount of fluorescence quenching, which is affected both by photochemical (CO_2 fixation) and by non-photochemical processes (thermal energy dissipation of the excited state of chlorophyll molecules). Index $(F_m - F_{st})/F_{st}$ closely correlates with the efficiency of the initial enzyme in the Calvin cycle, ribulose bisphosphate carboxylase, and characterises the plant adaptability to environmental conditions (Chen et al. 2019). In the studied *A. platanoides* plants, this parameter was varied within the range of 0.14–0.22: The lowest efficiency of photochemical processes was recorded in affected maple leaves sampled from Location 2; the value was 30% less compared to unaffected ones.

Based on the fact that indices F_m and F_{st} and the calculated index $(F_m - F_{st})/F_{st}$ determine the shape of the descending part of the Kautsky curve, it is definite that the activation and flow of reactions in the Calvin cycle and the passage of substances through leaf membranes and vessels were more effective in Norway maple plants unaffected by powdery mildew.

The indicator of the photosynthesis process flow, $(F_p - F_o)/F_v$ (which characterises the relative number of inactive reaction centres with respect to the total number of reaction centres) in the experimental plants was within the range of 0.45–0.71. The effect of powdery mildew on Norway maple plants sampled from Location 1 led to an increase in the value $(F_p - F_o)/F_v$ by 22.2%. This parameter informs about the saturation rate of inactive reaction centres PSII responsible for water decomposition and oxygen release (Vasylenko et al. 2021). An increase in $(F_p - F_o)/F_v$ indices indicates a violation of both energy migration and electron transport, and a decrease indicates a possible acceleration of electron transport processes.

ANOVA made it possible to explain 10–82% of the variation in fluorescence indices by plant location and state (affected/unaffected); results of the analysis are represented in Table 2. These predictors were statistically significant for all fluorescence indices, except for F_v/F_m and $(F_m - F_{st})/F_{st}$ indices. The predictor for the interaction between location and plant state was statistically insignificant. This indicated that the effect of plant infection on photosynthetic physiology was not site-specific.

The F_v/F_o index was the most sensitive to the effect of a plant infection, and the role of the site in the variation of this trait was statistically insignificant (Figure 2). Also, such indices as F_m, F_v, F_{st}, F_o, F_p, and $(F_p - F_o)/F_v$ were sensitive to the influence of site-specific conditions.

Table 2. ANOVA of the effect of plant location and state on the variation of fluorescence parameters

Trait	Source of variation			Test of the whole model		
	location	state	location × state	R^2_{adj}	*F*-ratio	*P*-level
F_o	$F = 21.14$; $P < 0.001$	$F = 15.37$; $P < 0.001$	$F = 0.65$; $P = 0.430$	0.55	12.40	< 0.001
F_m	$F = 19.93$; $P < 0.001$	$F = 105.27$; $P < 0.001$	$F = 2.99$; $P = 0.100$	0.82	42.40	< 0.001
F_v	$F = 13.63$; $P < 0.001$	$F = 78.64$; $P < 0.001$	$F = 1.21$; $P = 0.280$	0.77	31.20	< 0.001
F_{st}	$F = 19.86$; $P < 0.001$	$F = 74.26$; $P < 0.001$	$F = 1.42$; $P = 0.240$	0.78	31.80	< 0.001
F_p	$F = 56.10$; $P < 0.001$	$F = 44.23$; $P < 0.001$	$F = 7.48$; $P < 0.001$	0.80	35.90	< 0.001
F_v/F_o	$F = 0.13$; $P = 0.720$	$F = 66.32$; $P < 0.001$	$F = 0.01$; $P = 0.900$	0.70	22.20	< 0.001
F_v/F_m	$F = 0.26$; $P = 0.610$	$F = 8.60$; $P < 0.001$	$F = 0.91$; $P = 0.350$	0.20	3.30	= 0.034
$(F_m - F_{st})/F_{st}$	$F = 2.05$; $P = 0.160$	$F = 2.76$; $P = 0.110$	$F = 1.21$; $P = 0.280$	0.10	2.00	= 0.140
$(F_p - F_o)/F_v$	$F = 90.71$; $P < 0.001$	$F = 8.65$; $P < 0.001$	$F = 3.63$; $P = 0.070$	0.79	34.30	< 0.001

F_o – the initial value of fluorescence induction after irradiation is turned on; F_m – the maximum value of fluorescence induction; F_v – variable chlorophyll fluorescence; F_{st} – the stationary value of fluorescence induction after light adaptation of a plant leaf; F_p – the value of 'plateau' fluorescence induction; F_v/F_o – the efficiency of the water-splitting complex on the donor side of PSII; F_v/F_m – the maximum efficiency of the primary processes of photosynthesis; $(F_m - F_{st})/F_{st}$ – the photochemical efficiency coefficient; $(F_p - F_o)/F_v$ – the share of QA acceptors of non-renewable PSII reaction centres

