

***Pyrola chlorantha* (Ericaceae) on self-overgrowing industrial dumps and in natural habitats in the Middle Urals**

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Received: 19 March 2026 / Accepted: 05 May 2026 / Available online: 14 May 2026



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Abstract

The study of ecological and biological characteristics and adaptation mechanisms of species in anthropogenically transformed habitats is an important aspect of biodiversity conservation. The aim of this study was to test the hypothesis that environmental conditions influence the population structure and anatomical and morphological traits of *Pyrola chlorantha* Sw. in anthropogenically disturbed and natural habitats in the Middle Urals. To address this, we characterised the habitats and analysed the population structure and anatomical–morphological features of the species. Studies have shown that *P. chlorantha* grows in mixed and small-leaved forest phytocoenoses dominated by *Pinus sylvestris* L., *Populus tremula* L. and *Betula pendula* Roth. Forest communities on industrial dumps are characterised by lower values of tree canopy density, projective cover of the shrub and the herb–shrub layer compared to natural habitats. In all studied sites, *P. chlorantha* grew in small groups. In anthropogenic habitats, density ranged from 21 to 62 shoots per 100 m², and in natural habitats from 33 to 106 shoots per 100 m². All studied populations of *P. chlorantha* are predominantly vegetative type. Only in the population growing on a reclaimed area of a hydrodump of alluvial gold deposits, the proportions of vegetative and generative shoots were equal. *P. chlorantha* plants, growing in anthropogenic and natural habitats, did not differ in most morphological characteristics. Adaptation of *P. chlorantha* to technogenic environmental conditions occurred through rearrangements of the anatomical and morphological parameters of the leaves of generative shoots, involving a decrease in leaf area, an increase in leaf thickness, and a decrease in the total assimilating surface. Correlation analysis demonstrated a statistically significant negative correlation between the total leaf area of generative shoots and habitat light availability, according to Ellenberg indicator values.

Key words: anthropogenic habitats, biometric parameters, disturbed lands, forest phytocoenoses, ontogenetic structure, population density, Pyroleae.

Introduction

Anthropogenic impact on the biosphere leads to profound changes in the vegetation cover of the Earth (including a reduction in the number of species due to the transformation or direct destruction of their natural habitats) (Young et al. 2022, Luneva 2023, Campbell et al. 2024). Restoration of biological diversity is fundamental for the sustainable development of plant communities. In many industrial regions, a source of disturbance to natural landscapes and their significant pollution are dumps formed as a result of the activities of mining and processing enterprises (Kupriyanov and Manakov 2016, Zheleva et al. 2016). The Middle Urals is a region with a long history of economic development. Large areas of industrial dumps have accumulated here. During the restoration of vegetation cover on industrial dumps in the Middle Urals, forest phytocoenoses are primarily formed. In these forest phytocoenoses, during succession processes, typical forest species colonise the area, including representatives of the Ericaceae Juss. family and the tribe Pyroleae (Glazyrina et al. 2024).

The tribe Pyroleae has a circumpolar boreal range, with species distributed mainly in the temperate and cool temperate regions of the northern hemisphere of the Earth (North America, Europe, and Asia) (Anchev 1982, Bobrov 2009, Dodds 2023). In the flora of Russia, Pyroleae is represented by 4 genera (*Chimaphila* Pursh, *Orthilia* Raf., *Pyrola* L. and *Moneses* Salisb. ex Gray) and 15 species (Bobrov 2009). In the Sverdlovsk Region (the Middle Urals), there are 9 of those species that are typical components of the herb-shrub layer of coniferous and mixed forests.

It is now established that Pyroleae

exhibit two trophic strategies that enable them to colonise shaded forest habitats (Tedersoo et al. 2007). As partially mycoheterotrophic plants, they obtain nutrients both through photosynthesis and via associations with fungi. The degree of dependence on fungal-derived carbon varies depending on developmental stage, habitat type, light availability, and the presence of specific mycobionts in the community (Tedersoo et al. 2007, Johansson et al. 2015).

Anthropogenically transformed ecosystems are typically characterised by low fertility due to reduced mineral content (especially nitrogen), low water-holding capacity, increased insolation, and limited availability of mycobionts (Chibrik et al. 2011). Such conditions can lead to changes in the population structure and influence the anatomical and morphological characteristics of plants (Tarshis 2005, Filimonova et al. 2021, Urazgildin and Kulagin 2021).

The study of the species composition of plant communities, identification of ecological and biological characteristics, adaptive mechanisms, and life strategies of species in anthropogenic habitats, as well as assessment of their population status, are important aspects of the preservation of biological diversity and rational use of plant resources. There are few publications devoted to the study of populations of the tribe Pyroleae, both in natural and disturbed habitats (Tarshis 2005, Polyanskaya 2012, Dubrovnyaya and Mavlyudova 2019, Ilyina et al. 2022).

The object of our study was a circum-boreal-ancient Mediterranean species – *Pyrola chlorantha* Sw. This species is included in the Red Data Books of 12 regions of Russian Federation. Limiting factors for the species distribution within its range are: economic usage of pine for-

ests, narrow phytocoenotic specialisation, or its position near the border of range (Il'yina et al. 2022, Dodds 2023).

P. chlorantha is a long-rhizomatous, wintergreen, rosette-forming perennial herbaceous plant. This species is a mesophyte, sciophyte, and partial mycoheterotroph (Bobrov 2009, Johansson et al. 2015). The life form of *P. chlorantha* is represented by a modular system that is typical of all species of the genus *Pyrola* (Bobrov 2009). *P. chlorantha* grows in coniferous (formed predominantly by *Pinus sylvestris* L.) and mixed green-moss forests, on relatively dry, slightly acidic, neutral, and slightly alkaline soils (Bagdasarova et al. 1983, Bobrov 2009). In the Middle Urals, it occurs in forests in small groups of individuals (Knyazev et al. 2018).

