

Photosynthetic characteristics of three species of the family *Plantaginaceae* growing on high and low tide coastal areas of the White Sea

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Abstract

CO₂ gas exchange, transpiration, stomatal conductance, water use efficiency and chlorophyll content were investigated at the leaves of three species of the family *Plantaginaceae*: *Plantago maritima* L., *Plantago subpolaris* Andrejev and *Plantago schrenkii* C.Koch under natural conditions of the habitat on high and low tide areas of the White Sea' coasts. The high rate of photosynthesis at saturating CO₂ (P_{Nmax}) at *P. maritima* (85.0±4.8 μmol m⁻² s⁻¹), as compared to *P. subpolaris* and *P. schrenkii* (45.2± 7.5 and 36.9±3.2 μmol m⁻² s⁻¹) was caused by high activity of ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBPCO), the rate of electron transport, the rate of triose phosphate utilization, TPU), as well as high efficiency of carboxylation. The rates of photosynthesis at ambient concentration of CO₂ (P_N) at *P. maritima* were 1.4 and 1.7 times higher compared to *P. subpolaris* and *P. schrenkii*. Plants of *P. schrenkii* are characterized by lower values of stomatal conductance and water use efficiency compared to *P. maritima* and *P. subpolaris*. In natural habitat, the limiting factor of CO₂ assimilation *P. subpolaris* is the rate of photosynthetic electron transport, the activity of RuBPCO in *P. schrenkii*.

Key words: *Plantago*, plant stress, resistance, photosynthesis, obligate halophytes

Abbreviations: ATP - adenosine triphosphate, C_a - ambient concentration of CO₂, C_i - internal concentration of CO₂, LHC I - light-harvesting complexes of photosystem I, LHC II - light-harvesting complexes of photosystem II, NADPH - nicotinamide adenine dinucleotide phosphate reduced, PAR - photosynthetically active radiation, P_N - net photosynthetic rate at ambient concentration of CO₂, P_{Nmax} - maximum rate of photosynthesis at saturating CO₂, RCs PSI - reaction centers of photosystem I, RCs PSII - reaction centers of photosystem II, RuBP - ribulose-1,5-bisphosphate, RuBPCO - ribulose-1,5-bisphosphate carboxylase/oxygenase, TPU - triose phosphate utilization, W_C - maximal rate of RuBP carboxylation, W_j - PAR saturated rate of electron transport in the light, W_p - rate of triose phosphate utilization, WUE - water use efficiency

Received November 11, 2012, accepted December 17, 2012.

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Acknowledgements: The work is executed with the financial supports of grant No. 5.5829.2011 AVCP, grant GK 14.740.11.0300 within the limits of FCP, grant from RFBR No. 12-04-01008-a.

Introduction

A group of plants species, which are typical for the coastal zone, is combined in a littoral-halophyte floral complex (Tzvelev 1979, Sergienko 2008). Within the coastal zone of the White Sea on silty and sand-silty drainage spots and rocks, three types from the family *Plantaginaceae* (plantain plants) dominate and codominate. Being obligate halophytes, *Plantago maritima* L., *Plantago subpolaris* Andrejev and *Plantago schrenkii* C. Koch differ in latitude-longitude distribution (Shipurov 1996, 1997) and their biomass (Davey *et al.* 2007). Participation of these species in adaptation of the photosynthetic apparatus to specific habitat conditions has not been studied in details, though there is some information on the other species of the genus reported by Drake (1989). Among the promising approaches in the study of the plants in the field, there is a group of methods based either on the investigation of the chlorophyll fluorescence parameters reflecting potential and actual effectivity of photosynthetic processes in photosystem II (*e.g.* Nieva *et al.* 1999, Lu *et al.* 2002, Naidoo *et al.* 2006) and/or analysis of the data on CO₂ exchange with use of mathematical photosynthetic models which take into account both physical and biochemical

processes (Farquhar *et al.* 1980, von Caemmerer *et al.* 1982). The application of modeling allows to estimate the functioning of photosynthetic apparatus and the main limiting factors of carboxylation efficiency: activity of ribulose-1,5-bisphosphate carboxylase / oxy-genase (RuBPCO), regeneration of RuBP pool, is the rate of electron transport in electron transport chain of the chloroplasts, the rate of triosphosphate utilization (TPU) and supply of inorganic phosphate in the chloroplasts.

