

ORIGINAL PAPER

Leaf traits variation in silver birch (*Betula pendula* Roth) across sites, crown positions, and tree social classes in the Western Carpathians

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Abstract

Silver birch (*Betula pendula* Roth) is a widely distributed, early-successional broadleaved species with ecological and partly also economic significance in Europe. Despite rather extensive research on its ecology and wood production, detailed studies on leaf traits remain limited. This study quantified basic leaf characteristics – leaf area, leaf mass, specific leaf area (SLA), and petiole mass – of young silver birches across ten naturally regenerated stands in Slovakia. A total of 204 trees were sampled, representing four tree social classes (dominant, codominant, intermediate, overtopped), and 3,672 leaves were collected from upper, middle, and lower crown positions. Leaf area and mass were measured after scanning and oven-drying, while SLA was calculated as the ratio of fresh leaf area to dry mass. Results revealed substantial variation in leaf traits among sites, social classes, and crown positions. Leaf area and mass were highest in dominant trees and in upper crown leaves, while overtopped trees produced smaller, lighter leaves. Conversely, SLA increased from dominant to overtopped trees and from upper to lower crown positions, reflecting morphological adaptation to reduced light availability. Analysis of petiole mass indicated that leaf blades accounted for over 93% of total leaf mass, with stalk allocation varying with crown position and tree social status. Significant interactions among sites, crown positions, and social classes highlighted the multifactorial control of leaf morphology. These findings demonstrate the pronounced morphological plasticity of silver birch leaves, enabling flexible resource-use strategies that optimize carbon gain under contrasting light environments. Such plasticity likely contributes to the species' competitive success, ecological amplitude, and potential role in climate-adaptive forestry. This study provides essential baseline data on leaf traits of silver birch and emphasizes the need for further research linking environmental conditions to variations in leaf morphology and physiology.

Key words: lamina; petiole; leaf mass; leaf area; specific leaf area; destructive sampling

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1. Introduction

Silver birch (*Betula pendula* Roth) is a relatively short-lived, medium-sized broadleaved species occurring throughout most of Europe (San-Miguel-Ayanz et al. 2016). This species has a light canopy composed of serrated, relatively small leaves. Its bark is typically silvery-white, containing horizontal dark grey or nearly black lenticels; vertical fissures often develop later, especially in the lower part of the stem (Pagan & Randuška 1987). Birch has low soil quality requirements but is intolerant of shaded conditions (Kula 2011). It often appears early in secondary succession due to its abundant seed production, with seeds that are very light and easily dispersed by wind over large areas (San-Miguel-Ayanz et al. 2016).

For example, in Central European countries such as the Czech Republic and Slovakia, silver birch colonized many sites following environmental disturbances (Martiník et al. 2018), especially air pollution-related dieback (Kula 2011), windthrow events (Šebeň et al. 2024), or bark beetle outbreaks (Kunca et al. 2015; 2019). Under Slovak conditions, Konôpka et al. (2021) reported that in northern Slovakia – after a large-scale wind disaster in the High Tatra Mountains in 2004 – silver birch, together with Norway spruce (*Picea abies* [L.] H. Karst.) and rowan (*Sorbus aucuparia* L.), was the most common species in post-disturbance young stands. At the same time, silver birch exhibited the highest diameter increment among all species. Moreover, Šebeň et al. (2018) documented that silver birch is very frequent on abandoned agricultural

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lands (non-forest areas) in Slovakia. The authors also observed that the proportion of silver birch is higher in young stands than in older ones on forest land, indicating its potential relevance for future mature stands.

Recently, many authors have shown that the presence of birch alongside other commercially important tree species can increase total wood production (Holmström et al. 2021; Huuskonen et al. 2023; Männistö et al. 2024), enhance flora and fauna biodiversity (Dubois et al. 2020), and provide numerous positive effects on soil conditions (Kula 2011) as well as bioclimatic properties (Dubois et al. 2020) in forest stands. Moreover, the authors demonstrated that the presence of silver birch as an admixture increased the abundance of ground vegetation and light-demanding woody plants, and could serve as a measure for climate change adaptation. At the same time, the high plasticity and genotypic variation of silver birch suggest a strong capacity for acclimation in changing environments and a rich genetic pool for sustainable forestry (Oksanen 2021).

Traditionally, birch wood has been widely used in industry, particularly in Scandinavia, the Baltic countries, Belarus, and Russia, but much less so – or not at all – in Central and Western Europe (San-Miguel-Ayanz et al. 2016). However, for instance, Cameron (1996), Dubois et al. (2021) and Martiník & Matoušková (2025) described silvicultural strategies to produce large-sized birch logs even in Central and Western Europe. In summary, considering all the above arguments, silver birch can be regarded as a promising tree species in the context of climate change, offering both ecological and economic benefits. Therefore, studies on various aspects of silver birch should be conducted not only in “northern” Europe – as has been done in the past – but also in other European countries such as Slovakia.