The aim of this study was to test the hypothesis that environmental conditions influence the population structure, as well as the anatomical and morphological traits of *P. chlorantha* in both industrially disturbed and natural habitats in the Middle Urals.

Study Sites and Habitats

We studied the habitats of 6 anthropogenic populations of *P. chlorantha* (AP1–AP6), growing in forest plant communities formed as a result of the self-overgrowth process on dumps of the mining and processing industry, and 2 populations (NP1, NP2) in natural forest phytocoenoses.

All habitats are located in the low-mountain part of the eastern slope of the Ural Mountains (Middle Urals), in the subzone of southern taiga of the Sverdlovsk region. The climate is temperate continental, characterised by sharp variability of weather seasons (with cold long winters and warm short summers). In terms of

heat supply, the climate is characterised as cool; in terms of moisture supply, it is characterised as humid. The average annual temperature in the Sverdlovsk region for the period 2013–2022 was +2.24 °C. The average annual precipitation for the same period was 533 mm. Most of the mountainous Urals are covered with coniferous and mixed forests.

The dump substrates are non-toxic and characterised by low concentrations of plant-available mineral nutrients. Soil reaction (pH) ranges from slightly acidic to slightly alkaline and, in many sites, is close to neutral (Chibrik et al. 2011).

Methodology

The study of *P. chlorantha* populations was conducted during the growing seasons 2021–2022. Geobotanical survey of forest phytocoenosis was carried out using the detailed route method. In *P. chlorantha* habitats, 2–3 sample plots (100 m²) were established. Indicators, such as species composition, tree canopy density, and shrub layer projective cover (PC), were assessed. Using Raunkiaer plots (0.25 m²), the following characteristics were determined: PC of the herb–shrub layer, moss–lichen cover (MLC), and species diversity. The age of plant communities was determined based on mine survey data, corresponding to the end of mining and the cessation of human activity. Latin names of plant species are given in accordance with the international taxonomic database Plants of the World Online (Royal Botanic Gardens, Kew 2026).

Population studies were conducted according to generally accepted methods (Zlobin et al. 2013). To study the spatial structure of *P. chlorantha* populations in the studied communities, shoots were

chosen as the counting unit. Vegetative and generative shoots were distinguished. The average population density was determined by the number of shoots per unit area, as well as the ecological density (abundance) over the entire area occupied by the population (Odum 1986). The following morphological traits were measured for vegetative and generative shoots: shoot height (cm), leaf area (calculated using the ellipse formula, cm²), number of leaves, and total leaf area per shoot (cm²). Additionally, inflorescence length (cm) and number of flowers were measured for generative shoots. Based on the morphometric parameters of generative shoots, the population vitality index (IVC) was calculated (Ishbirdin et al. 2005).

An assessment of conditions in *P. chlorantha* habitats was carried out using indicator methods for 5 direct-acting environmental factors, using Ellenberg's indicator values (Ellenberg et al. 1991): light (L), temperature regime (T), soil moisture (F), soil acidity (R), and soil nitrogen content (N). Values of ecological factors for the habitat of each population were calculated based on the species composition of the communities, taking into account species abundance.

Ten flowering plants from each population were used to study the leaf mesostructure. Transverse sections of leaf discs were obtained using a freezing microtome MZ-2 (JSC Kharkov plant 'Tochmedpribor', Kharkov, Ukraine). From mature leaves of generative individuals in 2021, about 30 leaf discs (3 discs per plant) were fixed in 70% ethanol to study mesostructural parameters: leaf thickness, mesophyll thickness, upper and lower epidermis thickness, and thickness of palisade and spongy tissue. All measurements were carried out in 30 replicates (3 measurements per plant) using a Meiji

MT 4300 L light microscope (Meiji Techno, San Jose, CA, USA) and determined with a computer-assisted protocol based on MesoPlant software (OOO SIAMS, Ekaterinburg, Russia).

Statistical data processing was performed using Microsoft Excel 2019 and STATISTICA 12 software packages. The significance of differences was assessed using the non-parametric Mann–Whitney test at a significance level of $p < 0.05$.

Results and Discussion

Characteristics of anthropogenic habitats of *P. chlorantha*

The AP1 population of *P. chlorantha* was found at the dam of the Shuralino–Yagodnoye hydro placer gold deposit, in a forming small-leaved forest phytocoenosis dominated by *Betula pendula* Roth, *Populus tremula* L. and single individuals of *P. sylvestris* (57°24'28" N, 60°10'26" E). The age of the plant community was 35. The site was characterised by a well-developed undergrowth (*Salix caprea* L., *Salix myrsinifolia* Salisb., *Sorbus aucuparia* L., *Chamaecytisus ruthenicus* (Fisch. ex Wolf.) Klásk.). The herb–shrub layer was dominated by *Lathyrus pratensis* L., *Vicia cracca* L., *Orthilia secunda* (L.) House, *Pyrola rotundifolia* L., and *Melampyrum pratense* L. The MLC was represented by single individuals of green mosses. The geobotanical characteristics of the studied sites are summarised in Table 1.

The AP2 population of *P. chlorantha* was found in a mixed forest phytocoenosis forming on a reclaimed site (covered with a layer of peat) of a hydraulic dump (57°24'28" N, 60°10'30" E). The age of the plant community was 32. The tree layer was dominated by *P. sylvestris*; the under-

Table 1. Geobotanical characteristics of the studied sites.

