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EFFECT OF PHOSPHORUS DEFICIENCY ON GAS EXCHANGE PARAMETERS, LEAF GREENNESS (SPAD) AND YIELD OF PERENNIAL RYEGRASS (*LOLIUM PERENNE* L.) AND ORCHARD GRASS (*DACTYLIS GLOMERATA* L.)

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Abstract

Phosphorus is essential for the growth and development of plants. It also determines the quantity and quality of plant yields. Phosphorus actively participates in many vital processes and forms part of numerous substances indispensable for a normal course of certain biochemical changes. Unfortunately, phosphorus deficiency is quite common in grasslands. As a result, the content of phosphorus in soil is insufficient to meet nutritional requirements of forage crops and, consequently, the concentration of this element in green forage is insufficient to meet nutritional requirements of ruminants. The aim of the present study was to determine the effect of phosphorus deficiency in soil on the rate of photosynthesis and transpiration, water use efficiency, leaf greenness and the yield of some cultivars of perennial ryegrass (*Lolium perenne* L.) and orchard grass (*Dactylis glomerata* L.). A greenhouse experiment was conducted to assess the rate of photosynthesis and transpiration, water use efficiency (WUE), leaf greenness (SPAD – Soil-Plant Analysis Development) and the yield of perennial ryegrass (*Lolium perenne* L.) and orchard grass (*Dactylis glomerata* L.) grown under conditions of phosphorus deficiency in soil. The rate of photosynthesis and transpiration was measured using a Li-Cor 6400 gas analyzer (Portable Photosynthesis System), and leaf greenness was estimated with a Minolta SPAD-502 chlorophyll meter. Dry matter yield was determined by drying green matter to constant weight at 105°C. The results of the study indicate that phosphorus deficiency significantly decreased the rate of photosynthesis, water use efficiency and the yield of

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perennial ryegrass and orchard grass. At the same time, it increased the rate of transpiration and leaf greenness values. Among the tested cultivars, orchard grass cv. Areda was found to be the most resistant to phosphorus deficiency in soil, which was confirmed by the slightest reduction in the examined parameters.

Key words: photosynthesis, leaf greenness (SPAD), orchard grass, phosphorus deficiency, transpiration, yield, water use efficiency (WUE), perennial ryegrass.

WPŁYW NIEDOBORU FOSFORU NA WSKAŹNIKI WYMIANY GAZOWEJ, INDEKS ZIELONOŚCI LIŚCI (SPAD) ORAZ PLONOWANIE ŻYCICY TRWAŁEJ (*LOLIUM PERENNE* L.) I KUPKÓWKI POSPOLITEJ (*DACTYLIS GLOMERATA* L.)

Abstrakt

Fosfor jest pierwiastkiem niezbędnym do prawidłowego funkcjonowania każdej rośliny i decyduje o ilości oraz jakości uzyskanego plonu. Bierze on udział w przebiegu podstawowych procesów życiowych, wchodzi w skład wielu substancji, ważnych z punktu widzenia przemian biochemicznych. W paszach uzyskiwanych na użytkach zielonych może występować niewystarczająca zawartość fosforu w kryteriach prawidłowego żywienia roślin i żywienia przeżuwaczy. Celem pracy jest ocena wpływu niedoboru fosforu w glebie na intensywność fotosyntezy i transpiracji, współczynnik wykorzystania wody, indeks zieloności liści oraz plonowanie wybranych odmian życicy trwałej (*Lolium perenne* L.) i kupkówki pospolitej (*Dactylis glomerata* L.). W doświadczeniu szklarniowym badano intensywność fotosyntezy, transpiracji, współczynnik wykorzystania wody (WUE– Water Use Efficiency), indeks zieloności liści SPAD (Soil Plant Analysis Development) oraz plonowanie życicy trwałej (*Lolium perenne* L.) i kupkówki pospolitej (*Dactylis glomerata* L.) uprawianych w warunkach niedoboru fosforu w podłożu. Intensywność fotosyntezy i transpiracji mierzono przenośnym analizatorem gazowym LI-COR 6400, a indeks zieloności liści optycznym chlorofilometrem Minolta SPAD-502. Plon suchej masy określono przez wysuszenie zielonej masy w temp. 105°C, do stałej wagi. Wykazano, że niedobór fosforu istotnie ograniczał intensywność fotosyntezy, współczynnik wykorzystania wody oraz plonowanie badanych odmian, natomiast zwiększał intensywność transpiracji i indeks zieloności liści. Spośród badanych odmian najbardziej odporną na niedobór fosforu w glebie okazała się odmiana Areda kupkówki pospolitej, która w najmniejszym stopniu ograniczała badane cechy.