In fact, specific parts of trees have been studied to varying degrees, with foliage being examined particularly frequently by physiologists (e.g. Ma et al. 2023). This focus is largely because foliage plays a central role in the development and growth of trees, being the only organ actively involved in photosynthesis. Moreover, foliage serves as a storage organ for carbohydrates and minerals and is critically important for carbon and biochemical cycles (Kozłowski & Pallardy 1997). The authors explained that a leaf is composed of two parts: the blade (lamina) and the stalk (petiole), each with specific functions. The leaf blade plays a principal role in photosynthesis, gas exchange, and transpiration. The leaf stalk connects the blade to the stem. It serves as a transport bridge, allows flexibility of the leaf, optimizes light exposure by orienting the leaf toward light, and plays a role in leaf shedding (abscission).

Despite these facts, a review of the available literature (e.g. Barna 2004; Konôpka & Pajtik 2014; Fellner et al. 2016; Blasiak et al. 2021; Zhu et al. 2022; Thomas et al. 2024; Hegedüs et al. 2025, among others) suggests that few, if any, studies have focused specifically on the

leaves of silver birch. This lack of research extends even to basic leaf traits such as dry mass (weight) and area. Some authors have focused on specific leaf area (SLA), defined as the ratio between fresh leaf area and leaf dry mass (e.g. Wang et al. 2019). Although the Global Atlas of Specific Leaf Area under Climate Change (Sun et al. 2026) provides SLA values for 5,687 vascular plant species across 282 families, no data for silver birch are included. The authors emphasize that SLA is a key plant functional trait linked to structural, physiological, and resource-use strategies. Despite its huge importance, spatially continuous datasets capturing SLA variation across global biomes remain scarce. The previous studies showed that SLA is a sensitive indicator of growth conditions, especially light intensity (Zhang et al. 2022). In general, lower light intensity increased value of SLA, it means that certain unit of dry leaf mass make up large area.

Considering the aforementioned facts, we designed our research with the following objectives:

- to quantify basic leaf traits related to the lamina, such as leaf mass, leaf area, and SLA, for young silver birches originating from various sites in Slovakia;
- to analyze differences in leaf mass, leaf area, and SLA among the sampling sites;
- to examine changes in basic leaf traits along the vertical crown profile, specifically the upper, middle, and lower crown parts;
- to investigate differences in basic leaf traits between silver birches of different social tree classes;
- to quantify the mass of the leaf stalk (petiole) for silver birches grown at one of the sampling sites.

Our main hypothesis was that SLA would vary with leaf position along the vertical crown profile and with the tree social classes. We assumed that the highest SLA values would be found in the lower crown and in overtopped trees, whereas the lowest SLA values would occur in the upper crown and in dominant trees. This hypothesis is based on the general understanding that SLA varies with light intensity.

2. Material and methods

According to Pagan & Randuška (1987), silver birch occurs in Slovakia from the lowest altitudes (approximately 100 m) up to slightly over 1,200 m above sea level. This altitudinal range was therefore used to search for forest stands suitable for sampling. The primary selection was performed using the current national database of forest stands based on data from Forest Management Plans (internal database of the National Forest Centre in Zvolen, Slovakia). In addition, the selected silver birch stands had to occur on moderately fertile sites in order to represent average site conditions in Slovakia. Hence, most of the selected stands were located on mesotrophic Cambisols.

The main criteria for the selection of sampling stands were as follows: (i) stands had to originate exclusively from natural regeneration, which is the prevailing situation for silver birch in Slovakia; (ii) the proportion of silver birch in the tree species composition had to be at least 50%; and (iii) silver birch had to form the main canopy layer. Because silver birch is a fast-growing species, it often dominates the main canopy, while other tree species (e.g. European beech, Norway spruce, sessile oak, common hornbeam, and Scot pine) occur in the subcanopy layer (see Fig. A1 as example). The study focused exclusively on young growth stages, with an upper age limit of 20 years.

Field surveys were subsequently conducted, and ten stands were finally selected for detailed tree sampling (Table A1). The mean age of the selected stands ranged from 4 years (Klokočov site) to 20 years (Štôla site). Most stands were situated at the edges of forest complexes and exhibited relatively sparse canopies, with silver birch showing height dominance. The forest stands in the main layer were relatively sparse because the birches grew faster than the other trees, but it was not the only species in the place. No previous silvicultural (precommercial) thinning had been carried out in any of the selected stands. Within each stand, approximately 20 silver birch individuals were randomly selected for further sampling, resulting in a total of 204 sampled trees (Table A1). Each tree was classified into one of four social classes: 1 = dominant, 2 = codominant, 3 = intermediate, and 4 = overtopped (see for instance Wertz et al. 2020).

