Original scientific paper
Šumarski list 150 (1–2): 19–26, 2026

Influence of the *Salix caprea* Genotype and Leaf Characteristics on the Occurrence of Fungus *Melampsora caprearum*

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Abstract
Leaf rust caused by *Melampsora caprearum* is one of the most important but understudied diseases of goat willow (*Salix caprea*). This research studied for the first time the effect of genotype and the morphology of goat willow leaves on the occurrence and abundance of *Melampsora caprearum* uredinia. The genotype showed a statistically significant impact on the occurrence and abundance of uredinia on goat willow leaves. The morphological characteristics of the leaves, leaf area, leaf circumference, and length and width of the leaves had a statistically significant effect on the occurrence of uredinia, while they did not impact the uredinia abundance on the leaves. On the same tree, leaves of larger dimensions showed greater resistance to the occurrence of infection symptoms. Based on leaf morphology, the results represent a realistic basis for selecting goat willow trees less susceptible to *Melampsora caprearum*. Measures that can be applied in goat willow habitats to regulate leaf dimensions and reduce damage from *Melampsora caprearum* are discussed.

Keywords: willow rust, development, uredinial stage, protection strategies

DOI:
https://doi.org/10.31298/sl.150.1-2.2

How to Cite:
Vemić, A., S. Lazić, A. Lučić, Z. Radulović, Lj. Rakonjac, S. Stajić, V. Popović, 2026: Influence of the *Salix caprea* genotype and leaf characteristics on the occurrence of fungus *Melampsora caprearum*. Šumarski list 150 (1–2): 19–32. https://doi.org/10.31298/sl.150.1-2.2

INTRODUCTION

The genus *Salix* L. comprises about 600 species of shrubs and trees that grow in moist habitats (Cvjetićanin et al. 2016). Species from the genus *Salix* represent a valuable source of biologically active components widely used for various therapeutic purposes (Ramos et al. 2019, Tawfeek et al. 2021). Goat willow (*Salix caprea* L.) is a pioneer, fast-growing honey plant adaptable to different habitat conditions and able to extract heavy metals from the soil (Enescu et al. 2016). Lands populated by goat willow trees demonstrate enhanced water retention potential and moisture buffering capacity compared to fallow soils, indicating that goat willow positively influences hillside hydrology (Gonzalez-Ollauri and Mickovski 2020).

Rust fungi (Pucciniomycotina, Pucciniales) constitute one of the most significant orders of fungi, accounting for about a quarter of the known Basidiomycota (Aime and McTaggart 2021). Rust fungi represent the most numerous plant pathogens, and many aspects of their biology remain unexplained (Lorrain et al. 2018). In certain parts of Europe, more than two hundred taxa of rust fungi have been recorded (Woods et al. 2015, Talhinhas et al. 2019). The genus *Melampsora* was first described in 1843; it represents heteroxeny Basidiomycetes with a complete development cycle characterized by the formation of a crust of sessile, laterally adherent single-celled teliospores (Pei et al. 2005). The fungi from the genus *Melampsora* are among the most important pathogens in poplar plantations and short-rotation coppice systems. Several species of the genus *Melampsora* are found on *Salix* spp. in Europe (Ciszewska-Marciniak and Jędryczka 2011). Also, it is known that *Melampsora caprearum* (DC.) Thüm occurs on goat willow in urban green spaces (Stankevičienė 2018). Research in Central Europe has identified several species of the genus *Melampsora* that affect willow biomass production (Bubner et al. 2014). However, the bioecology of species of the genus *Melampsora* has not been sufficiently researched, particularly regarding hosts that are not used for broad commercial purposes but mainly have environmental value.

A higher-rang classification of the order Pucciniales must also include various aspects of the development of these organisms (Aime and McTaggart 2021). Climate change has led to an increased spread of rusts to higher elevations (Dudney et al. 2021). Ecological and basic biological studies of rust development are necessary to develop new control methods (Yamaoka 2014). The literature lacks data regarding the influence of the goat willow leaf morphology (*Salix caprea*) on the spread of *Melampsora caprearum*. Understanding this relationship will help maintain better health conditions for goat willow and reduce the spread of *Melampsora caprearum*, particularly in goat willow stands and protective belts in natural settings. This is especially important due to the additional threat to goat willow from leaf chewers, leaf miners, and gall inducers (Veselkin et al. 2019). Genotypes tolerating these threats can provide a valuable source of quality reproductive material. Accordingly, this study aimed to investigate the life cycle of *Melampsora caprearum* depending on the genotypes and the morphology of the goat willow leaves. The occurrence and abundance of uredinia as the phases of rust development that cause the most damage to the goat willow were investigated.