Słowa kluczowe: fotosynteza, indeks SPAD, kupkówka pospolita, niedobór fosforu, transpiracja, plonowanie, WUE, życica trwała.

INTRODUCTION

Phosphorus is essential for the growth and development of plants. It also determines the quantity and quality of yield. Phosphorus actively participates in many vital processes and forms part of numerous substances indispensable for a normal course of certain biochemical changes. It can be found in compounds responsible for energy storage and flow in plant cells (ATP, NADPH). Phosphorus is also present in nucleic acids (DNA and RNA) so it takes part in the processes of genetic information transfer. It plays an important role in enzyme activation, thus participating in photosynthesis and synthesis of proteins and fats (GAJ, GRZEBISZ

2003). Phosphorus deficiency is quite common in grasslands. As a result, the phosphorus content of soil is insufficient to meet nutritional requirements of forage crops. Consequently, the concentration of this element in green forage is too low to meet nutritional requirements of ruminants (CZUBA 1998, GRZEGORCZYK et al. 2001, TRĄBA and WOLAŃSKI 2001). According to FALKOWSKI et al. (1990), the optimum phosphorus content of dry matter in grassland vegetation should be 0.3%. However, this level is often difficult to reach. Long-term investigations carried out by NICZYPORUK, JANKOWSKA-HUFLEJT (2001) indicate that adequate concentrations of phosphorus in green fodder may be maintained provided that equal doses of this element are supplied to soil over longer periods of time. Phosphorus contributes to changes in the botanical composition of sward, promoting dicotyledonous plants, which usually contain more phosphorus than grasses. Another way to increase the concentration of mineral components, including phosphorus, is growing legume-grass mixtures (KRYSZAK 2001) and legume-grass mixtures with herbs (BENEDYCKI et al. 2001).

The aim of the present study was to determine the effect of phosphorus deficiency in soil on the rate of photosynthesis and transpiration, water use efficiency, leaf greenness and the yield of some cultivars of perennial ryegrass and orchard grass.

MATERIALS AND METHODS

The experiment was conducted in a greenhouse of the University of Warmia and Mazury in Olsztyn. Kick-Brauckmann pots were filled with 10 kg of soil formed from loose sand, characterized by a low content of phosphorus (31 mg$\cdot$kg^{-1}), potassium (42 mg kg^{-1}) and magnesium (13 mg kg^{-1}). The soil reaction was slightly acidic – pH_{KCl} 5.8. The experiment involved two cultivars of perennial ryegrass (*Lolium perenne* L.): tetraploid Maja and diploid Argona, and two cultivars of orchard grass (*Dactylis glomerata* L.): tetraploid Dala and diploid Areda. Control pots were fertilized with a nutrient solution containing 1.00 g N as $CO(NH_2)_2$, 0.25 g P as KH_2PO_4, 1.00 g K as K_2SO_4 and 0.50 g Mg as $MgSO_4 \cdot 7H_2O$. A micronutrient solution (30 mg/pot), composed of 2.65 mg Fe in EDTA, 0.09 mg $MnCl_2 \cdot 4H_2O$, 0.1 mg $ZnCl_2$, 0.03 mg $CuCl_2 \cdot 2H_2O$, 0.12 mg H_3BO_3 and 0.01 mg $(NH_4)_6Mo_7O_{24} \cdot 4H_2O$ per kg of soil, was also applied. The remaining pots were not fertilized. During the growing season leaf greenness was estimated with a Minolta SPAD-502 chlorophyll meter, while the rate of photosynthesis and transpiration was measured using a Li-Cor 6400 gas analyzer (Portable Photosynthesis System), at air temperature of around 25^{o}C, a constant CO_2 concentration of 400 ppm and illumination of 1000 μmol m^{-2} s^{-1}. Four measurements were performed for each cut. Means for the cuts are presented in the paper. Water use efficiency (WUE) was calculated based on instantaneous values of photosynthesis and transpiration. The aerial parts of plants were cut three times over the growing season. Dry matter yield was determined by drying green matter to constant weight at 105°C. The results were processed statistically with the use of STATISTICA software.