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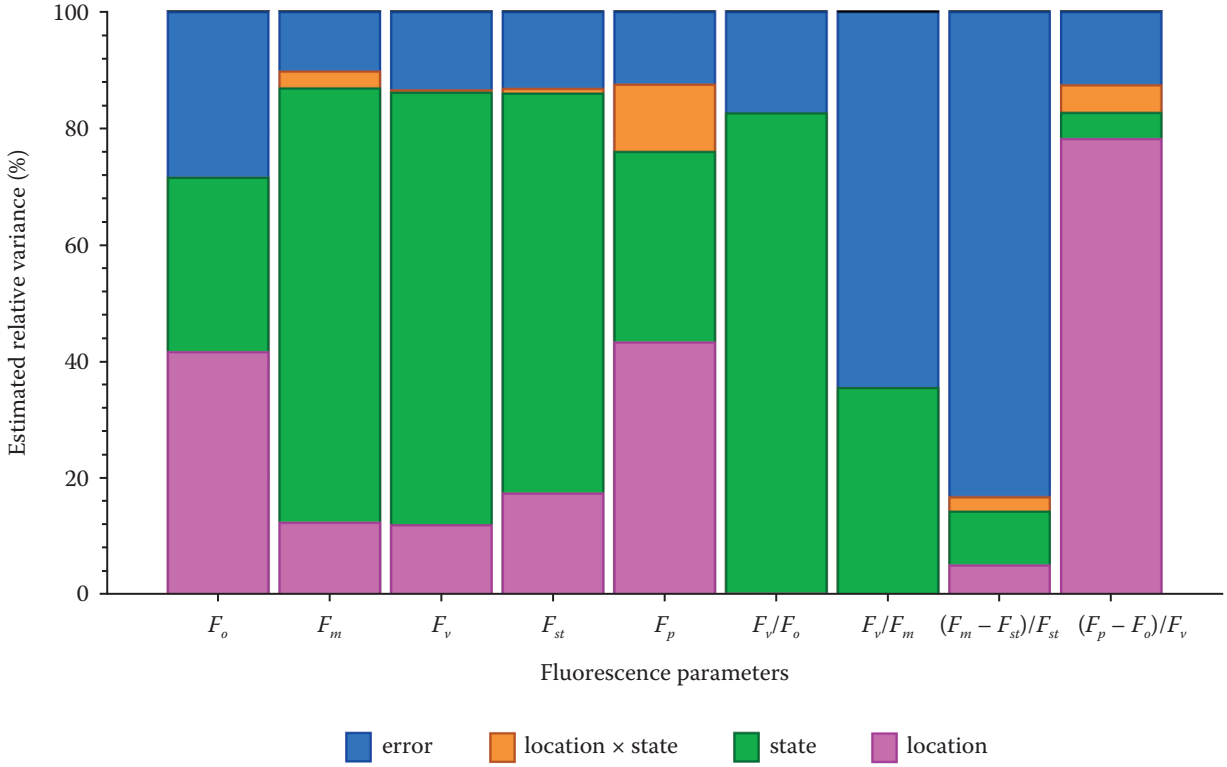

Figure 2. Relative variance components (in %) of the variation of fluorescence parameters according to the ANOVA method

F_o – the initial value of fluorescence induction after irradiation is turned on; F_m – the maximum value of fluorescence induction; F_v – variable chlorophyll fluorescence; F_{st} – the stationary value of fluorescence induction after light adaptation of a plant leaf; F_p – the value of 'plateau' fluorescence induction; F_v/F_o – the efficiency of the water-splitting complex on the donor side of PSII; F_v/F_m – the maximum efficiency of the primary processes of photosynthesis; $(F_m - F_{st})/F_{st}$ – the photochemical efficiency coefficient; $(F_p - F_o)/F_v$ – the share of QA acceptors of non-renewable PSII reaction centres

CONCLUSION

Analysis of the data obtained indicates a high sensitivity of chlorophyll fluorescence induction indices to the damage by diseases regardless of environmental conditions of local growth of *A. platanoides* seedlings. The high informativeness of induction changes in chlorophyll fluorescence was revealed for the structural organisation of chloroplasts in Norway maple leaves determined by the indices F_o, F_m, F_v, F_v/F_o, F_v/F_m, $(F_m - F_{st})/F_{st}$, $(F_p - F_o)/F_v$. Higher sensitivity of the index F_v/F_o to the impact of *S. bicornis* was detected compared to the index F_v/F_m, which should encourage the researchers to use it more frequently in assessing the impact of diseases on photosynthesis efficiency. In the leaves of Norway maple seedlings affected with the fungus by more than 50%, changes in the chlorophyll fluorescence induction were found quite different in intensity and direction compared to that in unaffected leaves. In addition, it turned out that all the studied parameters of the rapid kinetics of chlorophyll fluorescence were influenced significantly by the powdery mildew exposure. This indicates that all observed parameters can be used as indicators of the severe stress state in *A. platanoides* seedlings. However, there is a further need to conduct overtime studies throughout the growing season to determine the effectiveness of using these parameters to detect mild stress in the early stages of the fungal infection.

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