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Chlorophyll *a* fluorescence of perennial ryegrass (*Lolium perenne* L.) varieties under long term exposure to shade

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Abstract

The perennial ryegrass is the species widely used in Europe as forage as well as for creating lawns in urban areas. Unfavourable light conditions in cities are the principal reason of improper growth and functioning of grass communities. The aim of our work was to answer the following questions: what is the adaptive ability of photosynthetic apparatus of perennial ryegrass varieties to long-term reduction of solar radiation and which of the tested varieties has the best properties to be used for grassland establishment under reduced light conditions. A two-factor experiment was conducted with three varieties and three shading variants. Measurements of chlorophyll *a* fluorescence were provided, and the basic assessed parameters were: minimal fluorescence (F_0), maximal fluorescence (F_m), variable fluorescence (F_v) and maximal photosynthetic efficiency of photosystem II (F_v/F_m). Gas exchange was also measured. We explored the differences between the selected varieties in terms of their photosynthetic apparatus adaptation to light conditions. During May, all varieties were characterized by increase in minimal and maximal fluorescence levels under reduced light. The most significant changes were noticed for variety 'Taya'. During following months, a trend of decline in photosynthetic efficiency was observed for this variety. For this variety the most significant changes of CO_2 were also noted. The stomatal conductance was not affected by shading. On the basis of our results, we have assumed that each variety is unique in terms of threshold values and demand for light.

Key words: chlorophyll *a*, grasses, green infrastructure, lawns, light, *Lolium perenne*, photosynthesis, unfavourable light conditions.

Introduction

The perennial ryegrass (*Lolium perenne* L.) is one of the most popular grass species in Europe. It is widely used as a forage crop and as alternative and renewable bioenergy source (Jonavičienė et al., 2014). The lawn varieties of perennial ryegrass are commonly used for establishing of lawns in urban areas (Dąbrowski et al., 2013).

The urban green areas have multiple functions. Well-kept lawns enhance the aesthetic value of the entire city and they are involved in phytoremediation, which leads to improvement in the quality of air and soil (Wołejko et al., 2014). It was the reason of increasing, in recent decades, the demand for amenity grasses for ornamental lawns, grasslands, green areas in parks and for sports turf. Plant growth is hindered by various abiotic stresses – water deficit, light, heat and salt. The light conditions in urban areas are substantially modified by technical structures and trees, which leads to deterioration of the grass communities. Under such conditions, the amount of solar energy is reduced, and the wavelength spectrum is modified (Bell et al., 2000). In sporting arenas the shade is a significant factor correlated with the loss of grass cover to the turf and with algal invasion (van Huylenbroeck et al., 1999). In the parks and ornamental lawns, shade is most frequently combined with drought stress as a result of competition with trees and shrubs. The first physiological symptoms of negative impact of shade are reduction of the rate of photosynthesis and accumulation of pigments (van Huylenbroeck et al., 1999). The first morphological signs are leaf elongation and decreasing in leaf coverage. The results obtained by Gautier et al. (1998) suggest that the reduction of photon flux intensity had the significant impact on tillering of perennial ryegrass. Subsequently of photon flux intensity on grasses is the sodding reduction (Lewis, 2004). However, the effect of long-term reduction in the level of solar radiation, especially on functioning of the photosynthetic apparatus of lawn grasses in urban green areas, is still poorly recognized.

Photosynthetically active radiation (PAR) energy absorption by photosynthetic pigment molecules occurs in the antenna complexes located in the thylakoid membranes (Kalaji et al., 2012). The absorbed energy is then transferred as excitation energy to photosystem I (PSI) and photosystem II (PSII) reaction centre, where it is used to initiate photochemical reactions. A part of this energy is lost as heat and chlorophyll *a* fluorescence. The chlorophyll *a* fluorescence process can provide information on the functioning and structure of the photosynthetic apparatus (Kalaji, Łoboda, 2007; Akhkha et al., 2013; Stirbet et al., 2014; Živčák et al., 2014 a). Moreover, methods based on records of chlorophyll fluorescence are reliable, non-invasive, powerful and simple tools for assessment of photosynthetic electron transport (Živčák et al., 2014 b) and related photosynthetic processes and allow for detection of stress in plants (Baker, Rosenqvist, 2004; Borawska-Jarmułowicz et al., 2014). At the present time there is no research on the state of the photosynthetic apparatus in perennial ryegrass in terms of long term shading. The current research has focused on agricultural plants, such as lettuce (Fu et al., 2012), subterranean clover (Mauro et al., 2011), or wheat (Mitchell et al., 2006; Mu et al., 2010; Akhkha et al., 2013). Studies on the lawn varieties of perennial ryegrass were related only to drought and temperature stress (Borawska-Jarmułowicz et al., 2014), but there were no studies on the influence of unfavourable light conditions on perennial ryegrass lawn varieties. There was no attempt to select lawn varieties from this species, which could be used in unfavourable lighting conditions. The results obtained by Studer et al. (2008) showed that there was wide diversity within variety of perennial ryegrass in terms of response to habitat conditions.