Code	Tree canopy density	Under-growth cover, %	Herb-shrub cover, %	Moss-lichen cover, %	Species diversity, number of species, per 0.25 m ²	Evaluation of environmental factors based on the Ellenberg's indicator values, points				
						L	T	F	R	N
AP1	0.6–0.7	20–45	2.0–25.0	0–7	5.1	6.0	4.9	5.8	5.9	4.6
AP2	0.5–0.6	10–15	3.0–40.0	5–15	4.2	6.5	5.3	5.3	5.7	3.6
AP3	0.5–0.6	8–20	3.0–40.0	0–15	5.8	6.1	5.6	5.1	5.7	4.0
AP4	0.6–0.8	5–10	3.0–50.0	0–20	4.6	6.2	5.4	5.1	6.5	4.1
AP5	0.4–0.7	0	2.0–35.0	0–5	2.5	6.4	5.3	4.9	6.8	3.7
AP6	0.6–0.8	0	0.5–12.0	2–35	2.9	6.5	5.4	4.9	6.5	4.0
NP1	0.6–0.8	55–60	4.0–55.0	0–12	6.5	5.7	5.6	5.3	5.2	3.7
NP2	0.7–0.8	5–10	4.0–75.0	1–90	7.6	5.8	4.9	4.9	5.4	3.6

Note: AP – population in anthropogenic habitat, NP – population in natural forest community. Habitat factors based on Ellenberg's indicator values: light (L), temperature regime (T), soil moisture (F), soil acidity (R), soil nitrogen richness (N).

growth included *P. sylvestris*, *B. pendula*, *P. tremula*, and single individuals of *S. caprea* and *Ch. ruthenicus*. The herb-shrub layer was dominated by *O. secunda*, *P. rotundifolia*, *Trifolium medium* L., *Fragaria vesca* L., with single occurrences of *Antennaria dioica* (L.) Gaertn. and *Linnaea borealis* L. The MLC spread on stumps and tree bases.

The AP3 population of *P. chlorantha* was found in a small-leaved forest phytocoenosis forming on the ash substrate of a non-reclaimed area of the Verkhne-tagil'skaya thermal power station (VTTSP) (57°20'20" N, 59°56'31" E). The age of the plant community was 45. The tree canopy was dominated by small-leaved species (*B. pendula* and *P. tremula*) with an admixture of conifers (*P. sylvestris* and *Pinus obovata* Ledeb.). The undergrowth consisted of *S. myrsinifolia*, *S. aucuparia*, *Prunus padus* L., *Viburnum opulus* L., and *Ch. ruthenicus*. The herb-shrub layer was dominated by *Trifolium repens* L., *P. rotundifolia*, *O. secunda*, and *Calamagrostis epigejos* (L.) Roth; small groups of *Chimaphila umbellata* (L.) W.P.C. Barton,

Pyrola minor L., and *Moneses uniflora* (L.) A. Gray were found. The MLC was poorly developed, occurring only on the lower parts of tree trunks (Table 1).

The AP4 population of *P. chlorantha* was found in a mixed forest phytocoenosis forming on a reclaimed area (applying loam in strips on ash) of the VTTSP ash dump (57°20'46" N, 59°56'46" E). The age of the plant community was 50. The tree layer was dominated by *B. pendula*, *P. tremula*, *P. sylvestris* and *P. obovata*, with single occurrences of *Betula pubescens* Ehrh., *Alnus incana* (L.) Moench, and *Populus* sp. The undergrowth included *Pinus sibirica* Du Tour and *Larix sibirica* Ledeb. The herb-shrub layer was dominated by *F. vesca*, *O. secunda*, *L. pratensis*, *V. cracca*, and *Festuca rubra* L. The MLC was noted on the lower parts of tree trunks and on stumps.

The AP5 population of *P. chlorantha* was found in a mixed forest phytocoenosis forming on the upper tier of the dump of the Shabrovsky talc-magnesite deposit (56°37'45" N, 60°36'00" E). The age of the plant community was 55. The phyto-

coenosis was dominated by *B. pendula* and *P. sylvestris*, with single occurrences of *Acer negundo* L. The undergrowth included abundant seedlings of *P. sylvestris* and *A. negundo* and single individuals of *Ch. ruthenicus* and *S. aucuparia*. The herb–shrub layer included *O. secunda*, *P. chlorantha*, *V. cracca*, *T. medium*, *Trifolium lupinaster* L., *Epipactis atrorubens* (Hoffm.) Besser, and *Plantago media* L. The MLC spread on stumps and tree bases (Table 1).

The AP6 population of *P. chlorantha* was found in a mixed forest phytocoenosis forming on the middle tier of the dump of the Shabrovsky talc–magnesite deposit (56°37'44" N, 60°36'00" E). The age of the plant community was 60. The tree layer was dominated by *P. sylvestris* and *B. pendula*, with *B. pubescens* also present. The undergrowth was represented by single seedlings of *P. sylvestris*, *P. tremula*, and *A. negundo*. The herb–shrub layer was dominated by *O. secunda*, *P. rotundifolia*, *P. minor*, *Ch. umbellata*, *P. chlorantha*, *Pimpinella saxifraga* L., *Achillea millefolium* L., *T. pratense*, *T. medium*, *V. cracca*, *Platanthera bifolia* (L.) Rich., and *E. atrorubens*. In the recesses of the relief, the MLC was well-developed (Table 1).

Characteristics of natural habitats of *P. chlorantha*

The NP1 population of *P. chlorantha* grew in a natural forest massif located 68 km northwest of Yekaterinburg (57°22'05" N, 60°01'59" E). The tree layer was represented by *P. sylvestris*, *P. obovata*, with the participation of *Abies sibirica* Ledeb., *P. sibirica* and *B. pendula*. The understorey included *Rosa acicularis* Lindl., *S. caprea*, *Ch. ruthenicus*. The herb–shrub layer was dominated by *F. vesca*, *Rubus saxatilis* L., *Vaccinium vitis-idaea* L., as

well as *O. secunda*, *P. rotundifolia*, *Calamagrostis arundinacea* (L.) Roth, *Poa angustifolia* L., *Aegopodium podagraria* L. The MLC spread over the stumps and tree bases. The geobotanical characteristics of the studied natural habitats are summarised in Table 1.

