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Photosynthetic performance and mycorrhizal symbiosis of a coastal marsh plant, *Glaux maritima*, in conditions of fluctuating soil salinity

Ieva Druva-Lūsīte[1]*, Andis Karlsons[2], Anita Osvalde[2], Jevgenija Ņečajeva[1], Gederts Ievinsh[1]

[1]Department of Plant Physiology, Faculty of Biology, University of Latvia, Kronvalda Bulv. 4, Rīga LV-1586, Latvia
[2]Laboratory of Plant Mineral Nutrition, Institute of Biology, University of Latvia, Miera 3, Salaspils LV-2169, Latvia

*Corresponding author, E-mail: druva@lanet.lv

Abstract

The aim of the present study was to explore the effect of seasonal fluctuations of soil salinity on chlorophyll *a* fluorescence and mycorrhizal symbiosis of *Glaux maritima* L. plants in natural conditions. Two neighboring sites with different flooding regime and putatively different soil characteristics were chosen for the investigation. The two sites significantly differed in salinity and both macronutrient and micronutrient concentrations. The relatively more sea-affected site A had higher salinity and higher concentrations of most nutrients. Potential quantum yield of photosystem II (F_V/F_M) decreased to an extremely low level in plants at site A in July indicating photoinhibition of photosynthesis. In contrast, a relatively low increase of soil salinity did not affect F_V/F_M at site B. Decreased photosynthetic performance at site A in July was reflected also by a drastic decrease both in photosystem II activity as well as in the ratio of active reaction centres. *G. maritima* plants were characterized by a low level of intensity of mycorrhizal symbiosis throughout the vegetation season while the frequency of infection in general was higher. Both parameters showed significant changes during the season. Anatomy of root colonization showed distinct patterns at the two study sites with mostly intracellular hyphae forming hyphal coils in roots of *G. maritima* at site A in contrast to site B where predominantly external hyphae were found. Mycorrhizal symbiosis could be regarded as a significant part of the adaptive mechanisms of *G. maritima*.

Key words: chlorophyll fluorescence, *Glaux maritima*, mycorrhizal symbiosis, salinity, soil mineral content

Introduction

Understanding of adaptive characteristics of wild plants from heterogeneous environments is extremely important for both conservation of plant diversity as well as for selective improvement of agriculturally important traits of cultivated plants. Soil salinity is a major concern in many regions (Pitman, Läuchli 2002). In this respect wild plants from habitats with a high natural level of soil salinity could be used as models in studies of physiological adaptations to salinity (Redondo-Gomez et al. 2006; Brown, Pezeshki 2007; Ksouri et al. 2007).

Glaux maritima L. (Primulaceae) is a perennial herb distributed on saline coastal areas of the northern hemisphere. The main natural factor causing variation in the distribution of *G. maritima* plants in coastal areas is flooding frequency, which in turn affects salinity, nutrient level, and oxygen content of the soil (Jerling 1988). *G. maritima* is characterized as a weak competitor and an opportunist. While *G. maritima* is considered to represent halophytic species having typical characteristics of a salt excluder (Rozema et al. 1978; Rozema et al. 1981) no study so far relates increased soil salinity with particular cellular adaptive mechanisms of salt tolerance besides osmotic adaptation (Rozema 1975). Protection of photosynthetic machinery in conditions of fluctuating soil salinity has recently been described as an important adaptive response for plants from heterogeneous environments (Marcile et al. 2007). Photochemistry of photosynthesis, which can be easily assessed in field conditions by means of chlorophyll *a* fluorescence measurement, is a sensitive process reflecting suboptimal changes in environmental conditions (Maxwell, Johnson 2000.).

It is generally believed that mycorrhizal symbiosis enhances plant tolerance to salinity mostly by improving uptake of mineral nutrients (Juniper, Abbott 1993; Tsang, Maun 1999). Studies with plant species native to saline environments indeed show a relatively high level of mycorrhizal colonization of halophytic plants (Hildebrandt et al. 2000).