Our work was conducted to answer the following question: what is the adaptive ability of the photosynthetic apparatus in the chosen varieties of perennial ryegrass to long-term reduction of solar radiation and which of the tested varieties have the best properties to be used for grassland establishment under unfavourable light conditions. The result will contribute to the development of grasslands in cities under diverse light intensity.

Material and methods

The experiment lasted from April 20, 2010 to September 24, 2012 and it was conducted at the vegetation hall at Warsaw Agricultural University (52°259′ N, 21°020′ E), in a two-factor split-plot system. Each treatment was replicated three times in special boxes (213 × 107 × 15 cm) with a permeable bottom. Boxes were divided into 9 plots (71 × 35 cm and an area of 0.25 m^2). Two research factors were applied. The level of shade was the first one, expressed by quantity of solar irradiance (W m^{-2}): absence of shade – sun (control), half shade and shade. The second factor was the lawn variety of perennial ryegrass (*Lolium perenne* L.). The study involved three varieties: ‘Nira’ (HBP Sp. zo.o., Poland), ‘Henrietta’ (Feldsaaten Freudenberger GmbH & Co Kg, Germany) and ‘Taya’ (DLF-Trifolium Group, Denmark).

The level of shading was simulated by layers of agrotextiles, which were constantly spread on a wooden frame above the plants (at the height of 50 cm). Solar irradiance was measured by a meter TM-206 (Tenmars, Taiwan). Measurements were performed once a month during the entire vegetation period in 2012, and once per hour between 7.00 and 17.00. Measurements of the light spectrum were also carried out using a spectrophotometer SpectraPen SP 100 (Photon Systems Instruments, Czech Republic) in August. The results were presented in Figure 1.

Ground moisture and ground temperature were monitoring permanently, measurements were performed every hour around the clock by using a TDR (time domain reflectometry) technique. Device MIDL (multi interface data logger) was used with field probes model FP/mts. The results were presented in Figure 2.

The sward was mowed regularly during the study period: 6–8 times during the vegetation period at the height of 4–5 cm, multi-components fertilizer Substral 100 was used at a dose of 30 g m^{-2}, twice during the vegetation period (132 kg ha^{-1} N, 30 kg ha^{-1} P_2O_5 and 66 kg ha^{-1} K_2O), irrigated in the case of lack of precipitation with 3 mm m^{-2} dose per day.

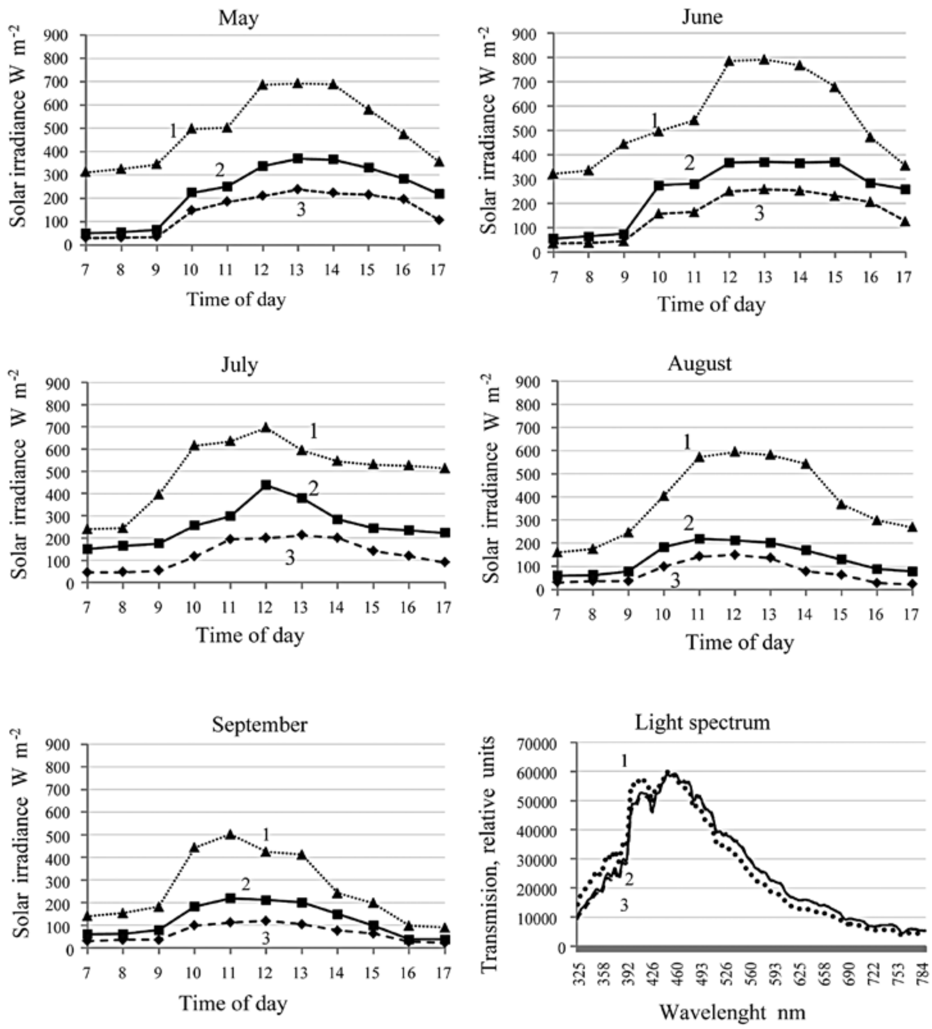
A fluorimeter OS5p (Optisciences, Great Britain) was used to estimate the efficiency of the photosynthetic apparatus. The leaves were adapted in the darkness for 25 minutes. The intensity of the light pulse was 3500 µmol m^2 s^{-1}, and the wavelength was 650 nm. Chlorophyll *a* fluorescence was measured in the middle part of the flag leaf. The measured parameters were: minimal fluorescence (F_0), maximal fluorescence (F_m), variable fluorescence (F_v) and maximum photosynthetic efficiency of PSII (F_v/F_m). There were 9 replicates per treatment. Gas exchange measurements were carried out by LCpro+ (ACD Bioscentific Ltd., Great Britain) on the middle part of the attached flag leaf in 9 replicates. The chamber surface was 6.2 cm^2. CO_2 assimilation and stomatal conductance were the measured parameter.