The NP2 population of *P. chlorantha* grew in a natural forest massif dominated by *P. sylvestris*, located 35 km southeast of Yekaterinburg (56°36'02" N, 61°03'10" E). In the sparse understorey and at forest edges, *B. pendula*, *S. aucuparia*, *P. padus*, *Rubus idaeus* L. occurred. The herb–shrub layer was dominated by *Vaccinium myrtillus* L., *V. vitis-idaea*, *R. saxatilis*, *F. vesca*, as well as *O. secunda*, *P. rotundifolia*, *Galium boreale* L., *Pulmonaria mollis* Wulfen ex Hornem., *Filipendula vulgaris* Moench, *C. arundinacea*, *Brachypodium pinnatum* (L.) Beauv. The MLC spread in spots at the recesses of the relief and the bases of tree trunks.

Our studies have shown that plant communities formed on industrial dumps (AP1–AP6) were characterised by lower species richness per unit area and a sparser cover of the herb–shrub layer compared to natural forest phytocoenoses (NP1–NP2). Plant communities in anthropogenic habitats (AP1–AP6) were characterised by higher total projective cover of the tribe Pyroleae species (22–50 %) and species of Fabaceae Lindl. family (11–36 %), while in natural forests (NP1–NP2) these indicators ranged from 14 to 19 % and from 1 to 11 %, respectively. The projective cover of *P. chlorantha* in anthropogenic habitats was higher (6–22 %) than in natural habitats (3–12 %).

It is known that the underground part of *P. chlorantha* is located in the litter or in the moss–lichen layer. In the studied forest phytocoenoses, both natural and those forming on dumps, litter thickness

varied between 3 and 7 cm, averaging 5 cm. According to previous studies, the pH of the litter in the studied habitats ranged from slightly acidic (pH = 5.3–5.6) to neutral (pH = 5.7–6.1), while organic carbon content ranged from 22.4 % to 35.0 %, and nitrogen content from 1.1 % to 1.7 % (Glazyrina et al. 2024).

Assessment of the ecological conditions of anthropogenic and natural habitats of *P. chlorantha* using Ellenberg indicator values (Ellenberg et al. 1991) showed that light availability varied from 10 % to 20 %, averaging 6.3 and 5.8 scores, respectively; the temperature regime was moderately warm (5.3 scores). The species inhabits dry and moderately moist habitats (5.2 and 5.1 scores), with soil reaction ranging from moderately acidic to slightly acidic and neutral (6.2 and 5.3 scores), and moderately supplied with mineral nitrogen (4.0 and 3.7 scores). In anthropogenic habitats of *P. chlorantha* in the Middle Urals, light availability indicators are slightly higher compared to natural habitats due to the lower degree of formation of the tree, shrub, and herb–dwarf shrub layers, as well as higher pH values of the substrates.

Characteristics of *P. chlorantha* populations

P. chlorantha exhibits a clumped spatial distribution of individuals. This is explained by the vegetative reproduction of the species, as well as its ability to disperse the vast majority of seeds (up to 95.7 %) to a distance of no more than 5 m (Johansson et al. 2014, Ilyina et al. 2022). In all studied habitats, *P. chlorantha* grew in small groups. The group size ranged from 2 to 7 per 100 m² in anthropogenic habitats and from 3 to 12 per 100 m² in natural habitats (Table 2). Groups included from 5.6 to 27.0 shoots per 0.25 m² in anthropogenic habitats, and from 7.8 to 9.6 shoots per 0.25 m² in natural habitats. The number of shoots per 100 m² in anthropogenic habitats ranged from 21 (AP1) to 62 (AP4), and in natural habitats from 33 (NP2) to 106 (NP1). The average shoot density of *P. chlorantha* in anthropogenic habitats was similar to that in populations of this species at the southern border of its range (Ilyina et al. 2022).

Studies showed that in most examined populations, the proportion of vegetative shoots was 1.1–49.0 times higher

Table 2. Density and ontogenetic structure of populations of *P. chlorantha*.

Code	Density of population, number			Distribution of individuals at different age stage, %			Population vitality in- dex (IVC)
	of groups		of shoots	vegetative	generative	vegetative/ generative	
	100 m ²	100 m ²	0.25 m ²				
AP1	2	21	10.5	90.5	9.5	9.5	1.06
AP2	2	54	27.0	46.3	53.7	0.9	0.88
AP3	7	40	4.5	77.8	22.2	3.5	1.01
AP4	7	62	5.6	67.8	32.2	2.1	0.87
AP5	6	55	9.2	90.9	9.1	10.0	1.11
AP6	3	50	8.3	98.0	2.0	49.0	0.97
NP1	12	106	9.6	82.1	17.9	4.6	1.05
NP2	3	33	7.8	51.5	48.5	1.1	1.20

Note: AP – population in anthropogenic habitat, NP – population in natural forest community.

than that of generative shoots (Table 2). In all populations, 2–3-year-old vegetative shoots bearing 3–7 leaves predominated, accounting for 55.6 % to 85.7 % of individuals. These findings are consistent with previous reports by Bagdasarova et al. (1983). In many shade-tolerant herbaceous species, vegetative reproduction predominates under conditions of limited light availability (Goryshina 1979).

An exception was observed in the population located in the reclaimed area of the Shuralino–Yagodnoye hydroplacer gold deposit (AP2), where the proportion of vegetative shoots was 1.2 times lower than that of generative shoots. This pattern is likely associated with the occurrence of *P. chlorantha* in relatively open stands within so-called ‘light windows’. In this site, herbaceous and shrub layer were lower and less dense than in the other, resulting in increased light availability. Elevated light levels are known to promote seed-based reproduction in shade-tolerant species (Goryshina 1979).