Sampling was conducted during the second half of the growing season (between early August and mid-September), when leaves were fully developed but not yet senescent. Before felling, the diameter at the stem base (hereinafter $d_{0,0}$) was measured in two perpendicular directions using a digital caliper, with a precision of 0.1 mm. Trees were then cut at ground level, and total height was measured using a metal tape with a precision of 1 cm. This destructive sampling approach was applied to quantify aboveground biomass and to construct allometric relationships (data not published). Leaf sampling represented only part of this effort but provided sufficient data for analyses focused exclusively on leaf traits.

From each sampled tree, 18 leaves were collected along the vertical profile of the crown: six leaves from the upper, six from the middle, and six from the lower crown third (see Fig. A1). Individual leaves were placed into paper envelopes labeled with specific codes (site, tree number, crown position, and leaf order). After transport to the laboratory, leaves were scanned (Fig. A2). Only leaf blades (lamina) were scanned, while petioles were excluded. Leaf area was calculated using the Easy Leaf Area software (Easlon & Bloom 2014). Leaves were subsequently dried in an oven at 95 °C for 24 hours and weighed using a high-precision laboratory balance (± 0.0001 g). In total, 3,672 leaves were processed.

An exception was made for leaves originating from the Štôla site. In this case, petioles were separated from lamina. Laminas were scanned, dried, and weighed, while petioles were dried and weighed separately. This procedure allowed the determination of both petiole mass and total leaf mass (lamina + petiole), enabling an analysis of the proportional contribution of individual leaf components. These data are important for calculating total tree-level fresh leaf area based on specific leaf area (SLA; see for instance Wang et al. 2019) and total foliage biomass. Sampling on this plot was conducted last of all sites. Based on previous experience, we realized that it is necessary to have information not only about the leaf blade but also about the petiole. The reason is that when linking SLA data with total leaf area, the proportion of these two components must be known. Data on total leaf biomass at the tree level, obtained from destructive sampling, actually include the weight of the petioles. Therefore, this portion needs to be subtracted from the combined weight of leaf blades plus petioles in order to correctly derive the total leaf area at the tree level.

SLA was calculated as the ratio of leaf area (cm^2) to dry leaf mass (g). SLA (expressed in $\text{cm}^2 \text{g}^{-1}$) was first determined at the individual leaf level, and then mean values and standard deviations were computed for each site, crown position, and tree social class.

Data archiving and processing, including nonlinear fitting, were performed using MS Excel. Statistical analyses, including one-way, two-way, and three-way ANOVA followed by Fisher's LSD test ($p < 0.05$), were conducted using Statistica 10.0. The analyses of leaf traits included the following factors: site/stand (without specifying an exact environmental or stand-related factors), crown position, and tree social class.

3. Results

Our sampled trees included young silver birches with diameters $d_{0,0}$ ranging from 4.6 mm to 358.5 mm and heights between 0.38 m and 18.36 m (Table A2). Across all sampled trees, the mean leaf area was $11.89 \pm 5.73 \text{ cm}^2$ ($\pm$ standard deviation), the mean leaf weight was 0.0812 ± 0.0475 g, and the mean SLA was $156.8 \pm 33.6 \text{ cm}^2 \text{g}^{-1}$.

Substantial differences in basic leaf traits were observed among sites/stands (Table A3). The lowest mean leaf area was recorded at the Klokočov site ($8.76 \pm 5.29 \text{ cm}^2$), while the highest was observed at the Slavošovce site ($15.77 \pm 8.15 \text{ cm}^2$). Leaf weight ranged from 0.0466 ± 0.0299 g in Klokočov to 0.1155 ± 0.0723 g in Slavošovce. The lowest SLA was $140.2 \pm 26.7 \text{ cm}^2 \text{g}^{-1}$ in Husárik, whereas the highest was recorded at Klokočov ($194.8 \pm 32.3 \text{ cm}^2 \text{g}^{-1}$).

Considering all sampled trees across sites, ANOVA analyses indicated that leaf traits were significantly influenced by site, tree social class, and leaf position within the

crown (Table A4). When considering any combination of two or all three factors, significant effects were found for leaf area, leaf mass, and SLA. The only exception was the combination of site and tree social class, which did not show significant effects on leaf mass and leaf area (Table A4).

Within tree social classes, leaf area was lowest in overtopped trees. Values were $13.38 \pm 5.75 \text{ cm}^2$, $9.80 \pm 4.38 \text{ cm}^2$, and $7.52 \pm 4.19 \text{ cm}^2$ in the upper, middle, and lower thirds of the crown, respectively (Fig. 1). Differences in leaf area among intermediate, codominant, and dominant trees were less pronounced. The highest leaf area ($16.15 \pm 8.46 \text{ cm}^2$) was found in the middle part of the crown of dominant trees.