Statistical analysis was performed by using software *STATISTICA*, version 10. Analysis of variance (ANOVA) was used to determine the significance of differences between the means, Fischer’s test was used as post-hoc test with level of significance α = 0.05. The Pearson procedure with level of significance α = 0.05 was applied to calculate the correlation coefficient.

Results

In the minimal fluorescence (F_0) parameter in perennial ryegrass variety ‘Nira’, differences were found only in the spring (May–June), but for varieties ‘Henrietta’ and ‘Taya’, growth in shade was greater also in the summer (Fig. 3). Variety ‘Taya’ was characterized by particularly large differences in F_0 parameter. The values were 30–70% higher in the shade than in the sun and 8–27% higher than in the half shade. Moreover, values were 12–23% higher in the half shade than in the sun.

The maximal fluorescence (F_m) parameter was dependent on light conditions from May to August (Fig. 4). There were no significant differences between F_m values measured in the sun and in the half-shade for ‘Nira’ and ‘Henrietta’. However, values measured for ‘Nira’ were significantly higher in the shade than in the half shade and in the sun (avg. 34%) in May and June, but they were lower than in the half shade and in the sun in July (avg. 14%). For ‘Henrietta’, F_m values were usually higher in the shade than in the sun. In May, these values were higher by 50%, in June – by 15%, and in August – by 22%. Response to the light conditions was even more visible in ‘Taya’ in comparison with ‘Henrietta’. F_m values were significantly higher in the shade and in the half shade than in the sun in May and August. In June and July F_m values were similar in the sun and in the half



Note. Solar irradiance measured in May, June, July, August and September, and light spectrum – in August.