MATERIAL AND METHODS

Research Locality

The goat willow trees infected with rust *Melampsora caprearum* were sampled at Ivica Mountain in Montenegro (43º01'13''N, 19º08'30''E). The trees belonged to the longitudinal belt of goat willow next to the stream, without pronounced exposure, at an elevation of 1,373 meters above sea level. The distance between the trees was less than 1 meter. The source of the inoculum was a larch tree (*Larix decidua* Mill.) situated less than 500 meters away from the goat willow trees (43º01'09''N, 19º08'27''E). No other (secondary) hosts for other rust species that can occur on goat willow were noticed, so the occurrence of other rust species can be excluded.

Plant Material

Eleven goat willow genotypes aged 11 to 12 years were selected to analyze the morphology of leaves infected by *Melampsora caprearum*. The leaves were sampled in August 2023, when the infection period for the uredinial stage was over, and the uredinia were visible on the infected leaves. Uredinia were dark yellow and orange, 1–2 mm in size, primarily hypophyllous, while in terms of arrangement, they were scattered and aggregated. Urediniospores had a colorless cell wall; some were completely colorless, ovoid, and ellipsoid 14–20 × 12–15 µm in size (Figure 1). The cell wall was echinulate, which was less noticeable on some spores. The morphological characteristics of fruiting bodies and spores matched the description of Bagyanarayana (2005) and Pei (2005).

Due to the high tree density, trees were sampled at a 30 m distance to avoid collecting genetically identical trees. Each genotype represented a separate individual, that is, a genotypically different individual. Individuality was estimated based on the distance between sampled trees. A random sample of 20 leaves was taken from each tree at a height of 2 meters from the southwest side and the middle of the branch. The collected leaves were packed in plastic bags and stored in the refrigerator for 48 hours. The uredinia occurrence on the leaves, an indicator of the beginning of rust, and the uredinia abundance on the leaves, an indicator of the intensity of rust, were examined. The uredinia occurrence is defined as binary, based on the occurrence or absence of leaf rust. Afterward, the fungal uredinia were counted on the lower side of each leaf to determine their abundance. All the leaves were scanned, and their lamina length, width, circumference, and area were calculated using LAMINA software (Umea University) (see Table 1, Figure 1).

Statistical Methods

Binary logistic regression was used to examine how factors such as genotype, leaf length, width, circumference, and area influence the occurrence of uredinia.

A general linear model (GLM) was used to compare the abundance of uredinia depending on the same factors tested for the uredinia occurrence. The normality of the residuals for the general linear model was assessed using the Lilliefors-corrected Kolmogorov–Smirnov test. At the same time, the homogeneity and linearity were checked through the point scatter diagram. Fisher's least significant difference (LSD) post hoc test was used to compare the abundance of uredinia between goat willow genotypes.

Table 1 Leaf dimensions of the tested goat willow leaves.

Number of Trees	Area (mm^2)	Circumference (mm)	Leaf Width (mm)	Leaf Length (mm)
1	1986.1680 ± 1027.48	156.8930 ± 41.58	39.2195 ± 8.74	69.6220 ± 19.17
2	1857.6105 ± 566.31	159.6730 ± 33.74	38.6405 ± 5.50	67.9620 ± 13.70
3	1694.7970 ± 487.39	149.8365 ± 24.59	34.7420 ± 4.25	67.7735 ± 11.09
4	2309.7147 ± 774.83	172.2079 ± 35.61	42.7147 ± 7.14	75.4311 ± 15.32
5	1700.4610 ± 346.81	150.1135 ± 16.34	36.2895 ± 4.02	68.4530 ± 7.47
6	1846.6125 ± 308.57	151.6980 ± 14.78	39.1695 ± 3.80	66.2260 ± 6.15
7	2410.4360 ± 822.41	171.2705 ± 34.39	44.0260 ± 8.15	73.9495 ± 15.12
8	1576.7890 ± 313.24	145.1575 ± 14.54	34.5415 ± 4.25	64.3510 ± 6.40
9	1415.5765 ± 568.58	134.2135 ± 24.41	32.6535 ± 6.27	59.5105 ± 10.37
10	2467.7885 ± 1598.97	178.4155 ± 67.92	41.1080 ± 11.83	78.6025 ± 29.18
11	2209.8581 ± 806.59	176.3514 ± 34.15	40.0243 ± 7.31	77.8781 ± 14.85