A similar pattern was observed for leaf mass (Fig. 2). Leaf mass was significantly lowest in overtopped trees and highest in dominant trees. The clearest differences among social classes were in the upper crown, where leaf mass values were $0.092 \pm 0.047 \text{ g}$, $0.117 \pm 0.049 \text{ g}$, $0.123 \pm 0.066 \text{ g}$, and $0.128 \pm 0.057 \text{ g}$ for overtopped, intermediate, codominant, and dominant trees, respectively.

For SLA (Fig. 3), trends were opposite to those observed for leaf area and leaf mass. SLA increased from dominant to overtopped trees and from the upper to lower parts of the crown. This pattern was most pronounced in the upper crown, where SLA values were $121.68 \pm 1.80 \text{ cm}^2 \text{ g}^{-1}$, $137.74 \pm 28.34 \text{ cm}^2 \text{ g}^{-1}$, $138.86 \pm 4.67 \text{ cm}^2 \text{ g}^{-1}$, and $152.49 \pm 32.18 \text{ cm}^2 \text{ g}^{-1}$ for dominant, codominant, intermediate, and overtopped trees, respectively. Across all tree social classes and crown positions, the highest SLA ($173.87 \pm 29.21 \text{ cm}^2 \text{ g}^{-1}$) was recorded in the lower crown of overtopped trees.

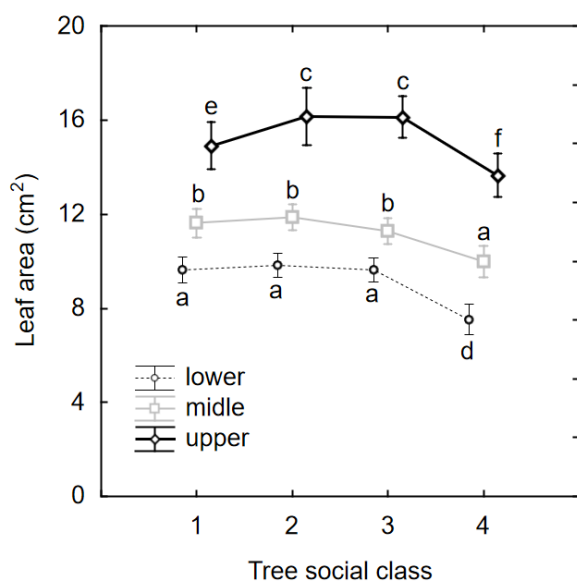


Fig. 1. Leaf blade area of silver birch in relation to crown position and social tree class. While error bars are standard errors, different letters indicate significant differences (two-way ANOVA followed by Fisher's test, $p < 0.05$).

At the Štôla site, we studied not only the leaf blade and its traits, but also the leaf stalk. The relationship between leaf stalk mass and leaf blade mass was nonlinear and showed a moderately strong correlation ($R^2 = 0.619$; Fig. 4). At the same time, the relationship between leaf blade mass and its area was strong ($R^2 = 0.736$; Fig. 5).

ANOVA analyses conducted for leaves at the Štôla site (Table A5) confirmed the same patterns observed for

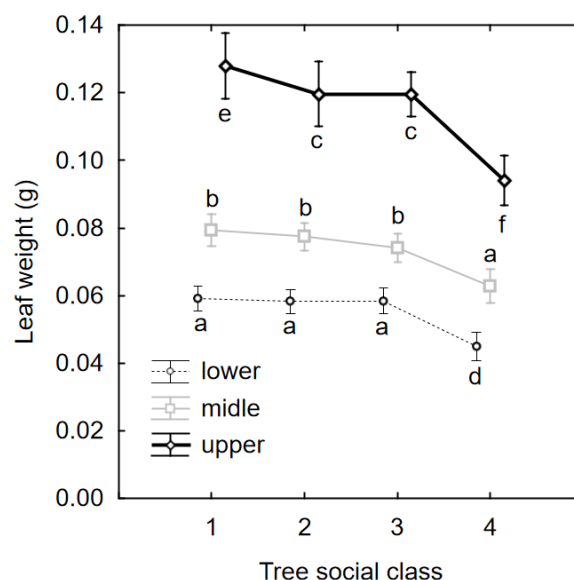


Fig. 2. Leaf blade weight (mass) of silver birch in relation to crown position and social tree class. While error bars are standard errors, different letters indicate significant differences (two-way ANOVA followed by Fisher's test, $p < 0.05$).