Figure 1. Light conditions in sun (1), half shade (2) and shade (3) treatments

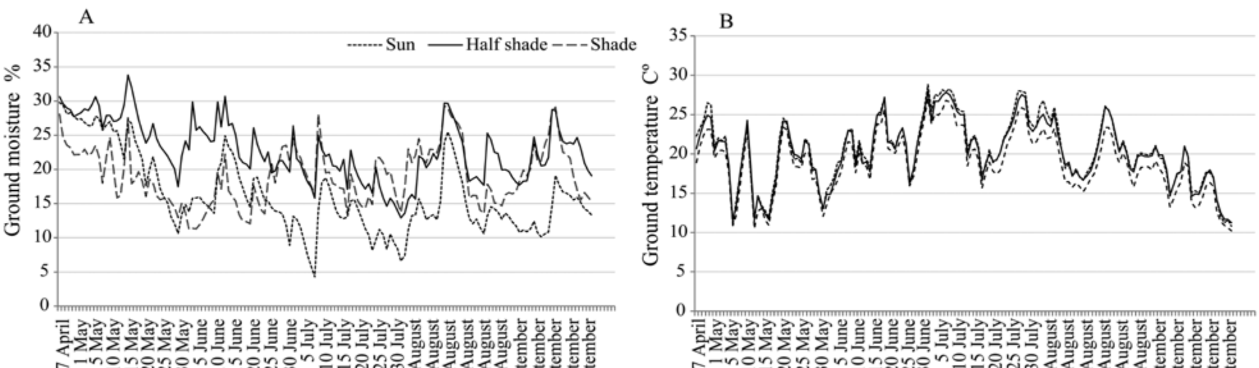
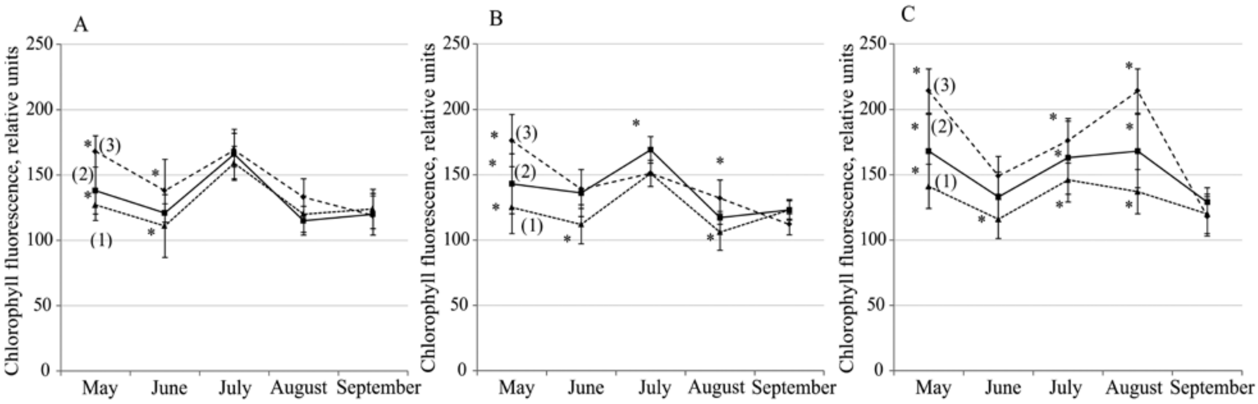


Figure 2. Ground moisture (A) and ground temperature (B) during experiment

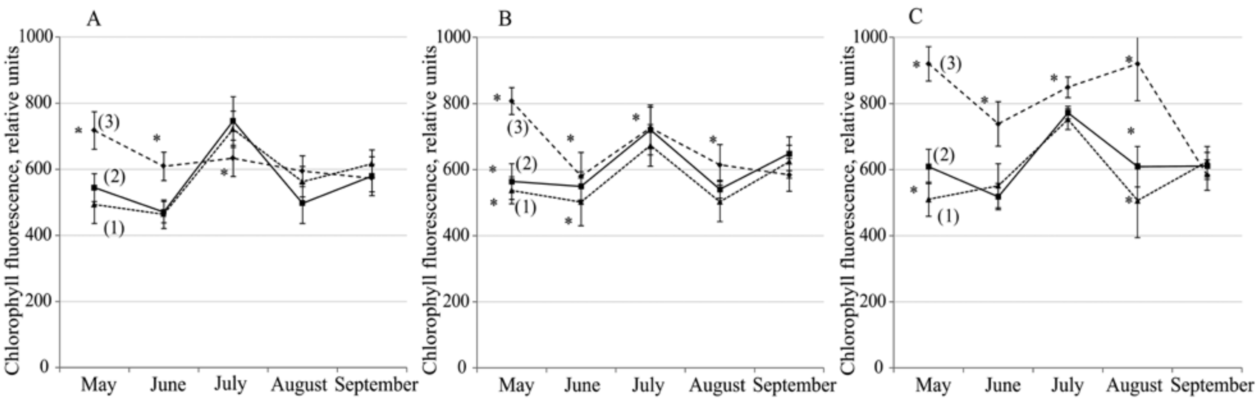
shade, but were higher in the shade (in June – by 38% and in July – by 11%).