This work aimed to study comparatively functional activity of photosynthetic apparatus of the three dominant species from the family *Plantaginaceae* under natural conditions of their habitats. Field measurements were made at the coastal zone of high tidal seas of the Arctic and Holarctic in the high and low tide areas. We hypothesized that there would be interspecific differences in photosynthetic parameters in the studied species.

The goal of the work was to study the activity of photosynthetic apparatus of *Plantago* leaves under natural habitat conditions, to determine the content of pigments and to give comparative estimation of the characteristics of CO₂ gas exchange.

Material and Methods

Object under study and environmental conditions

Plant intact leaves of three species of the family *Plantaginaceae* were under investigation: *Plantago maritima* L., *Plantago subpolaris* Andrejev and *Plantago schrenkii* C. Koch. They grown under natural conditions in the intertidal zone of the gulf area near the settlement Kolezhma (64° 14' N, 35° 53' E). All three species of plantain plants are the perennial herbaceous plants with a taproot. The plants of

Plantago maritima are 15-60 cm in height. The leaves are located in the root outlet, rare-toothed, linear, glabrous, having more or less the same size. The ears have long cylindrical shape, equal to or slightly shorter than a sterile part of flower-bearing stem. The lobes of corolla are often with cilia, a boll is elongate – ovate in shape, 2.5-3.0 mm in length with 2-3 seeds. The plants of *Plantago subpolaris* are 12-

30 cm in height. The leaves are located in the root outlet without teeth, linear, glabrous, having more or less the same size. The ears have a middle cylindrical shape, 1/3 shorter than the sterile part of flower-bearing stem. The lobes of corolla are without cilia, a boll is ovate or elongate – ovate in shape, 3.2-3.5 mm in length with 2-3 seeds. The plants of *Plantago schrenkii* are 5-12 cm in height. The leaves are located in the root outlet without teeth, linear-lanceolate, slightly pubescent, the lower leaves considerably shorter than the upper ones. All the leaves have often a small dark brown spots. The ears have an ovate shape, much shorter than the sterile part of flower-bearing stem. The lobes of corolla are without cilia, the egg-shaped boll is 2.0-2.5 mm in length with 2 seeds.

The field measurements of photosynthesis were made at the beginning of July 2010 at high solar radiation (PAR range of 1200-1400 $\mu\text{mol m}^{-2} \text{s}^{-1}$) and air temperature 30-35/25-30°C (day/night). The rates of CO₂ assimilation and plant transpiration were measured with LC portable photosynthetic system (ADC BioScientific, UK) in the afternoon under natural environmen-

tal conditions. All coastal biotopes in the estuarine zone of the Kolezma river were described by 3 transects: The first transect was located on the flat mud coast of the inner part of the jumpers from the shore to the island. General projective cover of vegetation was 50%. The dominant species were *Tripolium vulgare* (15%), *Plantago* s.l. (30%), *Triglochin maritima* (10%), *Salicornia europaea* (5%); The second transect was located on the sand-and-shingle coast in the inner part of the estuary. General projective cover of vegetation was 80%. The dominant species were *Juncus atrofuscus* (50%), *Triglochin maritima* (30%), *Plantago* s.l. (25%), *Glaux maritima* (15%), *Carex glareosa* (10%). The third transect was located on the marsh meadows with muddy soils on the right coast of the river. General projective cover of vegetation was 90%; the projective cover of water was 15%. The dominant species were *Eleocharis uniglumis* (50%), *Bolboshoenus maritimus* (30%), *Hippuris tetraphylla* (15%), and especially in salt depressions with water cover, *Carex mackenziei* (25%), *Triglochin maritima* (20%), *Plantago* s.l. (20%).