The aim of the present study was to understand if seasonal fluctuations in soil salinity in different sites can affect photosynthetic performance of *G. maritima* in natural conditions. Changes of the performance as reflected by nondestructive chlorophyll *a* fluorescence measurements were analyzed during a growth season. In parallel both quantitative and qualitative aspects of mycorrhizal symbiosis were determined.

Materials and methods

Study area and sampling

Study area was located in western part of Latvia, on the western coast of Riga Gulf near Mersrags, Latvia (N 57°20‘ E 23°08‘). Typical habitats are coastal meadow, coastal salt marsh and coastal lagoons. Two neighboring sites with different flooding regime and putatively different soil characteristics were chosen with a 200-m distance between them. The plant community was dominated by *Festuca rubra*, *Carex nigra*, *Juncus gerardii*, *Potentilla anserina*. Site A was more affected by flooding by sea water during the season in comparison to site B. Soil and plant analysis was performed once a month during the vegetation season. As plants at the beginning of vegetation season in the middle of May were extremely small, only soil samples were taken at that time.

Measurement of chlorophyll a *fluorescence*

For continuous chlorophyll *a* fluorescence measurement, a Handy PEA (Hansatech, UK) was used. Intact leaves were dark adapted for 30 min using leaf clips provided by the manufacturer. Five measurements of individual plants were made per experimental site. The data were analyzed by appropriate software (Hansatech, UK). The ratio F_V/F_M was calculated, where F_V is the difference between the maximum fluorescence and the minimum fluorescence level F_0. Chlorophyll *a* fluorescence parameter F_V/F_M measured after a dark adaptation period reflects the potential quantum yield of photosytem II (PSII) and thus is indicative of photoinhibition (Maxvell, Johnson 2000). F_V/F_0 charaterizing the

ratio of variable fluorescence per initial fluorescence was used as an indication of PSII activity.

Performance index (PI) is a combination of the three independent parameters summing the respective responses of PSII – total number of active reaction centers per absorption, yield of primary photochemistry and efficiency with which a trapped exciton can move an electron into the electron transport chain (Appenroth et al. 2001).

To characterize energy fluxes for reaction centres, the ratio between total chlorophyll and that of antenna complexes of reaction centres could be used. The ratio Chl RC/Chl antenna can be replaced by the ratio RC/ABS, where RC is the number of active PSII reaction centres, and ABS is the quantity of light absorbed (Clark et al. 2000).

Root sampling and assessment of arbuscular mycorrhizal colonization

Root samples with soil were excavated from individual plants. Roots of at least nine individuals per site were sampled. Collected root samples were placed in a polyethylene bag and stored at 4 °C until analysis. Roots were carefully rinsed with running tap water and cut into 1-cm-long fragments. Samples for mycorrhizal assessment were prepared according to a modified method of Hayman (1970). Roots were boiled for 1 h in 10 % KOH, then washed with tap water. Staining was performed in 0.05 % trypan blue for 5 min followed by washing with tap water. Samples were stored in lactoglycerol [mixture of lactic acid, glycerol, water 1:1:1 (v/v/v)]. Root pieces were mounted on glass slides and examined under a Nicon Eclipse E200 microscope. Photographs were taken by a digital camera. Mycorrhizal colonization (abundance of hyphae, vesicles and arbuscules) was estimated after Trouvelot et al. (1986) at 400 × magnification using 10 root segments of each plant. Intensity of mycorrhizal colonization in the root system (M%) and frequency of mycorrhiza in the root system (F%) were calculated with the computer program Mycocalc (Trouvelot et al. 1986). M% was calculated according to the formulae

$$M\% = (95 \times n_5 + 70 \times n_4 + 30 \times n_3 + 5 \times n_2 + n_1)/(\text{total nb}),$$

where n_5 = number of fragments with a degree of colonization rated as "5", n_4 = number of fragments with a degree of colonization rated as "4", etc.; nb = number of eyeshots. F% was calculated according to the formulae

$$F\% = (\text{nb of fragments with mycorrhiza/total nb}) \times 100.$$

In a particular study the number of eyeshots was 100.