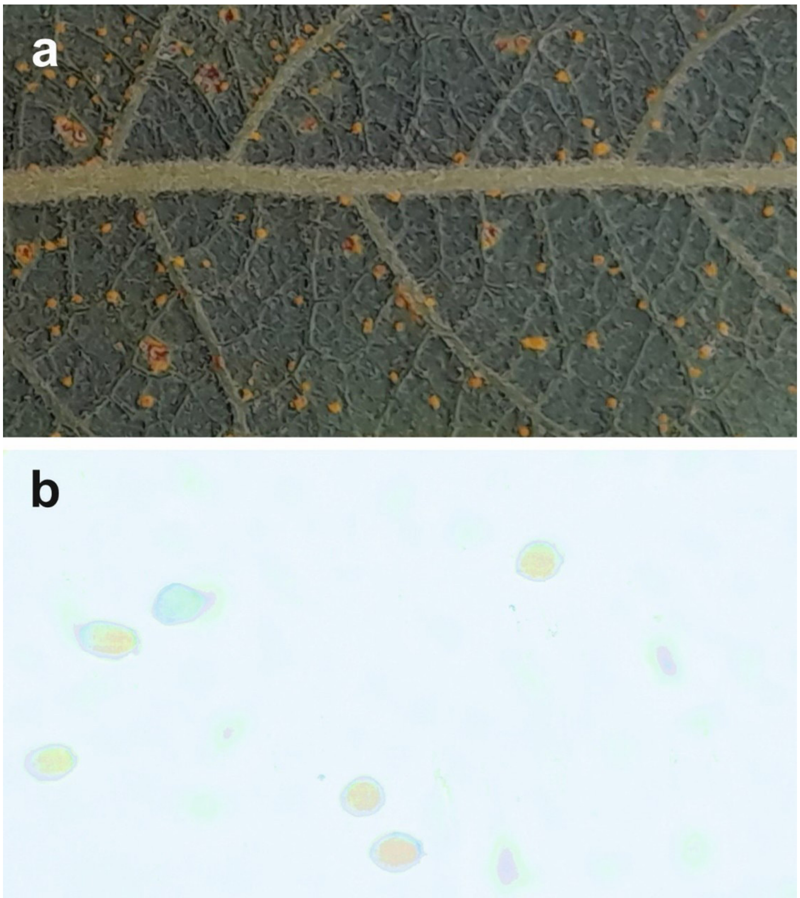

Figure 1 Uredinia and urediniospores of *Melampsora caprearum*.

RESULTS

Uredinia Occurrence on the Goat Willow Leaves

Infected leaves showed apparent symptoms in the form of yellow spots on the upper side and necrotic spots on one or both sides of the leaf (Figure 2). Abundant uredinia were found on the lower side of the leaves (Figure 2). Nevertheless, the binary logistic regression showed a statistically significant influence of the goat willow genotype, as well as the leaf's area, circumference, length, and width on the uredinia occurrence caused by *Melampsora caprearum* (Table 2, Figure 2, Figure 3). The odds ratio in binary logistic regression shows that different genotypes influence a higher or lower probability of the uredinia occurrence. According to the odds ratio from the binary logistic regression, an increase in leaf dimensions corresponds to a lower likelihood of symptoms caused by *Melampsora caprearum*, indicating a reduced probability of uredinia occurrence (Figure 3).

Table 2 Influence of the goat willow genotype and leaf dimensions on the occurrence of the *Melampsora caprearum* uredinia.

Source	Wald Chi-square	Type III df	*p*
Genotype	21.334	10	0.019
Leaf area	4.776	1	0.029
Leaf circumference	11.274	1	< 0.001
Leaf width	19.350	1	< 0.001
Leaf length	14.038	1	< 0.001