Analysis of morphological traits of *P. chlorantha* showed that, across the studied populations, the mean height of vegetative shoots ranged from 5.1 ± 1.2 to 7.4 ± 1.3 cm, while generative shoots ranged from 12.6 ± 1.0 to 16.6 ± 1.2 cm. Inflorescence length varied from 1.6 ± 0.3 to 2.6 ± 0.3 cm. Inflorescences bearing 2–5 flowers predominated, although shoots with a single flower or with 7–8 flowers were also recorded. This variation suggests generally favourable mineral nutrition conditions in the studied habitats. Overall, the results are in consistent with previous reports (Bagdasarova et al. 1983, Tarshis 2005, Knyazev et al. 2018).

Correlation analysis revealed a statistically significant positive correlation between the light factor (according to Ellenberg et al. 1991) and inflorescence

length ($r = 0.76$, $p < 0.05$). Light availability in the studied habitats was strongly influenced by tree canopy density and by the percentage cover of the shrub and herb–shrub layers. Accordingly, a statistically significant negative correlation was found between these parameters and inflorescence length ($r = -0.71$, $r = -0.75$, $r = -0.78$, respectively; $p < 0.05$).

The leaves of *P. chlorantha* are winter-green, subcoriaceous, elliptical, clustered in a rosette at the base on long petioles, and live for several years without signs of ageing (Lallemant et al. 2017). Leaves are often reduced to the size of scales, while retaining both the blade and the petiole parts. Leafless shoots are often formed (Bagdasarova et al. 1983, Bobrov 2009, Dodds 2023).

The studies have shown that in anthropogenic habitats, the proportion of leafless generative shoots of *P. chlorantha* varied from 7 to 19 %; in contrast, in natural habitats, no leafless shoots were found. Correlation analysis revealed a statistically significant direct dependence between the proportion of leafless generative shoots and habitat light conditions (according to Ellenberg et al. 1991) and an inverse dependence on the PC of the herb–shrub layer ($r = 0.79$, $r = -0.78$; $p < 0.05$).

The number of developed leaves in rosettes of vegetative and generative shoots varied from 1–2 to 5–7. In 1-year-old vegetative shoots, the leaf area was often less than 0.7 ± 0.2 cm², but larger leaves also occurred. In 2–3-year-old vegetative shoots, the area of a developed (mature) leaf varied from 1.6 ± 0.4 to 4.8 ± 0.5 cm². The maximum leaf sizes were found in AP5, AP6, NP1, and NP2. Correlation analysis revealed a statistically significant positive correlation between the average leaf area of vegetative shoots and litter

pH ($r = 0.76$, $p < 0.05$). It is known that *P. chlorantha* is more pH-demanding than other *Pyrola* species. It does not occur on very acidic soils and prefers alkaline, base-rich soils (Bagdasarova et al. 1983).

The average area of a developed (mature) leaf on generative shoots in all studied populations varied from 2.3 ± 0.3 to 4.9 ± 0.4 cm². Leaves reached maximum sizes in the natural habitat (NP2). The total leaf area per generative shoot was also greater in natural forest communities (Fig. 1).

Assessment of population vitality based on the average size spectrum of individuals (expressed by IVC) showed that plants from NP2, NP1, and AP5 reached the largest sizes, whereas the smallest sizes were observed in plants from AP2 and AP4 (Table 2).

The study of cross-sections of mature leaves of generative shoots of *P. chlorantha*, growing in natural forest communities, showed that leaf thickness was statistical-

ly significantly smaller than that of plants on dumps (Table 3). An exception were plants from AP3 and AP6, which had the same leaf thickness as plants from NP1.

Thus, under dump conditions, *P. chlorantha* exhibited a decrease in leaf area accompanied by an increase in leaf thickness. Such adaptive plant leaf rearrangements typically occur under different amounts of solar radiation (Goryshina 1979). We obtained similar results earlier (Chukina et al. 2017). Correlation analysis showed a statistically significant negative correlation between the total leaf area per generative shoot and habitat light conditions (according to Ellenberg et al. 1991) ($r = -0.74$, $p < 0.05$). Shading of *P. chlorantha* in natural habitats was due to a well-developed herb-shrub layer. Correlation analysis revealed a statistically significant positive correlation between the leaf area of generative shoots and the PC of the herb-shrub layer ($r = 0.76$, $p < 0.05$).

It is known that the photosynthetic

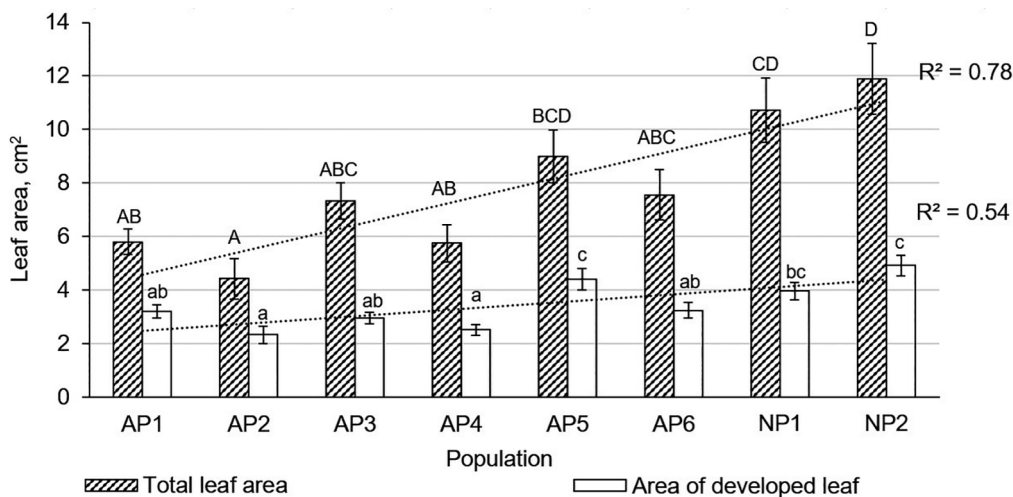


Fig. 1. Morphometric parameters of *P. chlorantha* generative shoots in the studied populations: total leaf area and area of developed leaf.

