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BOTANY

Structural and Functional Peculiarities of Plants from the Genus *Betula* L. at Early Stages of Ontogenesis

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Abstract—The morphological, biochemical, and physiological characteristics of silver birch (*Betula pendula* Roth), curly birch (*B. pendula* Roth var. *carelica*), and downy birch (*B. pubescens* Ehrh.) at early stages of ontogenesis in natural conditions were investigated. Some intra- and interspecific peculiarities of the morphophysiological properties were determined. Priority development of the underground mass for the seedlings of curly birch and that of the aboveground mass for the seedlings of silver birch and downy birch were found. The leaf of curly birch is developed more actively as compared with those in the other two species under equal potential possibility of the growth of their leaves by elongation. A high similarity of the mineral composition (C, N, P, K) of different forms and species of birches was demonstrated. For silver birch the maximum values of the stomatal conductance, rate of photosynthesis, and transpiration under similar atmospheric and soil conditions were obtained. In downy birch we found a higher efficiency of water use. The highest values of the maximum rate of ribulose 1,5-bisphosphate carboxylase/oxygenase carboxylation were found in curly birch. This may serve as an indicator of its shade tolerance, as compared with silver birch and downy birch.

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INTRODUCTION

At present, in the context of changes in climatic conditions and increasing anthropogenic activity, problems in the conservation of species diversity and structural and functional organization of ecosystems are especially relevant. The species diversity of forest communities is determined by hydrometeorological and edaphic conditions, as well as by the edificial role of forest-forming tree species. Forests of northwestern Russia are represented mainly by pine, spruce, and birch formations. Silver birch *Betula pendula* Roth and downy birch *B. pubescens* Ehrh. are most widespread on the territory of Karelia (Ermakov, 1986; Vetchinnikova, 2004). Curly birch *B. pendula* Roth var. *carelica* (Merclin) Hämet Ahti is also an indigenous representative of the flora. It growths alone or in groups in mixed forest stands. Different growth conditions have determined the high level of polymorphism of phenotypic characteristics in the genus *Betula*. In addition, differences in the strategies of adaptation to environmental factors and ecological and physiological peculiarities of plants from the genus *Betula* were indicated (e.g. Evstigneev, 2004). For example, silver birch has higher competitive capabilities, which is manifested in its high potential growth rate allowing active capturing of life space by the plant. Downy birch has higher morphological and physiological plasticity and a broad range of reaction in unfavorable cenotic conditions. Curly birch with figured wood is especially interesting for researchers (Hintikka, 1941; Lyubavskaya, 1978; Vetchinnikova, 2004; Novitskaya, 2008; and others) in relation to studies of the mechanisms of formation of structural anomalies.

Our previous studies of the water regime in silver birch and curly birch in natural conditions demonstrated similarities in the daily and seasonal dynamics of water cycle parameters in these two forms of *B. pendula* Roth (Sazonova et al., 2012). An increase in the differences of water deficiency and saturating water content in the leaves of silver birch and curly birch with an increase in the appearance of a veiny structure in the trunk wood in curly birch ontogeny were found. A similarity in the “biological” and “economic” optima of N : P : K in the seedlings of silver birch and curly birch was found in laboratory conditions (Pridacha et al., 2012). Intraspecific peculiarities in the distribution of the plant biomass under varied conditions of the availability of macroelements were revealed. Comparative analysis of the dependence of photosynthesis on light intensity, temperature, and air humidity revealed lower CO_2 consumption in the seedlings of curly birch as compared to those of silver birch under the conditions of atmospheric drought (Bolondinskii, 2010). It should be noted that study of the developmental peculiarities of plants in ontogeny allows us to determine the mechanisms of plant adaptation to particular growth conditions.

This work aims at a complex study of the morphological, biochemical, and physiological peculiarities of silver birch, curly birch, and downy birch in natural conditions of growth at early stages of ontogeny.

MATERIALS AND METHODS

The experimental studies were conducted on experimental plots of the Forest Research Institute on the area of the Agrobiological Station, of the KarRC of RAS (61°45′ N, 34°20′ E). Three-year-old seedlings of silver birch *B. pendula* Roth, curly birch *B. pendula* Roth var. *carelica,* and downy birch *B. pubescens* Ehrh., grown in similar soil and climatic conditions, were investigated.