Measurement of soil parameters and mineral nutrients

Soil samples were taken from the root zone near *G. maritima* plants (0 - 10 cm depth). For each sample five to eight subsamples were collected and thoroughly mixed to form one sample. Soil pH was measured in a 1 : 2.5 soil to 1M KCl volume ratio using a PB-20 pH meter (Sartorius). Soil electrical conductivity was determined in a 1 : 5 soil to deionized water volume ratio with a EC 215 conductometer (Hanna Instruments).

Soil samples were air-dried and sieved through a metal sieve (2-mm mesh size). Samples were extracted with 1M HCl in a 1:5 soil to extractant volume ratio. The levels of Ca, Mg, Fe, Cu, Zn, and Mn were measured by atomic absorption spectrophotometer AAnalyst 700 (Perkin Elmer) with an acetylene-air flame (Haswell 1991). The amount of N, P, Mo and B was assayed by colorimetry, concentration of S by turbidimetry. K and Na was measured by a flame photometer PFP7 (Jenwey) with an air-propane/butane flame. Chloride was determined by $AgNO_3$ titration (Patnaik 1997).

Table 1. General soil properties and concentrations of nutrients and Na and Cl (mg L^{-1}) at two sites with *Glaux maritima*. Data are means from 5 measurements throughout the season ± SE. *, significant differences between the sites ($P < 0.01$)

Parameters / nutrients	Site A	Site B
pH*	6.2 ± 0.1	6.5 ±0.1
Electrical conductivity (dS m^{-1})*	10.8 ± 1.1	4.2 ± 0.7
N*	40 ± 3.7	21.6 ± 3.3
P*	94.6 ± 2.4	134.2 ±12.9
K*	260 ± 10	120 ± 22
Ca*	2195 ± 91	965 ± 183
Mg*	1393 ± 53	538 ± 89
S*	293 ± 61	88 ± 19
Fe	503 ± 32	507 ± 114
Mn	21.4 ± 1.8	36.7 ± 15.3
Zn*	14.8 ± 0.9	2.9 ± 0.5
Cu*	2.7 ± 0.1	0.8 ± 0.1
Mo*	0.04 ± 0.00	0.03 ±0.0
B*	7.3 ± 1.3	2.5 ± 0.5
Na*	2310 ± 163	969 ± 139
Cl*	2838 ± 280	1132 ± 200

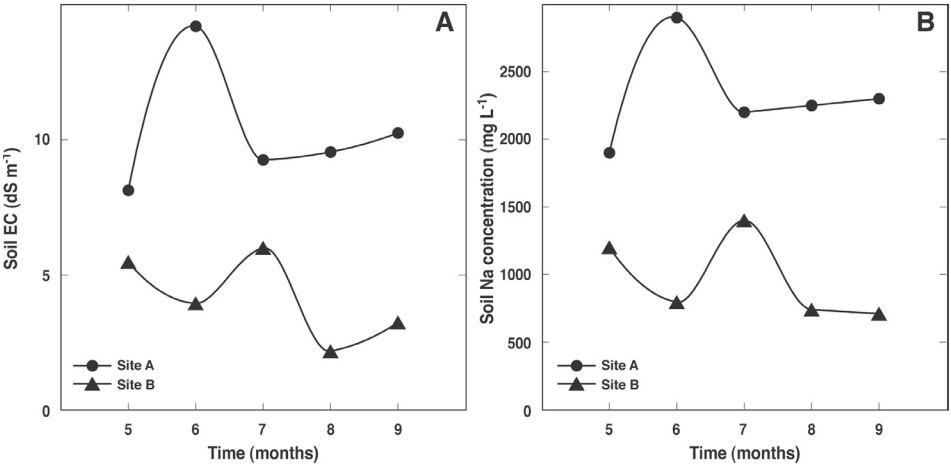

Fig. 1. Seasonal changes of soil electrical conductivity (A) and soil Na concentration (B) at two experimental sites with *Glaux maritima*.