Note: the dotted line indicates the trend line (linear function); different letters indicate significant differences between sites at $p < 0.05$.

Table 3. Anatomical features of *P. chlorantha* leaf.

Co- de	Sheet thick- ness, μm	Mesophyll thickness, μm	Thickness of palisade mesophyll, μm	Thickness of spongy meso- phyll, μm	Thickness of the upper epidermis, μm	Thickness of the low- er epider- mis, μm
AP1	266.1 c $\pm$ 6.2	208.3 c $\pm$ 6.7	44.8 a $\pm$ 1.7	163.5 c $\pm$ 7.6	29.6 a $\pm$ 1.6	28.2 a $\pm$ 0.9
AP2	274.7 d $\pm$ 8.7	216.2 cd $\pm$ 9.5	44.2 a $\pm$ 2.3	171.9 c $\pm$ 10.9	29.4 a $\pm$ 1.0	29.1 a $\pm$ 4.0
AP3	240.1 b $\pm$ 5.3	179.0 b $\pm$ 5.0	50.6 bc $\pm$ 2.3	128.4 bd $\pm$ 4.7	33.2 a $\pm$ 1.1	27.9 a $\pm$ 0.8
AP4	264.9 c $\pm$ 18.1	205.7 c $\pm$ 18.1	48.8 bc $\pm$ 1.5	157.0 bcd $\pm$ 18.1	31.2 a $\pm$ 1.0	28.0 a $\pm$ 1.0
AP5	255.2 c $\pm$ 6.0	197.4 cd $\pm$ 5.4	59.7 b $\pm$ 9.4	137.7 d $\pm$ 4.9	28.9 a $\pm$ 0.5	28.9 a $\pm$ 0.7
AP6	232.7 b $\pm$ 2.7	174.7 b $\pm$ 3.0	46.7 b $\pm$ 1.5	128.1 b $\pm$ 3.1	31.2 a $\pm$ 0.7	26.7 a $\pm$ 0.6
NP1	236.6 b $\pm$ 2.3	181.2 b $\pm$ 2.8	48.6 b $\pm$ 2.4	132.6 bd $\pm$ 3.5	28.8 a $\pm$ 0.9	26.7 a $\pm$ 1.1
NP2	206.0 a $\pm$ 4.0	151.2 a $\pm$ 3.6	42.0 a $\pm$ 0.7	109.2 a $\pm$ 3.5	29.7 a $\pm$ 1.3	25.1 a $\pm$ 1.2

Note: AP – anthropogenic population; NP – natural population. The arithmetic mean values (M) $\pm$ standard error of the mean are presented ($n = 30$). Different letters indicate significant differences between sites at $p < 0.05$.

function of plants is mainly carried out by leaves. The leaf is the most sensitive and, at the same time, informative organ of a plant organism, reflecting the influence of variable environmental conditions. The anatomical and morphological features of leaf structure are the result of plant adaptation to environmental factors, the main of which are light, temperature, humidity, and mineral nutrition.

It was established that the leaves of *P. chlorantha* have a dorsiventral type of mesophyll structure. These features have been noted in our previous research, as well as by other authors (Stoyanov and Raycheva 2005, Chukina et al. 2017). Beneath the upper epidermis are one to two layers of palisade mesophyll, composed predominantly of rectangular cells; its thickness in AP1, AP2, and NP2 did not differ significantly (Table 3). The cells of the spongy mesophyll are loosely arranged, resulting in a well-developed system of intercellular spaces in the leaf. It was shown that for plants growing on dumps, the thickness of spongy mesophyll exceeded that of the palisade mesophyll by 2.5–4.0 times, and it was sig-

nificantly greater than in the control habitat NP2. Correlation analysis showed a statistically significant positive correlation between spongy mesophyll thickness and habitat moisture conditions (according to Ellenberg et al. 1991) ($r = 0.74$, $p < 0.05$). The epidermis of *P. chlorantha* leaves is uniseriate; the thickness of the upper ($31.2 \pm 1.0 \mu\text{m}$ – $109.2 \pm 3.5 \mu\text{m}$) and lower ($25.1 \pm 1.2 \mu\text{m}$ – $29.1 \pm 4.0 \mu\text{m}$) epidermis in plants from AP1–AP6 and NP1–NP2 did not differ significantly (Table 3). Stomata were located only in the lower epidermis.

It is known that under different light conditions, functional rearrangements of the photosynthetic apparatus can occur in the same species. In our previous studies, it was shown that in *P. chlorantha*, growing on the VTTPS ash dump (AP3), there was an increase in the number of chloroplasts per unit leaf area, as well as an increase in chlorophyll *b* content compared to the control habitat (NP2) (Chukina et al. 2017). Such rearrangements of the internal assimilating surface of the leaf are characteristic of shade-loving plants under conditions of strong shading (Goryshi-

na 1979). Furthermore, under conditions of low irradiance, photosynthesis is a key prerequisite for the synthesis of organic matter, supporting both vegetative growth and the generative phase (flowering and seed formation).

Based on the obtained results, it can be concluded that *P. chlorantha* has successfully adapted to technogenic environmental conditions through rearrangements of leaf anatomical and morphological parameters.