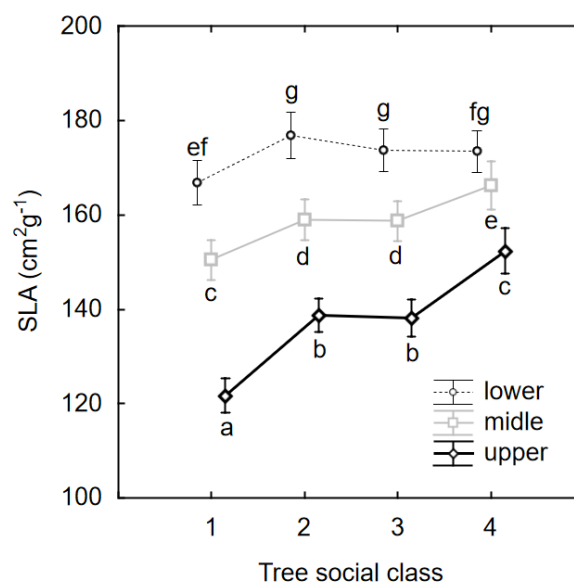


Fig. 3. Specific leaf area (SLA) of silver birch in relation to crown position and social tree class. While error bars are standard errors, different letters indicate significant differences (two-way ANOVA followed by Fisher's test, $p < 0.05$).

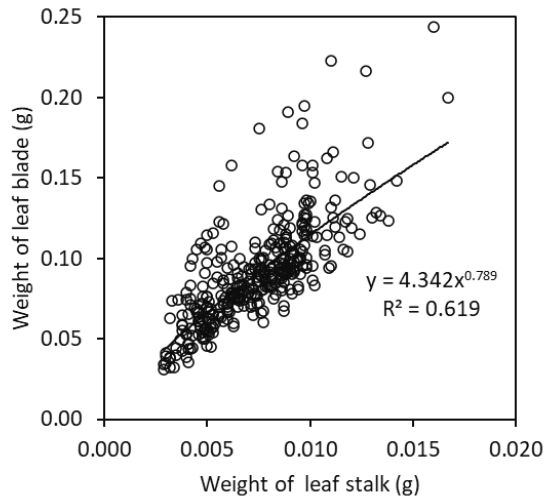


Fig. 4. Relationship between leaf stalk weight (mass) and leaf blade weight (mass) in silver birch at the Štôla site.

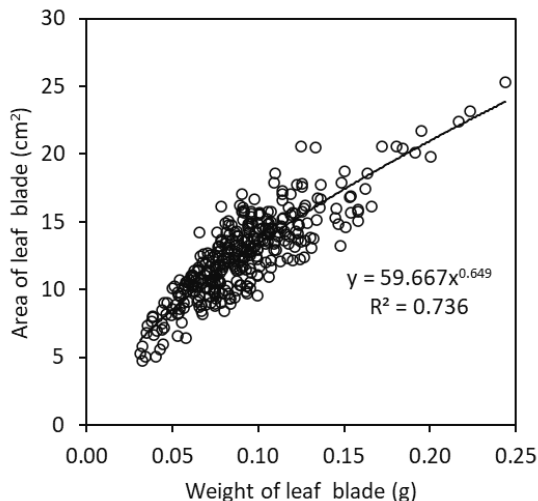


Fig. 5. Relationship between leaf blade weight (mass) and leaf blade area in silver birch at the Štôla site.

all sites combined (Table A4). This means that leaf mass, leaf area, and specific leaf area (SLA) were significantly related to both tree social class and position within the crown. In addition, the same significant relationships were found for stalk mass as well as for the combined mass of the leaf blade and stalk.

The mean leaf blade mass was 0.0937 ± 0.0384 g, while the stalk mass was 0.0074 ± 0.0028 g. Thus, leaf blade mass accounted on average for $93.26 \pm 16.83\%$ of the total leaf weight, whereas stalk mass accounted for $6.74 \pm 2.28\%$. Moreover, we found that the proportion between stalk and blade masses varied significantly with tree social class and crown position (Table A5). The highest proportion of stalk mass relative to total leaf mass was observed in the upper crown of dominant trees ($8.04 \pm 2.27\%$), whereas the lowest proportion occurred in the lower crown of overtopped trees ($6.71 \pm 2.16\%$).

4. Discussion

The wide range of tree traits observed in this study reflects substantial structural and environmental heterogeneity within and among silver birch stands. Significant differences in leaf traits among sites highlight the strong influence of local environmental conditions on leaf traits. Similar site-dependent variation in leaf area and SLA has been reported in some other tree species (e.g. European beech Norway spruce, and sessile oak) often linked to differences in soil fertility, moisture availability, and microclimate (e.g. Niinemets & Kull 1995; Poorter et al. 2009). The combination of low leaf area and mass with high SLA observed at the Klokočov site suggests the formation of thinner leaves, which is a common response to nutrient-poor or otherwise stressful conditions (Wright et al. 2004). Alternatively, it might be related to low light intensity for instance due to high stand density (Zhang et al. 2022). In contrast, the large and heavy leaves found at some sites might indicate higher biomass investment per leaf, consistent with more favorable growing conditions including light sufficiency. In fact, light availability influence not only qualitative traits of leaves, but also their total quantity (Barna 2001; Jarčuška & Barna 2011).