Results

Differences in soil edaphic factors and fluctuations of salinity

The two study sites with *G. maritima* significantly differed in salinity and both macronutrient and micronutrient concentrations (Table 1). The relatively more sea-affected site A had higher salinity and higher concentrations of most nutrients except P, Fe and Mn. The

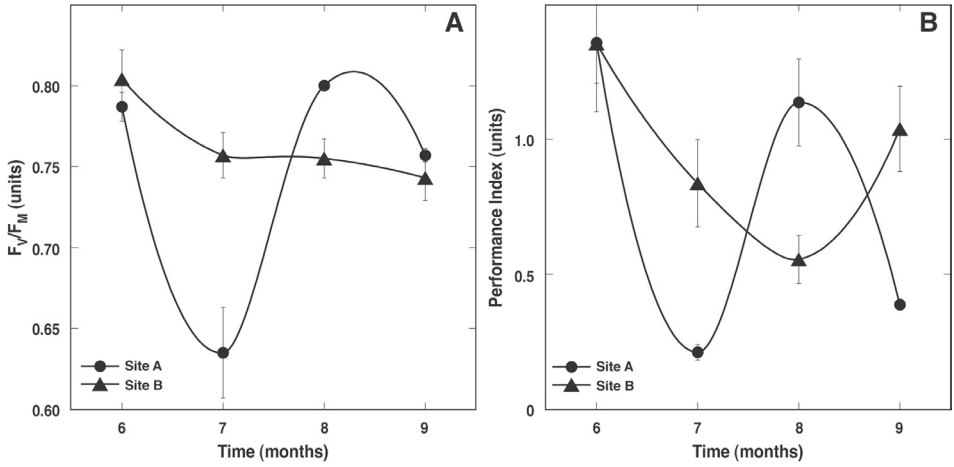

Fig. 2. Seasonal changes of potential quantum yield of photosystem II (F_V/F_M) (A) and performance index (PI) (B) of *Glaux maritima* plants at two experimental sites.

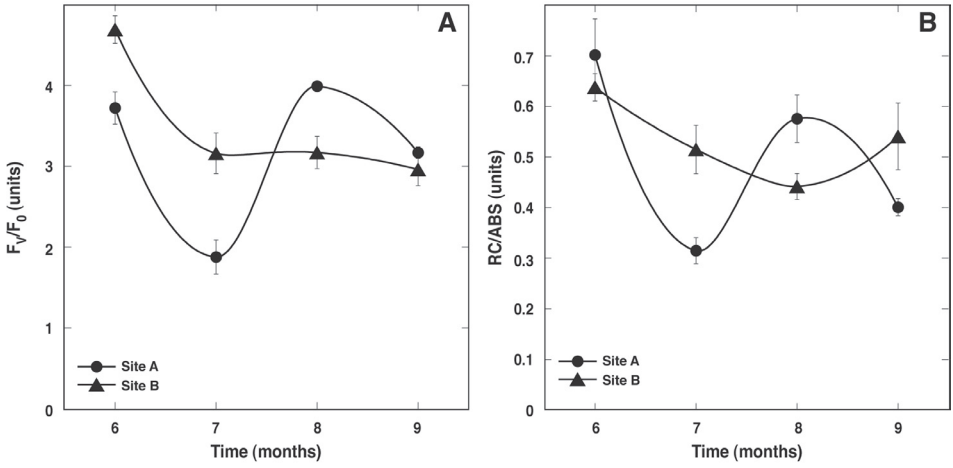

Fig. 3. Seasonal changes of photosystem II activity (F_V/F_0, A) and ratio of active reaction centres (RC/ABS, B) of *Glaux maritima* plants at two experimental sites.

most pronounced increase at site A was evident for Mg (< 3-fold), Zn (5-fold), Cu (> 3-fold), B (3-fold). Na and Cl concentrations at the site A was 2.4 and 2.5 times those at the site B, respectively. Higher ion content at site A was reflected by a 2.6-fold soil electrical conductivity and more acidic soil pH value.

Soil salinity at the two sites fluctuated significantly during the vegetation season as reflected by changes in the soil electrical conductivity (Fig. 1A) and Na concentration (Fig. 1B). Changes of a similar character was evident for Cl concentration (data not shown). Soil salinity at site A peaked in June while two significantly smaller peaks were evident for site B in May and July.