CO₂ gas exchange curves and calculated parameters.

Key characteristics of the CO₂ exchange were derived from P_n/C_i responses. To obtain the P_n/C_i response, the CO₂ concentration (C_a) was initially set to 65 $\mu\text{mol mol}^{-1}$ and than initial photosynthetic rate was measured. After that, the steady-state photosynthesis was measured at increased C_a; 100, 200, 400, 800, 1200, 1600 $\mu\text{mol mol}^{-1}$. The analysis of CO₂ response curves was made according to the model of Farquhar et al. (1980), modified by von Caemmerer et Farquhar (1982), Harley et Sharkey (1991), using a Photosyn Assistant Ver. 1.1.2 program, Parsons et Ogston (1999).

According to the authors' equations, the model enabled us to determine maximal rate of RuBP carboxylation (W_C), PAR saturated rate of electron transport in the light (W_j), the rate of triose phosphate utilization, (W_p), photosynthetic capacity at light saturation (P_{Nmax}), the rate of non-photorespiratory CO₂ efflux in the light and a number of other parameters.

The experiments were carried out in 3–4 replicates with 4–5 assays each. Mean values of photosynthetic parameters with their standard errors were calculated. The significance of differences was determined from Student's *t*-test at *P* = 0.95.

Results and Discussion

A comparison of different photosynthetic characteristics in the species of the family *Plantaginaceae* under study showed that higher rates of CO₂ assimilation, stomatal conductance and water use efficiency (WUE) were typical for *Plantago maritima* compared to *P. subpolaris* and *P. schrenkii* (Table 1). Photosynthetic rate calculated per unit of fresh biomass of the leaf was higher in

Plantago subpolaris relative to *Plantago schrenkii*, however, it was lower when calculated per unit of the leaf area. A decrease of stomatal conductance for gases efflux in *P. schenkii* and *Plantago subpolaris* resulted in a decrease of transpiration rate and more water use efficiency (WUE) by individual plants (Table 1).

| Object, conditions of measurement | P _N μmol m ⁻² s ⁻¹ , μmol g ⁻¹ s ⁻¹ | E mmol m ⁻² s ⁻¹ mmol g ⁻¹ s ⁻¹ | WUE μmol mmol ⁻¹ | C _i μmol mol ⁻¹ | G _s mmol m ⁻² s ⁻¹ |
|-----------------------------------|--|---|--------------------------------|--|--|
| <i>Plantago maritima</i> | 36.9±1.1 | 9.4±0.4 | 4.0 | 255±6 | 320±25 |
| <i>Plantago schrenkii</i> | 26.7±0.8 23.8±0.6 | 7.4±0.3 6.6±0.3 | 3.73 3.60 | 264±4 | 230±15 |
| <i>Plantago subpolaris</i> | 21.2±0.2 28.3±0.3 | 8.0±0.1 10.7±0.2 | 2.65 2.64 | 270±4 | 250±20 |

Table 1. The rate of photosynthesis (P_N), transpiration (E), stomatal conductance (G_s), water use efficiency (WUE), and intercellular CO₂ concentration (C_i) by the plants of genus *Plantago* L.: *P. maritima*, *P. subpolaris*, *P. schrenkii* under natural habitat conditions (PAR range of 1200-1400 μmol m⁻² s⁻¹), the air temperature day/night 30-35/25-30°C.

CO₂ concentration in the intercellular spaces of *P. subpolaris* and *P. schrenkii* leaves was at the same level that might testify the absence of stomatal photosynthetic limitation in these species. However, the lower photosynthetic rates in these species as compared to *P. maritima* pointed out the other limiting factor than G_s. In the leaves of *P. subpolaris* and *P. schrenkii* compared to *Plantago maritima*, the lower content of chlorophylls (Table 2) depended on the higher values of the Chl_a/Chl_b ratio. In the chloroplasts of the leaves of the higher plants, four types of the chlorophyll-protein complexes are formed. The reaction centers of photosystem I (RCs PSI) and photosystem II (RCs PSII) contain almost exclusively chlorophyll *a* (Ladygin *et al.* 1981) and the light-harvesting complexes bound to photosystem I (LHC I) or photosystem II (LHC II) comprise short-wave species of the chlorophyll *a* and the chlorophyll *b*