Across all sites, leaf area and leaf mass were lowest in overtopped trees and increased with improving social status, particularly in the upper and middle crown. This pattern agrees well with previous studies showing that suppressed trees produce smaller leaves due to reduced light availability and carbon limitation (Sellin & Kupper 2007; Niinemets et al. 2014). The relatively small differences among intermediate, codominant, and dominant trees suggest that the strongest functional differentiation occurs between overtopped and non-overtopped individuals, as also observed in mixed and even-aged stands of light-demanding species dominance (Pretzsch 2014). Vertical gradients within the crown further influenced leaf traits (see also Barna 2004). The decrease in leaf area and mass from the upper to the lower crown parts is documented within-crown acclimation to light availability (Ellsworth & Reich 1993). Leaves in the upper crown are exposed to high irradiance and thus benefit from greater biomass investment, whereas shaded lower-crown leaves remain smaller and lighter. From a physiological perspective, the leaves in the upper crown, which are thicker, and characterized by lower SLA, represent sun-type foliage with a higher photosynthetic capacity and, therefore, usually have greater production potential. In contrast, shade-type foliage is typically thinner, with higher SLA and lower photosynthetic capacity (e.g. Barna 2004; Legner et al. 2013; Martin et al. 2020).

SLA showed trends opposite to those of leaf area and mass, increasing from dominant to overtopped trees and from the upper to the lower crown. This inverse relationship between SLA and light availability is a well-established response across woody species (Poorter et al. 2009). High SLA values in shaded crown positions

indicate thinner leaves with lower construction costs, which enhances light use efficiency under low irradiance (Niinemets et al. 2014). The exceptionally high SLA observed in the lower crown of overtopped trees reflects extreme shade acclimation, a pattern previously reported for suppressed individuals growing under dense canopies (Touzot et al. 2025).

The significant interaction effects among site, tree social position, and crown position emphasize the multifactorial control of leaf morphology. Similar interactive effects have been reported in studies demonstrating that vertical light gradients often override site-level influences, while site conditions modulate the magnitude of within-crown responses (Niinemets et al. 2014).

The detailed analysis at the Štôla site revealed strong coordination between leaf area and leaf mass, consistent with previous findings that leaf size in birch is primarily driven by blade biomass investment (Niinemets & Kull 1995). The nonlinear relationship between blade mass and stalk mass indicates that support tissues do not scale proportionally with blade size, a pattern also reported in other deciduous tree species (Pickup et al. 2025). On average, the leaf blade accounted for more than 93% of total leaf mass, confirming that silver birch prioritizes photosynthetic tissue over structural support. However, variation in the proportion of stalk mass with social position and crown depth suggests adaptive allocation. Higher stalk proportions in the upper crown of dominant trees likely reflect increased mechanical and hydraulic demands associated with larger leaves, higher wind exposure, and elevated transpiration rates (Kozłowski & Pallardy 1997). In contrast, shaded lower-crown leaves of overtopped trees showed lower relative investment in stalk tissue, consistent with reduced mechanical stress and smaller leaf size.

Taken together, these results demonstrate pronounced morphological plasticity of silver birch leaves in response to both external environmental conditions and internal canopy gradients. The observed coordination among leaf area, mass, and SLA supports the concept of a flexible resource-use strategy, allowing silver birch to optimize carbon gain under contrasting light environments. Such plasticity is widely recognized as a key trait contributing to the competitive ability and broad ecological amplitude of silver birch (San-Miguel-Ayanz et al. 2016).

5. Conclusions

Silver birch leaves exhibited substantial variation in leaf area, mass, and SLA across sites, tree social classes, and crown positions, reflecting responses to both environmental conditions and within-canopy light gradients. Overtopped trees produced smaller, lighter leaves with higher SLA, whereas dominant trees had larger,

heavier leaves, particularly in the upper crown. Leaf blades accounted for over 93% of total leaf mass, with stalk allocation varying according to mechanical and hydraulic demands. The observed coordination among leaf traits highlights the morphological plasticity and flexible resource-use strategy of silver birch, enabling adaptation to contrasting light and growth conditions. At the very end of this study, it is necessary to acknowledge its limitation: the absence of detailed characteristics of the stands and sites. Such information could help explain inter-stand (site) differences in leaf traits. Addressing this gap presents a promising challenge for future research.

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Appendix

Table A1. Basic characteristics of the sites and sampled silver birch.