Conclusions

This study demonstrated that industrial dumps in the Middle Urals, specifically 40–60-year-old mixed and small-leaved forest phytocoenoses, form ecotopes suitable for colonisation by the typical boreal species *P. chlorantha*. Low herb–shrub projective cover, reduced phytocoenotic stress, and the presence of a developed litter layer create favourable conditions for the growth of *P. chlorantha* in technogenic ecotopes, where the species exhibits considerable ecological plasticity.

In response to increased light availability in anthropogenic habitats, *P. chlorantha* undergoes adaptive changes in the anatomical and morphological traits of generative shoot leaves. These changes, likely associated with the mitigation of light stress, include a reduction in leaf area, an increase in leaf thickness, and a decrease in total assimilative surface area.

Further research is needed to better understand population characteristics and adaptive modifications of the photosynthetic apparatus in Pyroleae species, particularly under anthropogenically disturbed conditions.

Acknowledgement

This work was carried out with the financial support of the Ministry of Science and Higher Education of the Russian Federation (theme No. FEUZ-2026-0017).

References

- ANCHEV M. 1982. Pyrolaceae Lindl. In: D. Yordanov D. (Eds). Flora of the Republic of Bulgaria. Publishing House of the Academy of Sciences, Sofia. VIII: 279–287 (in Bulgarian).
- BAGDASAROVA T.V., VAKHRAMEEVA M.G., NIKITINA S.V., DENISOVA L.V. 1983. Genus *Pyrola* [Rod Grushanka]. In: Biological flora of the Moscow region. Publishing house of Moscow State University, Moscow, 7: 153–176 (in Russian).
- BOBROV YU.A. 2009. Pyroloideae of Russia [Grushankovye Rossii]. Publishing House of Vyatka State University for the Humanities, Kirov. 137 p. (in Russian).
- CAMPBELL T., DIXON K.W., BRADSHAW S.D., GANN G.D., HARTLEY W., LAMBERS H., WARDELL-JOHNSON G. 2024. Standards-based evaluation inform ecological restoration outcomes for a major mining activity in a global biodiversity hotspot. *Restoration Ecology* 32(8), e14236. <https://doi.org/10.1111/rec.14236>
- CHIBRIK T.S., LUKINA N.V., FILIMONOVA E.I., GLAZYRINA M.A. 2011. Ecological basis and experience in the biological reclamation of lands disturbed by industry [Ekologicheskie osnovy i opyt biologicheskoi rekultivatsii narushennykh promyshlennost'yu zemel']. Ural State University Publishing, Ekaterinburg. 268 p. (in Russian).
- CHUKINA N.V., LUKINA N.V., BORISOVA G.G., YARINA U.S. 2017. Structural and functional features of the photosynthetic apparatus in Pyrolaceae family plants from technogenic habitats [Strukturno-funktsional'nye osobennosti fotosinteticheskogo apparata ras-

- tenii semejstva Pyrolaceae v tekhnogen-nykh mestoobitaniyakh]. Scientific Notes of Petrozavodsk State University 165(4): 81–89 (in Russian).
- DODDS J. 2023. *Pyrola chlorantha* Rare Plant Profile. New Jersey Department of Environmental Protection, State Parks, Forests & Historic Sites, State Forest Fire Service & Forestry, Office of Natural Lands Management, New Jersey Natural Heritage Program, Trenton, NJ. 18 p.
- DUBROVAYA S.A., MAVLYDOVA L.U. 2019. Ontogenetic structure and analysis of the state of *Pyrola rotundifolia* and *Orthilia secunda* coenopopulations in separate parts of their range [Ontogeneticheskaya struktura i analiz sostoyaniya cenopopulyacij *Pyrola rotundifolia* i *Orthilia secunda* v otdelnykh chastyakh areala]. Proceedings of Higher Educational Institutions. Volga Region. Natural Sciences 28(4): 35–49 (in Russian).
- ELLENBERG H., WEBER H.E., DÜLL R., WIRTH V., WERNER W., PAULISSEN D. 1991. Zeigerwerte von Pflanzen in Mitteleuropa. Scripta Geobotanica 18. 248 p.
- FILIMONOVA E., GLAZYRINA M., LUKINA N., MALEVA M., BORISOVA G., CHUKINA N. 2022. Demographic structure and morphological features of *Malaxis monophyllos* (Orchidaceae) populations colonizing technogenic substrates. Forestry Ideas 28(1): 100–111.
- GLAZYRINA M.A., LUKINA N.V., FILIMONOVA E.I. 2024. *Chimaphila umbellata* (Ericaceae) in natural and technogenic habitats in the Middle Urals [*Chimaphila umbellata* (Ericaceae) v estestvennykh i tekhnogennykh mestoobitaniyakh na Srednem Urale]. Vestnik of Orenburg State Pedagogical University. Electronic Scientific Journal 51(3): 21–40 (in Russian). <https://doi.org/10.32516/2303-9922.2024.51.2>
- GORYSHINA T.K. 1979. Plant ecology [Ekologiya rasteniy]. Higher School, Moscow. 368 p. (in Russian).
- ILYINA V., SENATOR S., MITROSHENKOVA A., KOZLOVSKAYA O., KAZANTSEV I. 2022. Population Structure of *Pyrola chlorantha* (Family Ericaceae) at the Southern Range Margin (Samara Region, Russia). International Journal of Plant Biology 13: 634–643. <https://doi.org/10.3390/ijpb13040051>
- ISHBIRDIN A.R., ISHMURATOVA M.M., ZHIRNOVA T.V. 2005. Life strategies of the cenopopulation of *Cephalanthera rubra* (L.) Rich. on the territory of the Bashkir State Nature Reserve [Strategii zhizni tsenopopulyatsii *Cephalanthera rubra* (L.) Rich. na territorii Bashkirskogo gosudarstvennogo zapovednika]. Vestnik of Lobachevsky University of Nizhni Novgorod. Series: Biology 1: 85–98 (in Russian).
- JOHANSSON V., MIKUSINSKA A., EKBLAD A., ERIKSSON O. 2015. Partial mycoheterotrophy in Pyroleae: Nitrogen and carbon stable isotope signatures during development from seedling to adult. Oecologia 177(1): 203–211. <https://doi.org/10.1007/s00442-014-3137-x>
- JOHANSSON V.A., MÜLLER G., ERIKSSON O. 2014. Dust seed production and dispersal in Swedish Pyroleae species. Nordic Journal of Botany 32(2): 209–214. <https://doi.org/10.1111/j.1756-1051.2013.00307.x>
- KNYAZEV M.S., TREYAKOVA A.S., PODGAEVSKAYA E.N., ZOLOTAREVA N.V., KULIKOV P.V. 2018. Annotated checklist of the flora of the Sverdlovsk region. Part 3: Dicotyledonous plants (Aristolochiaceae – Monotropaceae) [Konspekt flory Sverdlovskoy oblasti. Chast III: Dvudol'nye rasteniya (Aristolochiaceae – Monotropaceae)]. Phytodiversity of Eastern Europe 12(2): 4–95 (in Russian).
- KUPRIYANOV A.N., MANAKOV YU.A. 2016. Regularities of restoration of plant cover on the dumps of the Kuznetsk Basin. Siberian Journal of Forest Science [Sibirskij Lesnoj Zhurnal] 2: 51–58 (in Russian with English abstract). doi: 10.15372/SJFS20160205
- LALLEMAND F., PUTTSEPP Ü., LANG M., LUUD A., COURTY P.-E., PALANCADE C., SELOSSE M.-A. 2017. Mixotrophy in Pyroleae (Ericaceae) from Estonian boreal forests does not vary with light or tissue age. Annals of Botany 120(3): 361–371. <https://doi.org/10.1093/aob/mcx054>
- LUNEVA N. 2023. On the conservation of phytodiversity in agroecosystems [K voprosu