(Anderson 1980, Ladygin 1998). The results obtained on the Chl *a/b* ratio and the content of light-harvesting complexes may indicate that photosynthetic unit in *Plantago maritima* contains higher quantity of the LHCs per a reaction center as compared to *P. subpolaris* and *P. schrenkii*. This may indicate its adaptation to the conditions of shading. This fact is in a good agreement with ecology of these plants, which are submerged regularly under the inflow for couple of hours at high tidal level. The species of the family *Plantaginaceae* showed no difference in carotenoids content, nevertheless the value of the chlorophyll/carotenoids ratio was lower in *P. subpolaris* and *P. schrenkii*. An increase of the relative content of carotenoids is often associated with their antioxidative activity (Krinsky 1979), the significance of which at *P. maritima* might be lower.

| Object | Plants species | | |
|--|---------------------------|--------------------------|----------------------------|
| | <i>Plantago schrenkii</i> | <i>Plantago maritima</i> | <i>Plantago subpolaris</i> |
| Place of collection | Coast, transect 1 | Coast, transect 1 | Coast, transect 1 |
| Chlorophyll <i>a</i> mg g ⁻¹ dry mass | 1.64±0.10 | 2.05±0.44 | 1.66±0.27 |
| Chlorophyll <i>b</i> mg g ⁻¹ dry mass | 0.74±0.04 | 1.25±0.21 | 0.80±0.18 |
| Total chlorophylls <i>a+b</i> mg g ⁻¹ dry mass | 2.38±0.14 | 3.30±0.59 | 2.46±0.43 |
| Carotenoids mg g ⁻¹ dry mass | 0.57±0.02 | 0.56±0.14 | 0.50±0.07 |
| Chlorophyll <i>a</i> /chlorophyll <i>b</i> | 2.22±0.24 | 1.64±0.60 | 2.07±0.71 |
| Chlorophylls/carotenoids | 4.17±0.15 | 5.89±0.74 | 4.90±0.62 |
| Light-harvesting complex | 41.49±1.86 | 52.22±8.85 | 49.77±8.80 |

Table 2. Pigment content in leaves of *Plantago* L. plants (calculated per g dry matter of leaves).

| Parameters | Plant species | | |
|---|--------------------------|----------------------------|---------------------------|
| | <i>Plantago maritima</i> | <i>Plantago subpolaris</i> | <i>Plantago schrenkii</i> |
| Rate of photosynthesis at saturating CO ₂ , μmol CO ₂ m ⁻² s ⁻¹ | 85.0 ± 4.8 | 45.2 ± 7.5 | 36.9 ± 3.2 |
| Maximum rate of carboxylation, μmol CO ₂ m ⁻² s ⁻¹ | 123.0 ± 20.9 | 142.9 ± 13.8 | 69.5 ± 18.4 |
| Carboxylation efficiency, μmol CO ₂ m ⁻² s ⁻¹ | 1.776 ± 0.235 | 0.527±0.142 | 0.477 ± 0.316 |
| PAR saturated rate of electron transport, μmol m ⁻² s ⁻¹ | 428.0 ± 93.7 | 181.1 ± 3.44 | 253.8 ± 14.5 |
| Rate of triose phosphate utilisation, μmol CO ₂ m ⁻² s ⁻¹ | 29.3 ± 46.8 | 14.62 ± 1.5 | 15.26 ± 1.45 |
| Rate of respiration in the light, μmol CO ₂ m ⁻² s ⁻¹ | -9.8 ± 1.7 | -7.0 ± 2.6 | -4.2 ± 1.7 |
| CO ₂ compensation point, μmol mol ⁻¹ | 115 ± 4 | 115.3 ± 3 | 98 ± 3 |

Table 3. Parameters of CO₂ response curves of the leaves of plants, genus *Plantago* L.: *P. maritima*, *P. subpolaris*, *P. schrenkii* at light saturation, calculated by a Farquhar model.