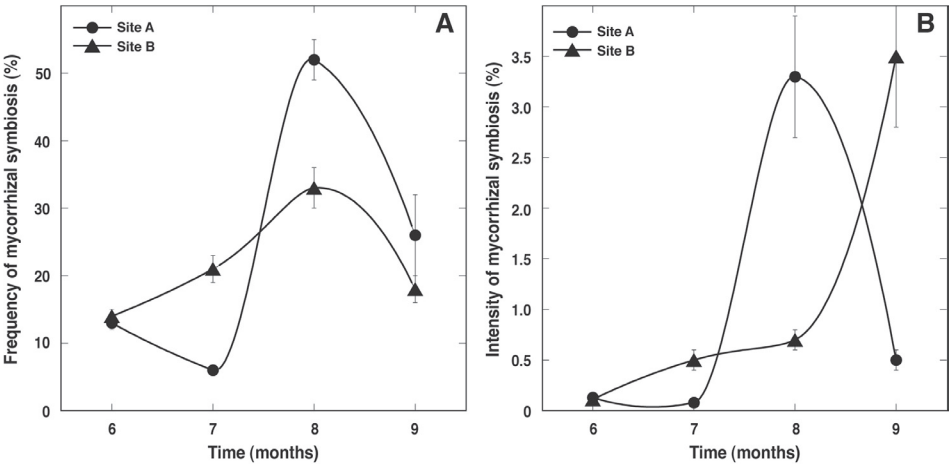

Fig. 4. Seasonal changes of frequency of mycorrhizal symbiosis (A) and intensity of mycorrhizal symbiosis (B) of *Glaux maritima* plants at two experimental sites.

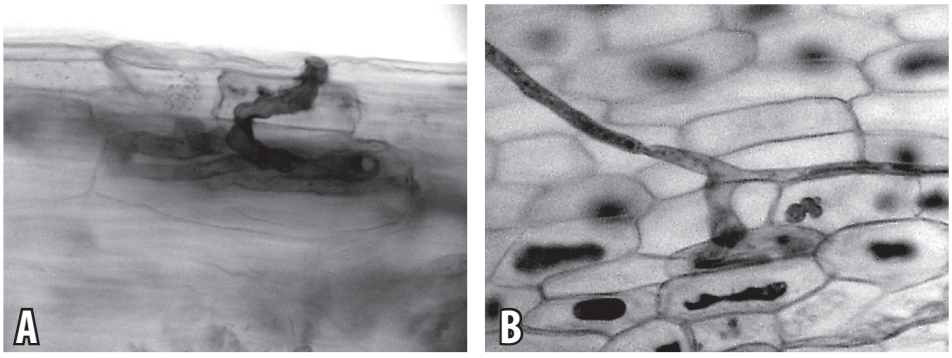

Fig. 5. Characteristic mycorrhizal fungal structures in roots of *Glaux maritima* from two experimental sites. A, intraradical hyphae forming hyphal coils at site A. B, external hyphae at site B.

Seasonal changes of chlorophyll a *fluorescence*

Potential quantum yield of PSII (F_V/F_M) decreased to an extremely low level in plants at site A in July indicating photoinhibition of photosynthesis (Fig. 2A). In contrast, a relatively low increase of soil salinity did not affect F_V/F_M at site B (Fig. 2A). However PI, which is a more complex parameter, decreased in *G. maritima* plants at site B until August followed by an increase in September (Fig. 2B) indicating that some aspects of photochemistry of PSII were affected. Indeed, a lower level of PSII activity (Fig. 3A) and decreasing ratio of active reaction centres of PSII (Fig. 3B) was evident at site B in July and August. Decreased photosynthetic performance at site A in July was reflected also by a drastic decrease both in PSII activity (F_V/F_0) and in the ratio of active reaction centres (RC/ABS; Fig. 3).