- sokhraneniya fitoraznoobraziya na terri-
toriyakh agroekosistem]. Phytodiversity of
Eastern Europe 17(2): 49–75 (in Russian).
doi: 10.24412/2072-8816-2023-17-2-49-75
- ODUM U. 1986. Ecology. Translated from Eng-
lish. Mir, Moscow, 2. 376 p. (in Russian).
- POLYANSKAYA T.A. 2012. Ecological diversi-
ty of cenopopulations of *Orthilia secunda*
(L.) House [Ekologicheskoe raznoobrazie
cenopopulyatsiy ortilii odnobokoj *Orthilia*
secunda (L.) House]. Bulletin of Voronezh
State University. Series: Chemistry, Biolo-
gy, Pharmacy 1: 125–131 (in Russian).
- ROYAL BOTANIC GARDENS, KEW 2026. Plants
of the World Online. Available at: [https://
powo.science.kew.org/](https://powo.science.kew.org/) (accessed:
12.01.2026).
- STOYANOV K., RAYCHEVA T. 2005. Anatomical
investigation of the leaf in Bulgarian repre-
sentatives of Pyrolaceae family [Anatom-
ichno izsledvane na lista pri balgarskite
predstaviteli na semeistvo Pyrolaceae].
Scientific Works of the Agricultural Univer-
sity, Plovdiv 50(5): 119–124 (in Bulgarian).
- TARSHIS L.G. 2005. On the variability of mor-
phological and anatomical characters of
species of the subfamily Pyroloideae (Er-
icaceae) in the Ural region [Ob izmenchi-
vosti morfologicheskikh i anatomicheskikh
priznakov u vidov podsemeistva Pyroloide-
ae (Ericaceae) na Urale]. Botanical Journal
[Botanicheskii Zhurnal] 8: 1197–1208 (in
Russian).
- TEDERSOO L., PELLET P., KÖLJALG U., SELOSSE
M.-A. 2007. Parallel evolutionary paths to
mycoheterotrophy in understory Ericace-
ae and Orchidaceae: Ecological evidence
for mixotrophy in Pyroleae. Oecologia
151(2): 206–217. [https://doi.org/10.1007/
s00442-006-0581-2](https://doi.org/10.1007/s00442-006-0581-2)
- URAZGILDIN R.V., KULAGIN A.YU. 2021. Struc-
tural and functional responses of woody
plants to anthropogenic environmental
changes: damage, adaptations and strat-
egies. Part 1. Effects on the macro- and
micromorphology of the assimilation ap-
paratus. Biosfera 13(3): 86–100 (in Rus-
sian). [https://doi.org/10.24855/biosfera.
v13i3.578](https://doi.org/10.24855/biosfera.v13i3.578)
- YOUNG R.E., GANN G.D., WALDER B., LIU J.,
CUI W., NEWTON V., NELSON C.R., TASHE
N., JASPER D., SILVEIRA F.A.O., CARRICK
P.J., HÄGGLUND T., CARLSEN S., DIXON K.
2022. International principles and stand-
ards for the ecological restoration and re-
covery of mine sites. Restoration Ecology
30(S2), e13771. [https://doi.org/10.1111/
rec.13771](https://doi.org/10.1111/rec.13771)
- ZHELEVA E., PETROV P., IVANOVA S. 2016.
Characterisation of soils and parentma-
terials from rehabilitated embankments in
the area of DPM Inc., Chelopech. Journal
of Environmental Protection and Ecology
17(4): 1324–1333.
- ZLOBIN YU.A., SKLYAR V.G., KLIMENKO A.A.
2013. Populations of rare plant species:
theoretical foundations and methods of
study [Populyacii redkikh vidov rasteniy: te-
oreticheskie osnovy i metodika izucheniya].
University book, Sumy. 439 p. (in Russian).