Measurements of the H_2O and CO_2 exchange parameters in birch leaves were conducted in diurnal dynamics from 9:00 to 15:00 in July 2011 on days with optimal external conditions. The meteorological parameters were registered using the system Li–Cor 6400XT (Li–Cor Inc., United States). In the period of measurements, the diurnal values of the photosynthetically active radiation varied from 600 to 1800 μmol/(m^2 s), the air temperature ranged from 22 to 28°C, and the water vapor deficit of the air varied from 0.8 to 1.8 kPa. The mean concentration of CO_2 in the air for the period of observations was about 370 μmol CO_2/mol.

Measurements of the stomatal conductance (g_s), rates of photosynthesis (A), and transpiration (E) were conducted on non-separated leaves from the middle part of the tree crown using the portative photosynthetic system Li–Cor 6400XT (Li–Cor Inc.). We used a standard leaf camera with a light source Li–Cor 6400-02B LED (Li–Cor Inc.). Observations in all trees were conducted on fully expanded leaves by the same methods in the leaf camera at light intensity of 1600 μmol/(m^2 s), CO_2 concentration of 400 μmol CO_2/mol, and air flow rate of 500 μmol/s. The air temperature in the measuring camera was 24°C. Each measurement was replicated three times.

The dependence of CO_2 assimilation rate on the CO_2 concentration in leaves was determined by the system Li–Cor 6400XT (Li–Cor Inc.) using the standard device program assuming the consecutive change in the concentration of CO_2 in the leaf camera (from 360 to 40 and from 40 to 1600 μmol CO_2/mol). Analysis of the CO_2 metabolic curve was conducted by the model of Farquhar et al. (1980) modified by Sharkey et al. (2007). This model allowed us to determine the maximum rate of carboxylation of ribulose 1,5-bisphosphate carboxylase/oxygenase (Rubisco) ($V_{c\ max}$), the maximum electron transport rate for ribulose-1,5-biphosphate (RuBP) regeneration (J_{max}), the rate of utilization of triosephosphates (TPU), and the rate of dark respiration (R_d).

After the end of intensive growth activity of plants in August, we collected plant samples for chemical analysis. Systematization of data was conducted for each tissue and organ: leaf, bark, wood, and root, as well as for the whole plant. Chemical analysis of plant samples was conducted using the scientific equipment of the Analytical Laboratory of the Forest Research Institute of Karelian Research Center of RAS. The carbon and nitrogen content was determined using the element analyzer PE-2410 (PerkinElmer, United States), potassium—by the method of atom-emission spectrometry (AES) on the AA-6800 series Atomic Absorption Spectrophotometer (Shimadzu, Japan), and phosphorus—by the spectrophotometric method with molybdenum blue. Threefold repletion was used.

The content of green pigments, chlorophylls *a* and *b* (Chl *a* and Chl *b*), respectively, were determined in the acetone extraction on a SF-2000 spectrophotometer (LOMO, Russia) according to generally accepted methods (Gavrilenko and Zhigalova, 2003). The photosynthetic efficiency of water use (WUE) was calculated by the ratio A/E (Wang et al., 1998). The water content of fresh leaf samples (W_{Cf}) was calculated with account of the fresh (W_f) and dry (W_d) mass of leaves by the formula $W_{Cf} = W_f - W_d/W_d$ (g water/g dry mass).

The methods of variation statistics were used for data analysis (Ivanter and Korosov, 2003). The tables and pictures provide the arithmetic means and their standard errors. To analyse the relationships between the parameters of carbon dioxide exchange and environmental factors, the regression analysis was used. Tests of hypotheses and estimations of significant differences between means were conducted at a 5% level of significance.

RESULTS AND DISCUSSION

Morphological peculiarities of the birches. Comparative analysis of biomass distribution did not reveal significant differences in birches of different species by this parameter ($p > 0.05$) (Fig. 1). However, it is possible to note a general tendency towards the development of a stronger extracting system (root) in curly birch, of a conducting system (trunk and branches) in downy birch, and of the conducting (trunk) and assimilating (leaf) systems in silver birch. It is confirmed by high values of the proportions of underground and aboveground biomasses of curly birch in comparison to those in silver birch and downy birch, 0.36, 0.3, and 0.29, respectively. It is possible to suppose that these peculiarities are conditioned by the different distribution of metabolites in the system of donor–acceptor relations of tissues and organs of the studied birch forms and species.

Comparison of the leaf size of the considered birch forms and species revealed significant differences ($p < 0.05$) in the leaf length and breadth of curly birch as compared with the other two species, which demonstrated similar values of these parameters ($p > 0.05$) (Table 1). The length and breadth of the leaf in curly birch exceeded the respective values in silver birch (by 9 and 8%) and downy birch (by 11 and 10%, respectively). These results are in good correspondence with the results of our previous studies (Pridacha and Pozdnyakova, 2010): a 30-year-old curly birch characterized by more active development of the leaf blade as compared to that in silver birch. Analysis of the leaf elongaton (i.e., the ratio of the leaf blade length to its breadth) in the birches under study did not reveal significant intra- and interspecific differences ($p > 0.05$). Most likely, this may indicate the equal potential growth capability of their leaves by elongation.