Site	Coordinates (N; E)		Altitude (m a.s.l.)	Vegetation belt	Number of sample trees	Mean diameter $d_{0.0}$ (mm)	Mean tree height (m)	Stand age (years)
Bacúrov	48.5271	19.0423	449	beech	20	56.3	5.52	11
Danielov dom	49.1149	20.1674	985	spruce	20	223.5	9.74	15
Gbely	48.7289	17.1025	171	oak	23	47.6	3.09	7
Husárik	49.4143	18.7692	750	spruce-fir-beech	20	45.3	2.62	5
Klokočov	49.4621	18.5413	692	fir-beech	20	23.7	2.03	4
Morovno	48.7368	18.7188	619	beech	17	39.9	3.83	8
Slavošovce	48.7301	20.2928	640	beech	22	33.9	2.42	5
Smokovec	49.1291	20.2310	890	spruce	23	41.8	3.76	9
Štôla	49.1121	20.1652	957	spruce	20	284.4	15.07	20
Výrava	49.2068	21.9747	505	oak-beech	19	34.7	3.01	6

Table A2. Mean tree characteristics and silver birch leaf traits (based on leaf blades) across all sites.

Characteristics	Mean	St. dev.	Minimum	Maximum	25 p.	75 p.
Diameter $d_{0.0}$ (mm)	106.7	109.7	4.6	358.5	26.6	186.0
Tree height (m)	6.15	4.93	0.38	18.36	2.38	9.60
Leaf area (cm ²)	11.89	5.73	1.26	61.40	8.34	14.22
Leaf weight (g)	0.0812	0.0475	0.0061	0.4570	0.0494	0.0998
SLA (cm ² g ⁻¹)	156.8	33.6	81.0	316.6	133.4	176.0

Table A3. Key silver birch leaf traits (based on leaf blades) by site.

Site	Characteristics	Mean	St. dev.
Bacúrov	Leaf area (cm ²)	13.03	3.33
	Leaf weight (g)	0.0863	0.0296
	SLA (cm ² g ⁻¹)	156.6	26.8
Danielov dom	Leaf area (cm ²)	11.45	2.92
	Leaf weight (g)	0.0742	0.0337
	SLA (cm ² g ⁻¹)	168.8	42.1
Gbely	Leaf area (cm ²)	13.01	7.43
	Leaf weight (g)	0.0876	0.0515
	SLA (cm ² g ⁻¹)	152.4	20.9
Husárik	Leaf area (cm ²)	6.86	3.30
	Leaf weight (g)	0.0532	0.0324
	SLA (cm ² g ⁻¹)	140.2	26.7
Klokočov	Leaf area (cm ²)	8.76	5.29
	Leaf weight (g)	0.0466	0.0299
	SLA (cm ² g ⁻¹)	194.8	32.3
Morovno	Leaf area (cm ²)	11.41	5.23
	Leaf weight (g)	0.0710	0.0388
	SLA (cm ² g ⁻¹)	169.1	29.9
Slavošovce	Leaf area (cm ²)	15.77	8.15
	Leaf weight (g)	0.1155	0.0723
	SLA (cm ² g ⁻¹)	147.4	28.1
Smokovec	Leaf area (cm ²)	13.05	6.80
	Leaf weight (g)	0.0866	0.0523
	SLA (cm ² g ⁻¹)	160.4	30.3
Štôla	Leaf area (cm ²)	12.73	3.57
	Leaf weight (g)	0.0937	0.0384
	SLA (cm ² g ⁻¹)	142.7	26.6
Výrava	Leaf area (cm ²)	11.26	5.51
	Leaf weight (g)	0.0809	0.0458
	SLA (cm ² g ⁻¹)	147.4	29.7

Table A4. ANOVA of silver birch leaf traits (based on leaf blades) across all sites. Significant relationships ($p < 0.05$) are highlighted in bold.

Dependent variable	Predictor	F value	p value
Leaf mass (weight)	site (S)	50.17	<0.001
	tree social class (TSC)	7.06	<0.001
	position in crown (PC)	335.21	<0.001
	S × TSC	2.76	<0.001
	S × PC	14.39	<0.001
	TSC × PC	1.52	0.168
	S × TSC × PC	1.95	<0.001
Leaf area	site (S)	52.28	<0.001
	tree social class (TSC)	14.16	<0.001
	position in crown (PC)	488.66	<0.001
	S × TSC	3.32	<0.001
	S × PC	10.89	<0.001
	TSC × PC	1.55	0.159
	S × TSC × PC	1.78	<0.001
SLA	site (S)	59.06	<0.001
	tree social class (TSC)	21.76	<0.001
	position in crown (PC)	265.71	<0.001
	S × TSC	5.42	<0.001
	S × PC	6.32	<0.001
	TSC × PC	4.19	<0.001
	S × TSC × PC	1.75	<0.001

Table A5. ANOVA of silver birch leaf traits at the Štôla site. Significant relationships ($p < 0.05$) are highlighted in bold.