Dynamics of mycorrhizal symbiosis and anatomical differences of symbiosis

G. maritima plants were characterized by a low level of intensity of mycorrhizal symbiosis throughout the vegetation season (Fig. 4B) while the frequency of infection in general

was higher (Fig. 4A). Both parameters showed significant changes during the season. At site A lower levels of mycorrhizal symbiosis in July was followed by a drastic increase in August. In September frequency of mycorrhizal symbiosis decreased at both sites while intensity showed an opposite pattern for the two sites with a significant increase at site B and decrease at site A (Fig. 4).

Anatomy of root colonization showed a distinct pattern at the two study sites. At the sea flooding-affected site A *G. maritima* plants had mostly intracellular hyphae forming hyphal coils (Fig. 5A). In contrast plants at site B predominantly had external hyphae usually with a relatively high level of branching (Fig. 5B). No arbuscules were found in the symbiotic root cells.

Discussion

As flooding by sea water resulting in drastic increase in soil salinity is a main factor affecting distribution of *G. maritima* plants (Jerling 1988b) one may ask what is the overall effect of these environmental changes on general performance of *G. maritima*. In terms of reproduction flooding episodes have been observed to positively affect the rate of vegetative propagation of *G. maritima* (Jerling 1988a). In the present experiments fluctuation of soil salinity induced temporal changes in photochemistry of PSII of *G. maritima* plants. In the most severe situations as at site A in June photoinhibition of photosynthesis was evident in July. However, recovery of photosynthetic performance at the later stages indicates that *G. maritima* plants are indeed well-adapted to subtle changes in soil salinity.

G. maritima is known as a typical salt eliminator, which is achieved by the means of salt-secreting glands (Rozema 1975; Rozema et al. 1978). On the other hand, it has been long known that *G. maritima* is a mycorrhizal plant (Mason 1928). Mycorrhizal symbiosis of *G. maritima* has been characterized as moderate to low intensity (Hildebrandt et al. 2001). Similarly, in the present study a low level of symbiosis was found for *G. maritima*. Low mycorrhizal colonization of plants in salt marshes does not imply ineffectiveness of mycorrhizal symbiosis (Füzy et al. 2008). In spite of the relatively low intensity of mycorrhizal symbiosis in roots of *G. maritima* clear seasonal change in colonization was found (Fig. 4). In general seasonal dynamics of mycorrhizal symbiosis is a well-known phenomenon and is thought to be dependent on both climate variation as well as host phenology (Lugo et al. 2003). In temperate regions periodically fluctuating low temperature affects function of mycorrhizal symbiosis in relation to edaphic conditions (Tibbett, Cairney 2007). On the other hand this may also reflect a seasonality of mycorrhizal fungi itself (Bever et al. 2001). Usually maximum intensity of colonization is at the phase of full photosynthetic capacity (Merryweather, Fitter 1995). In our study both frequency and intensity of the symbiosis increased during the vegetation season until August in roots of *G. maritima* (Fig. 4).

Soil at both sites was characterized by an extremely high Na, Cl, B and S content. However, the amount of N, Cu and Mo can be estimated as relatively low. Together with high soil electrical conductivity and fluctuating character of changes in these parameters this indicates a direct effect of flooding by sea water. Consequently, mineral disbalance could be predicted, especially at site A. However, a high S level in the soil is one of the factors leading to higher tolerance of salt-affected plants partly through reduction of B uptake (Baker, Pilbeam 2007).

In flooded soils reduced forms of N, Mn, Fe, S are produced due to activity of

anaerobic soil microorganisms (Cronk, Fennessy 2001). A decrease in redox potential can be stressful or toxic to plants. Reducing conditions also change the availability of mineral nutrients. Phosphate availability is increased due to conversion of Fe^{3+} to Fe^{2+}. In addition availability of positively charged ions e.a. K, Mg, Ca also increases in reduced conditions. Flooding also negatively affects mycorrhizal symbiosis (Carvalho et al. 2003; Šraj-Kržič et al. 2006). However, it was concluded that mycorrhizal symbiosis in salt marsh depends on soil salinity rather than on soil flooding (Carvalho et al. 2003).