Mineral composition of tissues and organs of birches. Comparison of the content of elements C, N, P, and K and the N : P : K ratio in tissues and organs of the birches did not reveal significant differences ($p > 0.05$) between the considered birch forms and species (Fig. 2). This result is in good correspondence with the existing data on the mineral composition of plants in the forests of Karelia (Morozova, 1991). It is also reasonable to note a tendency towards lower values of the N content in tissues of the bark and roots of curly birch, as compared with those in silver birch and downy birch (to 15 and 17%, respectively). However, in calculations for the whole plant, these differences are very smoothed.

Some authors (Shulyakovskaya et al., 2010) also reported similarity in physological and biochemical parameters in these three forms and species of birches at earlier stages of ontogenesis, in particular, lipid and fatty-acid composition, as well as nitrogen-containing substances. In addition, the range of variation of the ratio N : P : K in different tissues of the birches under study was fairly similar and amounted (44–61) : (7–12) : (32–48). The ratio of macroelements in the leaf was also similar for different birch forms and species and was equal 61 : 7 : 32. We should also indicate the similarity of the values of the ratio N : P : K as calculated for the entire plant. For silver birch and curly birch these were 52 : 9 : 39, for downy birch 54 : 9 : 37. Maximum differences in the ratio N : P : K in different organs were found for the roots of curly birch (5%), as compared with other two birch species.

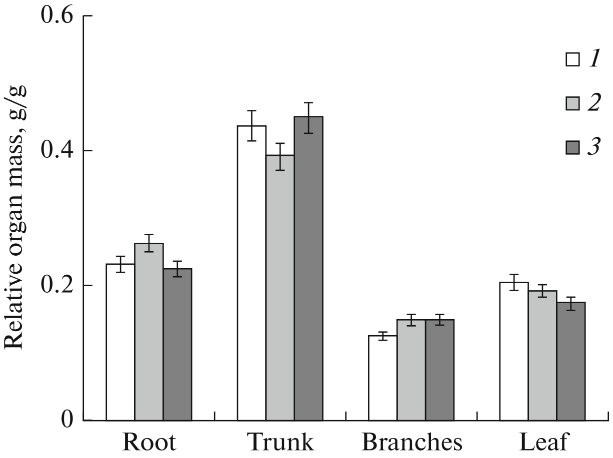

Fig. 1. Biomass distribution in organ seedlings of silver (*1*), curly (*2*) and downy (*3*) birches (it is presented as the ratio of organ mass to dry mass of whole plant).

Physiological peculiarities of the birches. Comparative analysis of the values of the main ecophysiological parameters characterizing peculiarities of CO_2 gas and water exchange in the leaf, as well as peculiarities of photosynthetic apparatus in relation to plant species, revealed a number of common features (Table 2). Maximum g_s were found in silver birch, whereas its values for downy birch and curly birch were significantly lower ($p < 0.05$), 15 and 11%, respectively. As compared to silver birch, downy birch displayed a small but significant ($p < 0.05$) decrease in the values of A and E (by 2 and 11%, respectively) and an increase in the values of WUE and W_{Cf} (by 6 and 30%, respectively). The values of these parameters were similar in silver birch and curly birch.

The content of CO_2 in intercellular air spaces of leaves (C_i) was also equal in different forms and species of birches. It was within the limits typical for C_3-type plants (Larcher, 1995). Some authors reported on variation of this parameter in dependence on the ambient conditions, in particular, light conditions, temperature, and air humidity, as well as the water potential of the plant and the availability of nutrients (Schulze, 2005; Hikosaka et al., 2006; Bernacchi et al., 2009; Niinemets et al., 2009; and others). Changes in the pigment content of curly birch as compared to that in the other two birches occurred mainly due to decrease in Chl *b* ($p < 0.05$), which led to an increase in the ratio of green pigments Chl *a*/Chl *b*.

Table 1. Linear parameters of the leaf in plants from the genus *Betula* L.