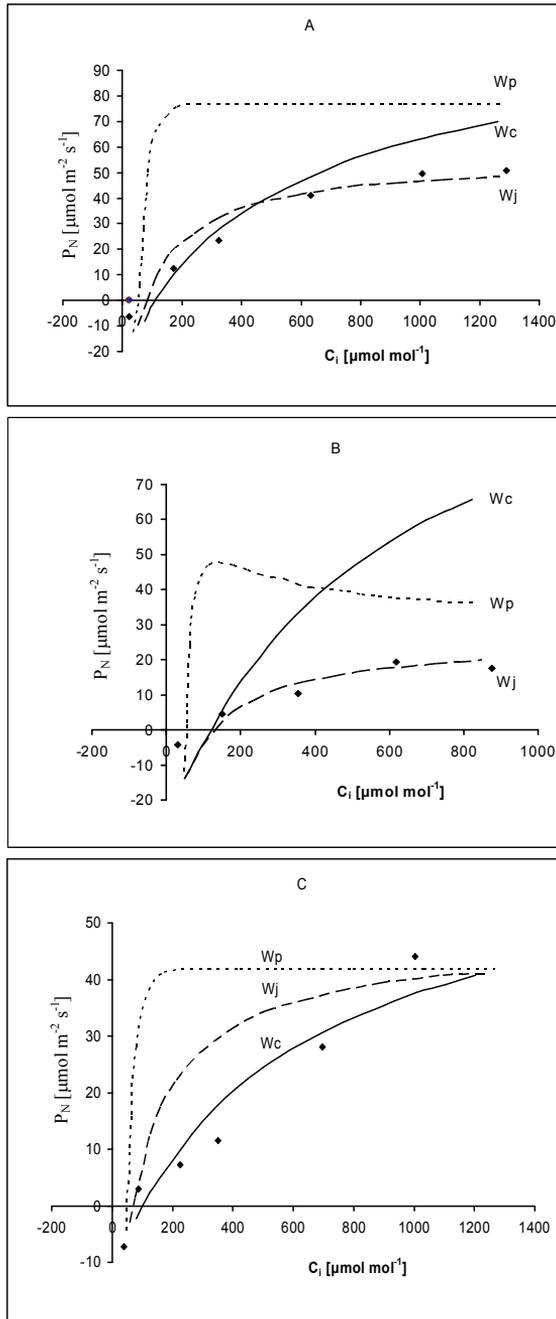


Fig. 1. Construction of the P_N/C_i curves. The P_N/C_i curves were constructed using the steady state P_N values and C_i values calculated by the *CIRAS*. Points represent the P_N values recorded; W_c model - (the unbroken line) characterises the carboxylation activity when the rate of carboxylation is limited on by activity of RuBPCO; W_j model - (the dashed line) represents the electron transport limits photosynthesis by regeneration of RuBP; and W_p model - (the dotted line) carboxylation is limited by regeneration of inorganic phosphate. A, B, C *Plantago maritima* L., *Plantago subpolaris* Andrejev and *Plantago schrenkii* C. Koch.

The results of CO₂ gas exchange were analyzed with a Farquhar model (Fig. 1 A, B, C,) to determine the limiting factors of the functioning of plant photosynthetic apparatus. The photosynthetic rate for plants *P. maritima* in the range of lower concentrations of CO₂ in the intercellular spaces of leaves was determined by the enzymatic activity of RuBPCO. Only at the higher concentrations of CO₂ (more than 500 μmol m⁻¹s⁻¹), the rate of RuBP regeneration was evaluated. A comparison of the values of functional activity of the photosynthetic apparatus of *P. subpolaris* and *P. schrenkii* showed that they differed in their components. Thus, in *P. subpolaris*, the limiting process of carboxylation both at natural and higher concentrations of CO₂ was the rate of electron transport. In *P. schrenkii*, it was functioning of the enzyme.