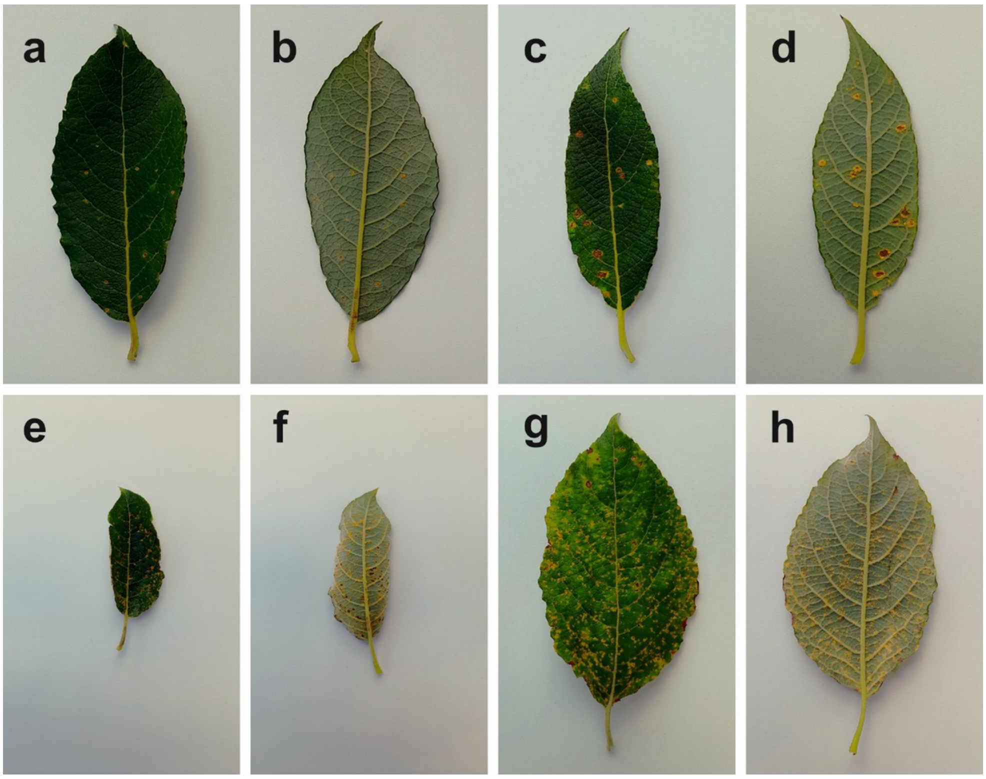

Figure 2 Damage to goat willow leaves (*Salix caprea*) caused by *Melampsora caprearum*; a – symptoms on the upper face of the leaf on less susceptible trees; b – the abundance of uredinia on the lower face of the leaf on less susceptible trees; c,e – symptoms on the upper face of the leaf on middle susceptible trees; d,f – the abundance of uredinia on the lower face of the leaf on middle susceptible trees; g – symptoms on the upper face of the leaf on sensitive trees; h – the abundance of uredinia on the lower face of the leaf on sensitive trees.

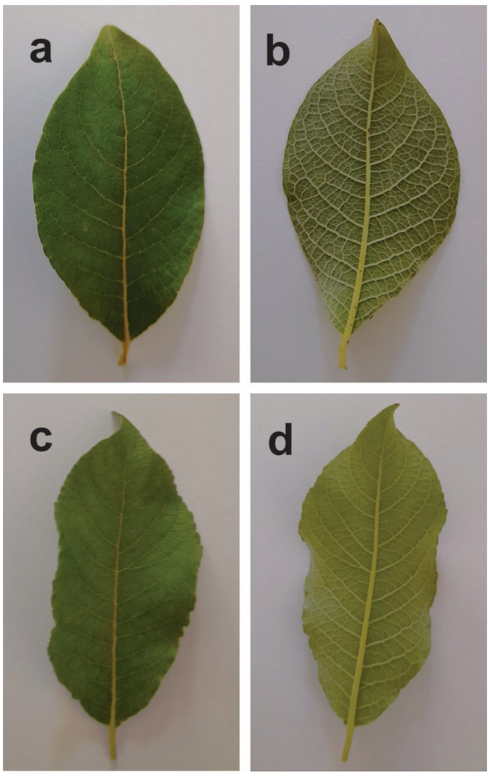

Figure 3 Resistant goat willow leaves (*Salix caprea*) without rust symptoms.

Uredinia Abundance on the Goat Willow Leaves

A statistically significant difference was observed in the number of *Melampsora caprearum* uredinia between different goat willow genotypes based on GLM results (Table 3, Figure 2, Figure 4). The lowest number of *Melampsora caprearum* uredinia on leaves was present on individual trees, with a prevalence of 9.09% (Figure 2 a–b, Figure 4, Figure 5). Also, the highest number of uredinia appeared in the same percentage of trees, again at 9.09% (Figure 2 g–h, Figure 4, Figure 5). The remaining 81.82% of trees were in the range between the highest and lowest sensitivity (Figure 2 c–d, Figure 2 e–f, Figure 4, Figure 5). However, leaf area, circumference, length, and width did not affect the abundance of uredinia based on GLM results (Table 3). This indicates that leaves of different dimensions showed a similar number of uredinia (Figure 2 d, f).