Parameter	*B. pendula* Roth	*B. pendula* Roth var. *carelica*	*B. pubescens* Ehrh.
Length, cm	5.67 ± 0.13	6.2 ± 0.13	5.5 ± 0.07
Breadth, cm	5.07 ± 0.12	5.49 ± 0.15	4.92 ± 0.09
Extent of oblongness	1.12 ± 0.02	1.14 ± 0.02	1.12 ± 0.01

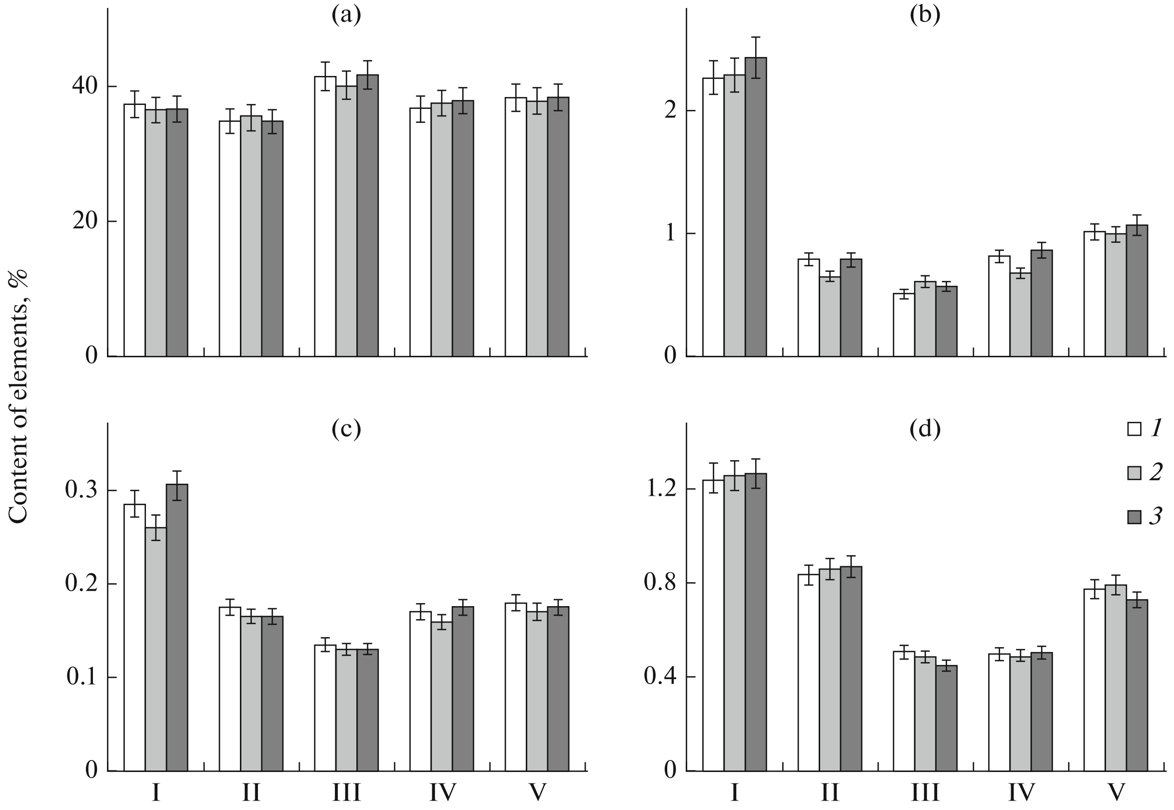

Fig. 2. The content (% dry weight) of carbon (a), nitrogen (b), phosphorus (c), potassium (d) in leaf (I), bark (II), wood (III), root (IV) and whole plant (V) of silver (*1*), curly (*2*) and downy (*3*) birches.

Analysis of the parameters of the carbon dioxide response curve (A/C_i), calculated according to method suggested by Sharkey et al. (2007), revealed that in silver, curly and downy birches characterized by fairly weak differences between the values of the maximum electron transport rate for RuBP regeneration (J_{max}= 162.9, 169.7, and 167.6 μmol/(m^2 s), respectively), the rate of utilization of triosephosphates (TPU = 11.7, 12.2, and 11.8 μmol/(m^2 s), respectively), and the rate of dark respiration (R_d = 2.6, 2.7, and 2.6 μmol/(m^2 s),

Table 2. Parameters of the CO_2/H_2O exchange and the content of green pigments in the leaves of plants from the genus *Betula* L.