Hence, the results of the analysis showed that higher photosynthetic rates at saturating CO₂ of *P. maritima* were associated with more efficient functioning of the photosynthetic apparatus at light and in dark (Table 3). The higher values of

RuBPC/O activity, rates of electron transport, utilization of triose phosphate and the higher efficiency of carboxylation response were typical for *P. maritima* as compared to *P. subpolaris* and *P. schrenkii*. High stomatal conductance of the species enabled the higher rate of transpiration. The data obtained in combination with the higher content of the pigments confirms more active functional state of the photosynthetic apparatus *P. maritima* as compared to *P. subpolaris* and *P. schrenkii* under conditions of their habitat. A comparison of the functional activity of the photosynthetic apparatus of *P. subpolaris* and *P. schrenkii* showed that they are different in their components. A low rate of photosynthesis in *P. subpolaris* was dependent on the low rate of electron transport photosynthetic and possible decrease in the synthesis of energy-storing compounds, *i.e.* ATP and NADPH. A decrease of phosphate supply in the chloroplasts stroma may affect these processes indirectly due to inhibition of triose phosphates utilization.

Concluding remarks

The analysis of the photosynthetic and ecophysiological characteristics showed that two groups of species can be distinguished according to their functional activities: the first one includes *P. maritima*, and the second one *P. schrenkii* and *P. subpolaris*. All investigated species are attributed to obligate halophytes, but have various geographical distributions. Thus, *P. maritima* enters the group of boreal Eurasian areal, invades a wide range of ecotopes along the coast of the White Sea in taiga, forming great biomass. This species often form oligodominant communities on the muddy and sand-muddy sublittoral and littoral zones. They firstly appear on muddy and sandy-muddy drainage areas and withstand long-term

(up to the 4-th hours) flood with sea waters. Eurybionity of the halophyte within a wide spectrum of ecotopes of intertidal zone is followed by a high functional activity that testified optimal conditions of its growth and high adaptation level to the conditions of intertidal zone in the middle taiga. The other two species are attributed to the group of hypoarctic and arctic types with European areal and, as compared to *P. maritima*, they occupy a narrower spectrum of ecotopes, since both grown out of the flood zone. *P. subpolaris* is able to form oligodominant communities on the silty drainage areas, on the maritime meadows. It grows beyond the tidal zone, and *P. schrenkii* grows in rock ecotopes, in the cracks of the rocks and is observed in

grass-serge-herbal communities above the tidal zone. As dependent on the degree of functional activity of the photosynthetic apparatus, and geographical distribution of plants, these species can be presented in the following sequence: *P. maritima*, *P. subpolaris*, *P. schrenkii*. It corresponds to a decrease in the range of their adaptation to the conditions of littoral and this sequence is in agreement with a decrease of their sizes and biomass.

In taxonomic literature, *Plantago maritima* L. s.l. represents a complex system of species which have been frequently described as special ones. Thus, dwarf arctic plants with elliptical few-flowered inflorescence are ascribed to *P. schrenkii* C. Koch (Andrejev 1930, Grigoriev 1958, Stankov et Taliev 1957). Tzvelev (1979, 1980, 1981) put these plants to *Plantago maritima* subsp. *borealis* (Lange) Blitt and Dahl. The

plants with numerous flower-bearing stems and large bolls from the coast of the White Sea are described as *P. subpolaris* Andrejev and also attributed to these subspecies.

According to the view of L. Sergienko (Sergienko 1977) and A. B. Shipurov (Shipurov 1996, 1997), the analysis of variability of *P. maritima* L. s.l. confirms the necessity to consider *P. schrenkii* C. Koch as a separate species. The investigation made by us in this study showed that along morphological features, there were differences in the functioning of photosynthetic apparatus in the plants under study that might be considered an additional argument for the acceptance of *P. maritima*, *P. subpolaris* and *P. schrenkii*, growing on the coast of the White Sea, as independent taxonomic units.

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