Dependent variable	Predictor	F value	p value
Leaf mass (blade weight)	tree social class (TSC)	2.68	<0.001
	position in crown (PC)	32.56	<0.001
	TSC × PC	2.56	0.020
Stalk mass (weight)	tree social class (TSC)	5.98	<0.001
	position in crown (PC)	30.30	<0.001
	TSC × PC	1.61	0.143
Mass of blade and stalk (weight together)	tree social class (TSC)	2.60	0,048
	position in crown (PC)	33.71	<0.001
	TSC × PC	2.55	0.020
Shares of stalk mass to blade and stalk mass	tree social class (TSC)	10.64	<0.001
	position in crown (PC)	5.12	0.006
	TSC × PC	1.73	0.113
SLA	tree social class (TSC)	10.18	<0.001
	position in crown (PC)	150.74	<0.001
	TSC × PC	2.74	0.013

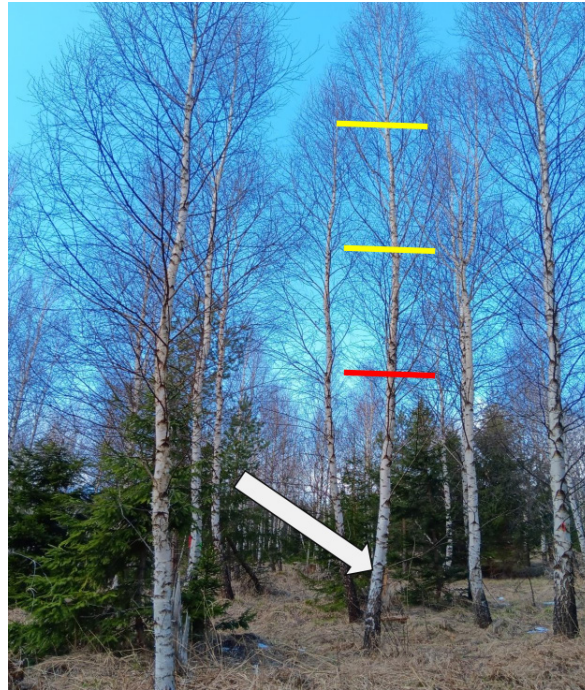


Fig. A1. Silver birch with a Norway spruce understory at the Štôla site (very early spring 2025, before leaf burst). The white arrow marks a sampled tree classified in tree social class 2, i.e., codominant. The red line indicates the lower limit of the live crown, while the yellow lines delineate the upper, middle, and lower thirds of the crown.

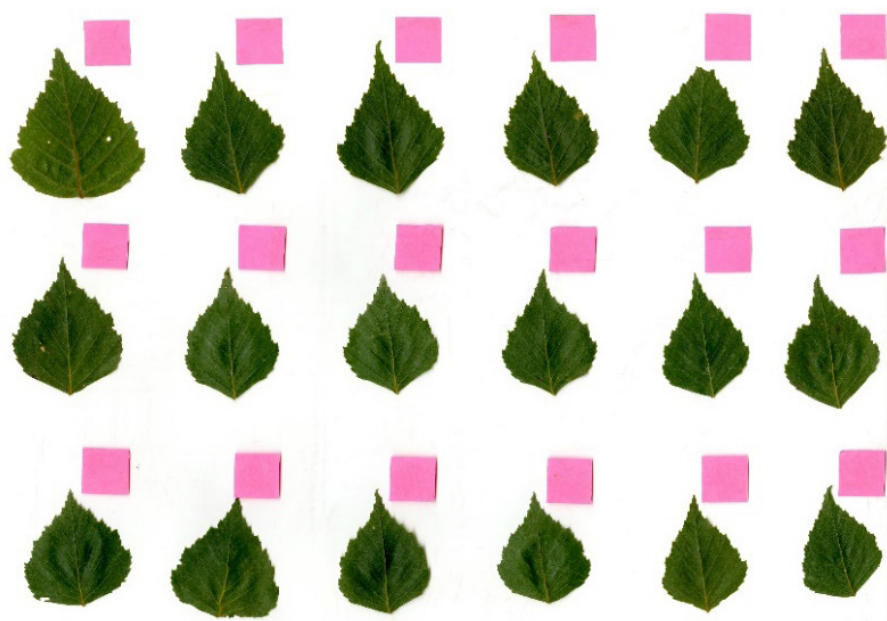


Fig. A2. Example of eighteen leaf blades sampled from a single silver birch tree. The upper, middle, and lower rows of leaves correspond to the upper, middle, and lower thirds of the crown, respectively. The pink squares represent a reference area measuring 2×2 cm.