Variable fluorescence (F_v). In May and June, the tested varieties were characterized by lower values of that parameter in the sun and in the half shade than in the shadow (avg. 30%) (Fig. 5). The reduced F_v values under greater solar radiation in spring may indicate a lower activity of PSII and dissipation of excitation energy, most likely due to the higher air temperature in these treatments. In the summer months, the response to light conditions was differentiated in particular varieties. In July a stress reaction in 'Nira' growing in the shade was observed, but in 'Taya' stress response occurred in the sun (F_v was significantly lower in the sun than in the



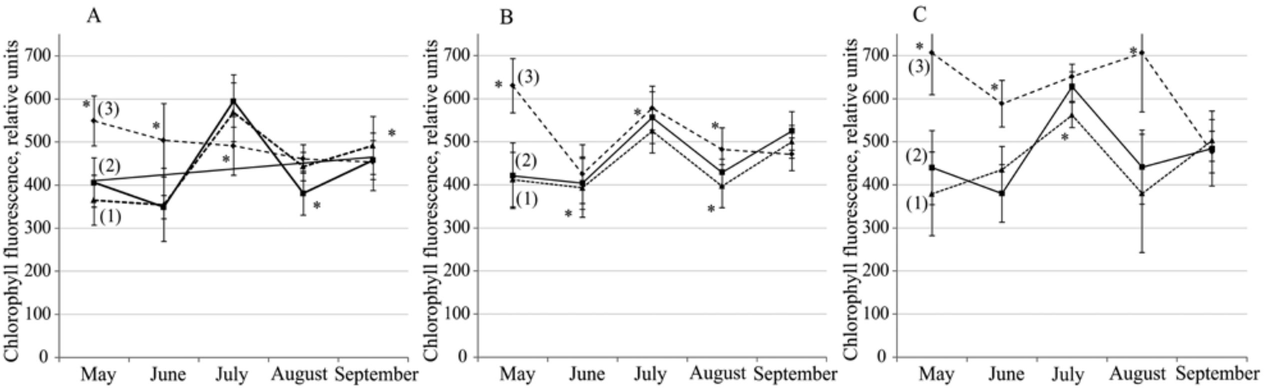
Note. The means marked by asterisks within one month and varieties differ significantly.

Figure 3. Minimal fluorescence (F_0) depending on light conditions: the sun (1), the half shade (2) and the shade (3) in varieties 'Nira' (A), 'Henrietta' (B) and 'Taya' (C) ± SD



Note. The means marked by asterisks within one month and varieties differ significantly.

Figure 4. Maximal fluorescence (F_m) depending on light conditions: the sun (1), the half shade (2) and the shade (3) in varieties 'Nira' (A), 'Henrietta' (B) and 'Taya' (C) ± SD

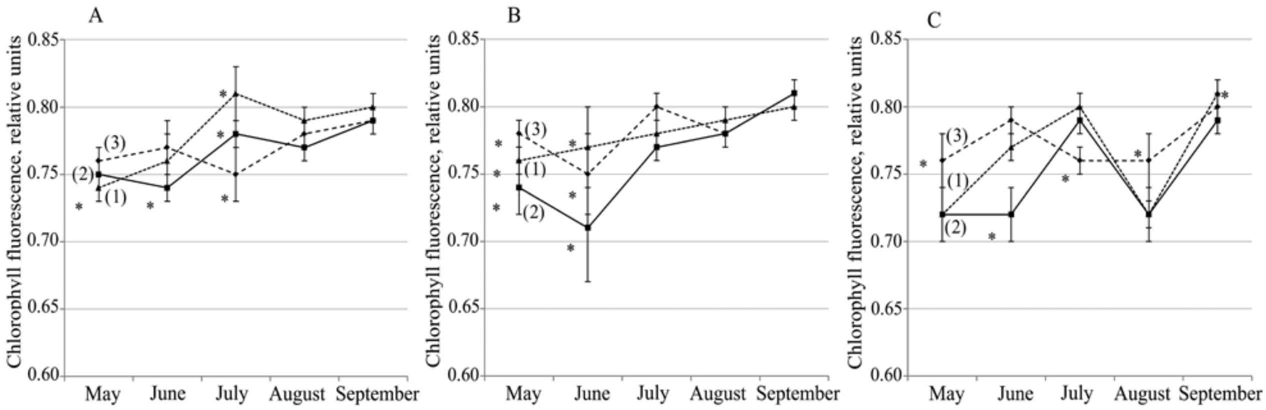


Note. The means marked by asterisks within one month and varieties differ significantly.

Figure 5. Variable fluorescence (F_v) depending on light conditions: the sun (1), the half shade (2) and the shade (3) in varieties 'Nira' (A), 'Henrietta' (B) and 'Taya' (C) ± SD

shade). Irradiance had no significant effect on the value of this parameter in the variety of 'Henrietta'. In August, the smallest F_v values in the sun were noticed in 'Henrietta', in 'Nira' – in the half shade, and in 'Taya' – in the sun and in the half shade. In September, all varieties were characterized by the lowest values in shade.