RESULTS AND DISCUSSION

The average rate of photosynthesis was comparable in all grass leaves, ranging from 6.45 to 7.00 µmol CO_2 $m^{-2}s^{-1}$ (Table 1). Cultivar Maja was characterized by the highest rate of photosynthesis. This process was widely differentiated in particular cuts. The lowest rate of photosynthesis was observed in the first cut, while the highest – in the second cut. Phosphorus deficiency in the soil significantly limited photosynthesis intensity in leaves of all the cultivars. Compared to the control, the rate of photosynthesis decreased by 24%. The strongest response to phosphorus deficit was recorded in the first cut, whereas in the successive cuts the differences in CO_2 assimilation between the control and experimental (phosphorus-deficient) treatments were smaller. This was most probably caused

Table 1

Intensity of photosynthesis (µmol CO_2 m^{-2} s^{-1})

Cultivars	Fertilization	1st cut	2nd cut	3rd cut	Mean
Areda	control object phosphorus deficiency	6.63 *b 4.58 a	8.15 cd 7.05 ab	6.65 c 5.68 ab	7.14 b 5.77 a
Dala	control object phosphorus deficiency	6.78 b 4.40 a	8.68 cd 6.80 a	6.45 bc 5.25 a	7.30 bc 5.48 a
Argona	control object phosphorus deficiency	7.48 b 4.55 a	9.25 d 7.00 a	6.75 c 5.40 a	7.83 bc 5.65 a
Maja	control object phosphorus deficiency	6.43 b 3.98 a	10.45 e 7.70 ab	7.10 c 6.38 bc	7.99 c 6.02 a
Mean for cultivars					
Areda Dala Argona Maja		5.60 ab 5.59 ab 6.01 b 5.20 a	7.60 a 7.74 a 8.13 a 9.08 b	6.16 a 5.85 a 6.08 a 6.74 b	6.45 a 6.39 a 6.74 ab 7.00 b
Mean for fertilization					
Control object Phosphorus deficiency		6.82 b 4.38 a	9.13 b 7.14 a	6.74 b 5.68 a	7.56 b 5.73 a

* homogeneous statistical groups

by changes in phosphorus content which occurred over the growing season, namely by a decrease in the concentration of this element observed during the growth and development of plants (FALKOWSKI et al. 1990). Among the tested cultivars, cv. Areda orchard grass was found to be the most resistant to phosphorus deficiency. The rate of photosynthesis decreased to the slightest degree in this cultivar, i.e. by 19% on average, compared to a 25–28% decline in the other cultivars. According to literature data, the effect of phosphorus on photosynthesis depends on plant species. OLSZEWSKI (2004) demonstrated that a reduction in phosphorus doses resulted in a significant photosynthesis intensity decrease in pea, and a slight increase in the rate of this process in faba bean. PSZCZÓŁKOWSKA et al. (2002) reported a decrease in the rate of photosynthesis in leaves of pea and yellow lupine under phosphorus deficit conditions. In a study conducted by FREDEEN et al. (1989), the rate of photosynthesis decreased by 55% due to phosphorus deficiency stress in soybean. DIETZ and FOYER (1986) postulated that the negative impact of phosphorus deficiency on photosynthesis in leaves may be reversible. In an experiment performed by these authors, CO_2 assimilation inhibited due to phosphorus deficit was restored to the normal rate following phosphorus supply to plants.