Mycorrhizal plants may have a higher salt tolerance than non-mycorrhizal plants (Feng et al. 2002; Al-Karaki 2006; Sharifi et al. 2007). Improved tolerance of mycorrhizal plants vs. non-mycorrhizal in saline conditions can be related to enhanced mineral nutrition and as a result improved physiological processes (Ruiz-Lozano, Azcón 2000). In addition, potential quantum yield of PSII (F_V/F_M) is higher in plants with a higher degree of mycorrhizal colonization, especially in suboptimal conditions (Pinior et al. 2005). Consequently, in spite of a putative negative effect of high soil salinity on mycorrhizal symbiosis of *G. maritima* plants at site A in July increased frequency and intensity of the symbiosis at later stages clearly indicates an adaptive potential of mycorrhizal symbiosis. Moreover, appearance of intercellular hyphal structures (hyphal coils) in roots of *G. maritima* at site A under the effect of high soil salinity may represent inducible adaptive response. Indeed, hyphal coils have been described as exchange structures indicating intense exchange activity between the symbionts (Lugo et al. 2003).

In conclusion, photochemistry of photosynthesis of *G. maritima* plants is negatively affected by elevated soil salinity leading to significant inhibition of photosynthesis in the most severe cases. However, relatively high long-term adaptive potential of the species leads to significant recovery of physiological processes during stabilization of the salinity. Mycorrhizal symbiosis could be regarded as a significant part of the adaptive mechanisms of *G. maritima*.

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Piekrastes mitrāju auga *Glaux maritima* fotosintēzes efektivitāte un mikorizu simbioze mainīga augsnes sāļuma apstākļos

Ieva Druva-Lūsīte[1]*, Andis Karlsons[2], Anita Osvalde[2], Jevgenija Ņečajeva[1], Ģederts Ieviņš[1]

[1]Augu fizioloģijas katedra, Latvijas Universitātes Bioloģijas fakultāte, Kronvalda bulv. 4, Rīga LV-1586, Latvija
[2]Minerālās barošanās laboratorija, LU Bioloģijas institūts, Miera 3, Salaspils LV-2169, Latvija
*Korespondējošais autors, E-pasts: druva@lanet.lv

Kopsavilkums

Dotā darba mērķis bija izpētīt sezonālo augsnes sāļuma izmaiņu ietekmi uz hlorofila *a* fluorescenci un mikorizu simbiozi dabiskos apstākļos augošiem *Glaux maritima* augiem. Pētījumam izvēlējās divus tuvu izvietotus parauglaukumus ar atšķirīgu applūšanas režīmu un iespējami atšķirīgām augsnes īpašībām. Parauglaukumi būtiski atšķīrās pēc augsnes sāļuma un makroelementu un mikroelementu koncentrācijām tajā. Relatīvi vairāk jūras ietekmētajā parauglaukumā A bija lielāks sāļums un augstākas lielākās daļas minerālelementu koncentrācijas. Fotosistēmas II potenciālais kvantu iznākums (F_V/F_M) parauglaukumā A jūlijā samazinājās līdz kritiski zemam līmenim, parādot fotosintēzes fotoinhibēšanu. Pretēji tam, relatīvi nelielais augsnes sāļuma pieaugums parauglaukumā B neietekmēja F_V/F_M. Samazinātā fotosintēzes efektivitāte parauglaukumā A jūlijā bija saistīta arī ar fotosistēmas II aktivitātes un aktīvo reakcijas centru proporcijas samazinājumu. G. maritima augiem bija raksturīga zema mikorizu simbiozes intensitāte visā veģetācijas sezonas laikā, bet simbiozes frekvence kopumā bija augstāka. Abi parametri būtiski mainījās sezonas laikā. Sakņu kolonizācijas veids bija atšķirīgs divos parauglaukumos – parauglaukumā A varēja novērot pārsvarā iekššūnas hifas, kas veidoja hifu tinumus. Savukārt, parauglaukumā B dominējā ārpussaknes hifas. Mikorizu simbiozi var uzskatīt par būtisku daļu *G. maritima* adaptīvajos mehānismos.