The value of ***maximal photosynthetic efficiency of photosystem II (F_v/F_m) parameter*** gradually increased along with progress of vegetation to reach the level of 0.80 in September (Fig. 6). In May, all varieties showed the highest photochemical efficiency of their photosynthetic apparatus in the shade. In June, the plants in the half shade were characterized by the lowest F_v/F_m values. In July and August F_v/F_m depends more on variety. For 'Nira' it was the highest in the sun, in 'Taya' in the sun in July, but in the shade in August. No influence of the light intensity

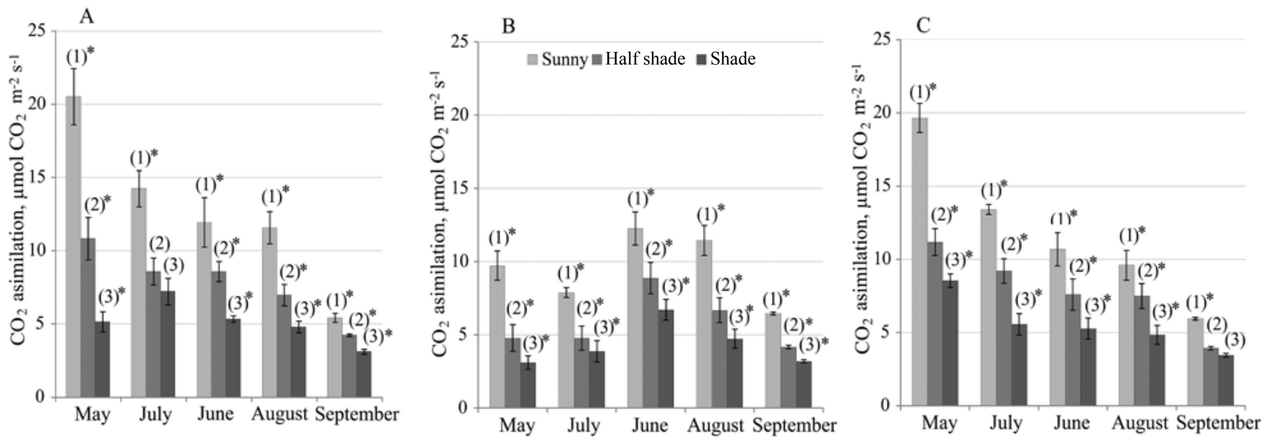


Note. The means marked by asterisks within one month and varieties differ significantly.

Figure 6. Maximal photosynthetic efficiency of PSII (F_v/F_m) depending on light conditions: the sun (1), the half shade (2) and the shade (3) in varieties 'Nira' (A), 'Henrietta' (B) and 'Taya' (C) ± SD

on F_v/F_m values in 'Henrietta' was found. In September, the light conditions had no significant influence on F_v/F_m, excluding 'Taya'.

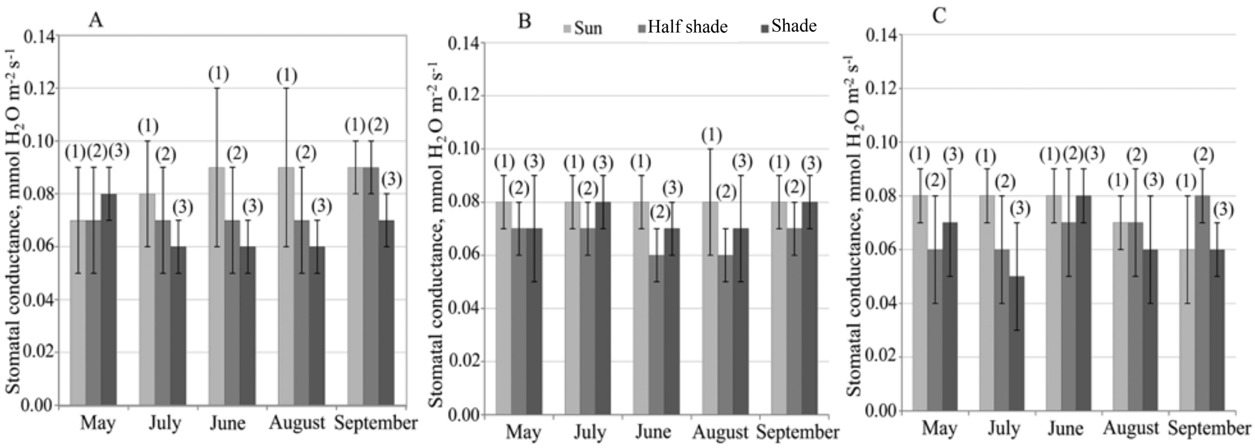
CO_2 assimilation and stomatal conductance. In May, for varieties 'Nira' and 'Taya' grown in the sun, assimilation was at level of 20 µmol CO_2 m^{-2} s^{-1} and decreased to 5 µmol CO_2 m^{-2} s^{-1} (Fig. 7). CO_2 assimilation was significantly lower in the half shade and in the shade than in the sun (by 46.3% in the half-shade and by 66.8% in the shade). The biggest difference between the sun and the shade was found in May, especially for 'Nira'. As opposed to 'Nira' and 'Taya', 'Hernietta' was characterized by lower CO_2 assimilation in the spring months. The quantity did not exceed 10 µmol CO_2 m^{-2} s^{-1} in the sun and 5 µmol CO_2 m^{-2} s^{-1} in the half shade and the shade. The quantities of CO_2 assimilation in other months were similar as in other varieties. Stomatal conductance values ranged from 0.06 to 0.08 mmol H_2O m^{-2} s^{-1} (Fig. 8). There were no differences between the values measured under different light conditions.