Parameter	*B. pendula* Roth	*B. pendula* var. *carelica*	*B. pubescens* Ehrh.
g_s, mol $H_2O/(m^2$ s)	0.33 ± 0.01	0.3 ± 0.01*	0.28 ± 0.01***
A, μmol $CO_2/(m^2$ s)	18.89 ± 0.11	18.85 ± 0.06	18.53 ± 0.07**
E, mmol $H_2O/(m^2$ s)	2.47 ± 0.07	2.37 ± 0.02	2.24 ± 0.03***
WUE, μmol CO_2/mmol H_2O	7.83 ± 0.19	7.96 ± 0.06	8.33 ± 0.13*
W_{Cf}, g water/g dry mass	1.1 ± 0.08	1.1 ± 0.06	1.46 ± 0.09*
C_i, μmol CO_2/mol	267.56 ± 3.82	261.01 ± 1.88	259.39 ± 3.9
Chl *a*, mg/g wet mass	2.06 ± 0.14	1.84 ± 0.11	2.23 ± 0.22
Chl *b*, mg/g wet mass	0.79 ± 0.09	0.56 ± 0.03*	0.76 ± 0.06
Chl *a* + Chl *b*, mg/g wet mass	2.85 ± 0.2	2.4 ± 0.12	2.98 ± 0.23
Chl *a*/Chl *b*	3.13 ± 0.17	3.4 ± 0.16	3.13 ± 0.36

g_s, stomatal conductance; *A*, photosynthesis rate; *E*, transpiration rate; WUE, efficiency of water use; W_{Cf}, water content; C_i, intercellular CO_2 concentration; Chl *a*, chlorophyll *a*; Chl *b*, chlorophyll *b*; Chl *a* + Chl *b*, sum of green pigments; Chl *a*/Chl *b*, pigment ratio. * $p < 0.05$. ** $p < 0.01$. *** $p < 0.001$.

respectively). At the same time, comparison of the values of the maximum rate of Rubisco carboxylation ($V_{\mathrm{c\,max}}$) revealed maximum values of this parameter for curly birch, 136.9 μmol $CO_2/(m^2\ s)$, as compared with those for silver birch and downy birch, whose values were less by 9 and 19%, respectively. This result seems very interesting because high values of $V_{\mathrm{c\,max}}$ in the leaf of curly birch might have provided potentially maximum photosynthetic rate as compared to that in other birch forms, which was confirmed by measurements of photosynthesis rate for silver birch and curly birch under shaded conditions (Bolondinskii and Vilikainen, 2014). In particular, it was shown that there is twofold decrease in the values of the light compensation point in curly birch as compared to those in silver birch, which allowed it CO_2 consumption at very low photosynthetically active radiation, PAR (<0.5% maximum values of solar radiation coming to the ground surface under sunny weather in midday hours), whereas in silver birch leaves under these light conditions the CO_2 emission (respiration) was observed. High values of $V_{\mathrm{c\,max}}$ explain the mechanism of adaptation of the photosynthetic apparatus in curly birch to the low light conditions. In addition, differences in the pigment apparatus, in particular, the lower number of green pigments in curly birch, responsible for consumption and transformation of light energy into chemical energy of organic substances may also result in decrease of the maximum rate of photosynthesis even under saturated light. It should be pointed out that differences in the A values may also be explained by leaf structure peculiarities of the considered birch species, in particular, by the relations among leaf photosynthetic tissues, its mechanical and conducting features (e.g. Niinemets, 1999).

CONCLUSIONS

Provided study of structural and functional characteristics of silver birch, curly birch, and downy birch at early ontogenetic stages allowed to find numerous intra- and interspecific differences. It was shown prefered development of the underground biomass in the seedlings of curly birch and of the aboveground biomass in the seedlings of silver birch and downy birch, which may also evidence the different distributions of metabolites in the donor–acceptor system of the forms and species of the birches under study. Analysis of the leaf blade parameters revealed more active development of the leaf in curly birch as compared with that in silver birch and downy birch under equal potential growth capability of their leaves by elongation. Comparison of the mineral composition of tissues and organs of birches revealed a similarity in the content and proportions of the main mineral elements, which indicates the closeness of the chemical compositions in these woody plants. This closeness is optimal for the life forms and species of birches under study and, evidently, is conditioned by their phylogenetic proximity.

Analysis of the main ecophysiological parameters characterizing the processes of CO_2/H_2O exchange revealed that the seedlings of silver birch are characterized by higher values of the stomatal conductance and the rates of photosynthesis and transpiration. Higher efficiency of water use was found in downy birch, which indicates lower water losses by transpiration under similar carbon assimilation rates. In addition, the estimation of the performance of the photosynthetic apparatus allowed determining the highest values of the maximum rate of Rubisco carboxylation for curly birch, which promotes tolerance to shaded conditions as compared with silver birch and downy birch.

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