In the present study, phosphorus deficiency increased transpiration intensity by 52% on average (Table 2). The tested cultivars differed in their responses to phosphorus deficit. The weakest response was recorded in cv. Areda, while the strongest in cv. Dala – the rate of transpiration

Table 2

Intensity of transpiration (m mol H_2O m^{-2} s^{-1})

Cultivars	Fertilization	1st cut	2nd cut	3rd cut	Mean
Areda	control object phosphorus deficiency	1.10 a 1.48 a	0.98 a 1.37 bc	0.60 a 0.85 bc	0.89 a 1.23 b
Dala	control object phosphorus deficiency	1.40 a 2.43 c	1.05 ab 1.96 d	0.73 ab 1.07c	1.06 ab 1.82 d
Argona	control object phosphorus deficiency	1.30 a 2.00 bc	1.05 ab 1.65 cd	0.58 a 0.95 bc	0.98 a 1.53 c
Maja	control object phosphorus deficiency	1.58 ab 2.38 c	1.40 c 1.98 d	0.85 bc 1.08 c	1.27 b 1.81 d
Mean for cultivars					
Areda Dala Argona Maja		1.29 a 1.91 bc 1.65 b 1.98 c	1.18 a 1.51 bc 1.35 ab 1.69 c	0.73 a 0.90 ab 0.77 a 0.96 b	1.06 a 1.44 c 1.26 b 1.54 c
Mean for fertilization					
Control object Phosphorus deficiency		1.34 a 2.07 b	1.12 a 1.74 b	0.69 a 0.99 b	1.05 a 1.60 b

increased in these cultivars by 38% and 72% respectively. The tetraploid cultivars evaporated more water than the diploid ones. Particular cuts differed with respect to the rate of transpiration, which was the fastest in the first cut and the slowest in the third cut. An increase in transpiration intensity caused by insufficient phosphorus supply was also reported by PSZCZÓŁKOWSKA et al. (2002).

The values of photosynthesis and transpiration provide information about plant water relations, reflected in water use efficiency (WUE). In the current experiment, water use efficiency was higher in the diploid rather than in the tetraploid cultivars (Table 3). Phosphorus deficit considerably affected water use efficiency in the analyzed grass cultivars. In comparison with the control treatments, WUE decreased by 48% on average. The cultivars differed in their responses to phosphorus deficiency. The weakest response was recorded in cv. Areda, and the strongest in cv. Dala – water use efficiency decreased in these cultivars by approximately 42% and 55% respectively. Water use efficiency was at the lowest level in the first cut, then improving gradually.

Table 3

Water use efficiency (μmol CO_2 $m^{-2}s^{-1}$ · m mol H_2O m^{-2} s^{-1})

Cultivars	Fertilization	1st cut	2nd cut	3rd cut	Mean
Areda	control object phosphorus deficiency	6.07 e 3.10 b	8.42 b 5.15 a	11.21 de 6.78 bc	8.57 de 5.01 b
Dala	control object phosphorus deficiency	4.90 de 1.81 ab	8.39 b 3.47 a	9.09 de 4.91 a	7.46 cd 3.39 a
Argona	control object phosphorus deficiency	5.79 e 2.30 ab	8.88 b 4.27 a	11.86 e 5.77 ab	8.84 e 4.11 ab
Maja	control object phosphorus deficiency	4.16 cd 1.70 a	7.48 b 3.90 a	8.47 cd 5.95 bc	6.70 c 3.85 ab
Mean for cultivars					
Areda Dala Argona Maja		4.59 c 3.36 ab 4.04 bc 2.93 a	6.79 a 5.93 a 6.57 a 5.69 a	9.00 a 7.00 a 8.81 a 7.21 a	6.79 b 5.43 a 6.48 b 5.28 a
Mean for fertilization					
Control object Phosphorus deficiency		5.23 b 2.23 a	8.29 b 4.20 a	10.16 b 5.85 a	7.89 b 4.09 a

Phosphorus deficiency in the soil had a non-significant effect on leaf greenness values, which increased by 3.5% on average. The response of the tetraploid cultivars was stronger than that of the dipolid ones (Table 4). Perennial ryegrass cultivars contained significantly more chlorophyll in leaves than orchard grass cultivars. The highest chlorophyll concentration

Table 4

Leaf greenness index (SPAD)