Note. The means marked by asterisks within one month and varieties differ significantly.

Figure 7. CO_2 net assimilation in differing light conditions: the sun (1), the half shade (2) and the shade (3) in varieties 'Nira' (A), 'Henrietta' (B) and 'Taya' (C) ± SD

The correlation coefficients between CO_2 assimilation and chlorophyll *a* fluorescence parameters are shown in Table. For 'Nira' in May, there was strongly negative correlation between CO_2 assimilation and all measured parameters. In June, the correlation coefficients were statistically significant between CO_2 assimilation and F_0, F_m and F_v parameters, but not for F_v/F_m (−0.24). In July, there was negative but not statistical significant correlation between CO_2 assimilation and F_0 parameter. For F_m and F_v the correlation was negative and statistically significant and for F_v/F_m was positive and significant. In August and September, the statistically significant correlation was between CO_2 assimilation and F_v/F_m parameters. For 'Henrietta' in May negative and significant differences were between CO_2 assimilation and F_0, F_m and F_v parameters. In June, negative and significant differences were between CO_2 assimilation and F_0 and F_m parameters, for F_v was not significant and for F_v/F_m was positive. The correlation coefficient was significantly positive for F_v/F_m parameter in July and in August as well. For the other parameters it was significantly negative in August. In September, the correlation coefficient was positive for all of parameters but significant only for F_v/F_m parameter. In 'Taya' in May, the correlation coefficient was significant negative between CO_2 assimilation and all of measured parameters. In June, the correlation



Note. The means marked by asterisks within one month and varieties differ significantly.

Figure 8. Stomatal conductance in differing light conditions: the sun (1), the half shade (2) and the shade (3) in 'Nira' (A), 'Henrietta' (B) and 'Taya' (C) ± SD

Table. Correlation coefficient between CO_2 assimilation and chlorophyll *a* fluorescence parameters in different months

Variety	Month	Chlorophyll *a* fluorescence parameters			
		F_0	F_m	F_v	F_v/F_m
'Nira'	May	−0.58*	−0.67*	−0.68*	−0.91*
	June	−0.39*	−0.55*	−0.41*	−0.24
	July	−0.29	−0.46*	0.45*	0.66*
	August	−0.29	−0.41	0.02	0.66*
	September	0.02	0.03	0.03	0.85*
'Henrietta'	May	−0.61*	−0.58*	−0.56*	−0.20
	June	−0.67*	−0.42*	−0.22	0.49*
	July	−0.10	−0.23	−0.26	0.89*
	August	−0.78*	−0.70*	−0.68*	0.83*
	September	0.38*	0.11	0.14	0.85*
'Taya'	May	−0.72*	−0.69*	−0.68*	−0.91*
	June	0.59*	−0.53*	−0.50*	−0.22
	July	−0.62*	−0.60*	−0.56*	0.95*
	August	−0.63*	−0.67*	−0.68*	−0.88*
	September	0.16	0.27	0.21	0.69*

Note. The coefficient values marked by asterisk are significant.

coefficient was significant positive between CO_2 assimilation and F_0, between CO_2 assimilation and F_m and F_v was negative. In July, the correlation coefficient was negative between CO_2 assimilation and F_0, F_m and F_v, but between CO_2 assimilation and F_v/F_m was positive. In August, the correlation coefficient was negative for all chlorophyll *a* fluorescence parameters and in September was positive for F_v/F_m.

Discussion

Sunlight is known to be one of the most powerful factors influencing plant growth and development. It determines not only the physiological, but also the morphological variations of the leaves. In this study, it was found that the significance of the impact of the shading level depended on both, the variety and the season. F_0 may be measured when all reaction centres are open and Q_A (plastoquinones located on D2 protein) is fully oxidized. The increase in the F_0 parameter is explained by loss of PSII reaction centres (Fu et al., 2012) and their inactivation (Cui et al., 2006). According to these authors, the value of this parameter is also correlated with chlorophyll content, which increases in the shade (Cavagnaro, Trione, 2007; Mauro et al., 2011). F_m may be detected when all centres are closed (Q_A fully reduced). This parameter showed a trend similar to F_0. Sarijeva et al. (2007) have proved a strong correlation of both parameters in plant leaves under different light treatment. Trend in changes of both parameters suggests the occurrence of photo-acclimation response of plants to shading, which has evolved to maximize light capture under unfavourable light conditions (Mauro et al., 2011; Reed et al., 2012). Variable fluorescence (F_v) is the difference between the value of fluorescence parameters F_m and F_0 and depending on maximum quantum efficiency of PSII. The low values of this parameter is evidence of low PSII activity and dissipation of excitation energy as heat. F_v/F_m is a reliable parameter to estimate the photochemical activity of PSII, and under stress-free conditions, it should be close to 0.83 (Kalaji et al., 2012). However, Mauro et al. (2011) reported a strong correlation between this parameter and the level of shading. Our results did not confirm this relationship.

Photoinhibition is probably the reason for lower values in the sun in May and June. The phenomenon of reduction of F_v/F_m parameter in the sun has been confirmed by Pollastrini et al. (2011). Higher CO_2 assimilation was observed in full sun by many authors (Mitchell et al., 2006; Sarijeva et al., 2007; Dai et al., 2009), but is also dependent on air temperature and wind. This is probably the reason for low values in September and fluctuation of correlation coefficient between CO_2 assimilation and F_v/F_m parameter. Mauro et al. (2011) suggest that decreasing of light intensity occurs at the expense of electron transport, photophorylation and carbon fixation components, resulting in the reduced ability of the leaf to assimilate CO_2. Li et al. (2014) have reported that under shading the decreased stomatal density, leaf thickness, cross-sectional area of the vascular bundle, contact area of the bundle sheath cells may be partially responsible for depressing photosynthetic capacity. The sun trapping leaves have a higher number of photosynthetic apparatus components providing the photosynthetic capability per unit of leaf area. The capacity of plants to adapt to shading was confirmed by (Miralles et al., 2011). Reed et al. (2012) have indicated that the entire photosynthetic apparatus in shade is more efficient at harvesting light, but it assimilates less CO_2 in comparison with the leaves in the sun. This may be the reason for the lack of correlation between assimilation and the F_v/F_m parameter (Table). Pollastrini et al. (2011) reported that stomatal conductance parameter was not affected by different light conditions, lack of this relationship and the fact that no such correlation exists have been confirmed by our results.

Conclusion

All varieties of perennial ryegrass showed the ability of photosynthetic apparatus to adapt to the long-term shading conditions. Varieties 'Nira' and 'Henrietta' displayed a comparable degree of adaptation to the shading, but 'Taya' showed higher adaptation ability, and this is variety recommended for establishment of lawns in shaded locations. Maximal photosynthetic efficiency of PSII (F_v/F_m) is not a sufficient parameter to determine adaptability of the plants to shade. The correlation coefficient between this parameter and CO_2 assimilation was changing during the whole season. At the beginning, the correlation was high positive, but it is necessary to analyze more parameters of the fluorescence induction curve, in particular, minimal (F_0), maximal (F_m) and variable (F_v) fluorescence.

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Daugiametės svidrės (*Lolium perenne* L.) veislių chlorofilo *a* fluorescencija ilgalaikio užpavėsinimo sąlygomis

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Santrauka

Daugiametė svidrė yra svarbus Europos pašarinis augalas (dėl šviesos trūkumo miestų vejos prastai auga). Tyrimo tikslas – nustatyti, kurios iš tirtų veislių pakančiausios silpnam apšvietimui, kokios yra daugiametės svidrės fotosintetinio aparato galimybės prisitaikyti prie ilgalaikės sumažintos saulės spinduliuotės. Trijų veislių daugiametės svidrės augintos esant trims užpavėsinimo variantams (dviejų veiksnių bandymas). Augalai buvo vertinti pagal chlorofilo *a* minimalią (F_0), maksimalią (F_m) bei kintančią (F_v) fluorescenciją ir II fotosistemos maksimalų fotosintetinį efektyvumą (F_v/F_m) bei dujų mainus. Gegužės mėnesį dėl sumažėjusio apšvietimo augaluose minimali ir maksimali fluorescencija padidėjo, ypač veislės ‘Taya’. Vėlesniais mėnesiais šios veislės svidrių fotosintetinis efektyvumas mažėjo. Patys didžiausi CO_2 pokyčiai taip pat buvo nustatyti šios veislės svidrių. Užpavėsinimas neturėjo įtakos žiotelių laidumui. Kiekviena tirta veislė pasižymėjo savitu šviesos stiprumo ir jo slenkstinių dydžių poreikiu.

Reikšminiai žodžiai: chlorofilas *a*, daugiametė svidrė, fotosintezė, nepalankios šviesos sąlygos, šviesa, vejos, žalioji infrastruktūra, žolės.