Cultivars	Fertilization	1st cut	2nd cut	3rd cut	Mean
Areda	control object phosphorus deficiency	35.83 a 37.10 ab	36.83 a 38.53 b	39.60 a 40.53 ab	37.42 a 38.72 b
Dala	control object phosphorus deficiency	37.68 c 38.80 c	38.98 b 41.33 cd	40.48 ab 41.58 c	39.04 b 40.57 cd
Argona	control object phosphorus deficiency	38.75 c 40.35 d	41.10 c 42.15 cd	40.00 ab 41.10 bc	39.95 c 41.20 de
Maja	control object phosphorus deficiency	40.98 d 43.08 e	42.43 d 43.83 e	40.65 ab 41.68 c	41.35 d 42.86 e
Mean for cultivars					
Areda Dala Argona Maja		36.46 a 38.24 b 39.55 c 42.03 d	37.68 a 40.15 b 41.63 c 43.13 d	40.06 a 41.03 b 40.55 ab 41.16 b	38.07 a 39.80 b 40.58 c 42.10 d
Mean for fertilization					
Control object Phosphorus deficiency		38.31 a 39.83 b	39.83 a 41.46 b	40.18 a 41.22 b	39.44 a 40.84 b

was noted in cv. Maja (SPAD 42.1 on average). The highest chlorophyll content of leaves was recorded in the second cut of perennial ryegrass and in the third cut of orchard grass. An increase in leaf greenness values under phosphorus deficiency conditions is most probably part of a physiological reaction. Phosphorus-deficient plants produce dark-green leaves due to inhibited cell growth and a higher number of cells per unit area (GAJ, GRZEBISZ 2003). The present results are consistent with the findings of PENG et al. (1999), who demonstrated that at the early development stages of rice, SPAD readings were by 1 to 2 units higher in phosphorus-poor soils compared to phosphorus-fertilized fields; those differences were no longer noticeable at the beginning of panicle emergence.

Under optimum fertilization conditions, the yield of cv. Maja was significantly higher than the yields of the other investigated cultivars, which remained at a comparable level, showing no statistically significant differences (Table 5). Deficit in soil P caused a highly significant yield decline. Dry matter yield decreased in all cultivars, by 36.5% on average. Orchard grass cv. Areda exhibited the weakest response to phosphorus deficit – the dry matter yield of this cultivar decreased by 21%. In all the cultivars the strongest response to phosphorus deficiency was noticed in the first cut. In the successive cuts the differences between the control and non-fertilized treatments with regard to yielding were substantially smaller.

Table 5

Dry matter yield (g·pot^{-1})

Cultivars	Fertilization	1st cut	2nd cut	3rd cut	Mean
Areda	control object phosphorus deficiency	9.38 d 6.08 b	8.08 cd 6.93 c	5.48 bc 5.08 ab	22.93 d 18.08 c
Dala	control object phosphorus deficiency	9.43 d 4.15 a	7.03 cd 3.70 a	5.43 bc 4.68 a	21.88 d 12.53 a
Argona	control object phosphorus deficiency	8.38 c 3.60 a	7.43 cd 4.05 a	6.30 d 5.20 bc	22.10 d 12.85 a
Maja	control object phosphorus deficiency	9.35 d 3.48 a	8.13 d 5.28 b	7.13 e 5.98 cd	24.60 e 14.73 b
Mean for cultivars					
Areda Dala Argona Maja		7.73 c 6.79 b 5.99 a 6.41 ab	7.50 c 5.36 a 5.74 a 6.70 b	5.28 a 5.05 a 5.75 b 6.55 c	20.50 b 17.20 a 17.48 a 19.66 b
Mean for fertilization					
Control object Phosphorus deficiency		9.13 b 4.33 a	7.66 b 4.99 a	6.08 b 5.23 a	22.88 b 14.54 a

CONCLUSIONS

1. Phosphorus deficiency significantly decreased the rate of photosynthesis, water use efficiency and the yield of perennial ryegrass and orchard grass, while increasing the rate of transpiration and leaf greenness values.

2. Among the tested cultivars, orchard grass cv. Areda was found to be the most resistant to phosphorus deficiency in soil, which was confirmed by the slightest reduction in the examined parameters.

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