Table3 Influence of the goat willow genotype and leaf dimensions on the abundance of the *Melampsora caprearum* uredinia.

Source	Type III Sum of Squares	df	Mean Square	F	*p*
Genotype	23755.738	10	2375.574	2.216	0.026
Leaf area	500.755	1	500.755	0.467	0.497
Leaf circumference	53.641	1	53.641	0.050	0.824
Leaf width	2188.638	1	2188.638	2.042	0.157
Leaf length	21.201	1	21.201	0.020	0.889

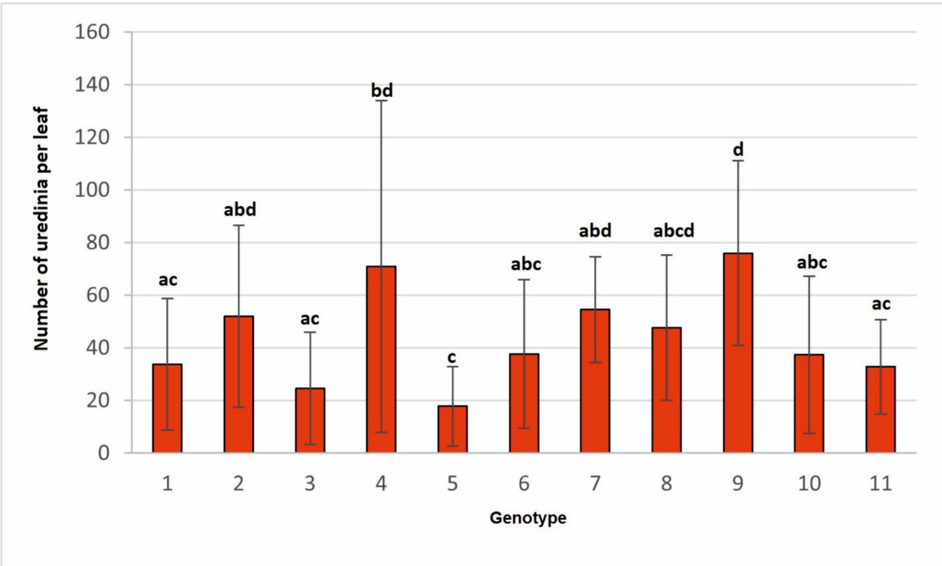

Figure 4 The abundance of uredinia on different goat willow genotypes.

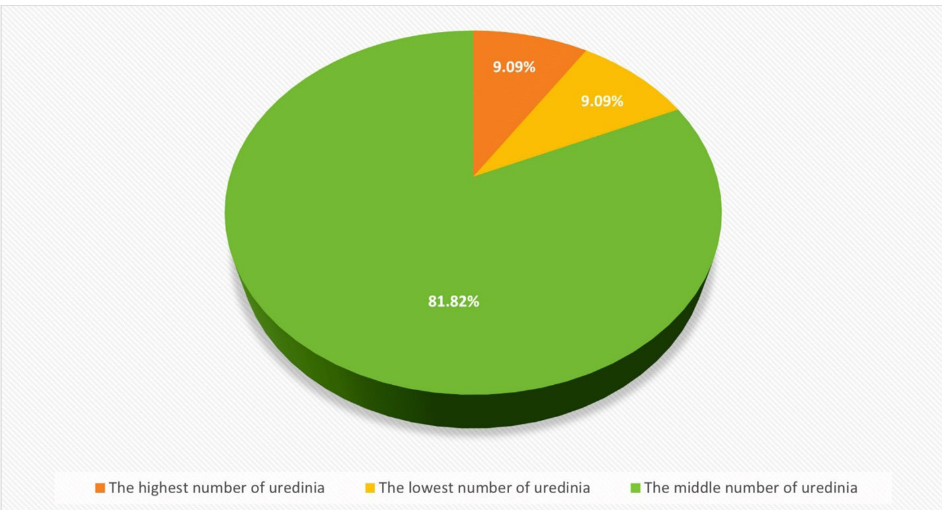

Figure 5 The percentage of goat willow trees with different uredinia abundance.

DISCUSSION AND CONCLUSIONS

Tree breeding and genomics development enable new rust control strategies worldwide (Hamelin 2022). This study showed a significant influence of various factors such as genotype, leaf length, width, circumference, and area on the occurrence of the uredinia of *Melampsora caprearum* fungus on goat willow leaves. Namely, different genotypes showed unequal intensity of rust occurrence on the leaves in the canopy. At this moment, it is impossible to determine the precise mechanism for this phenomenon. The reasons for this phenomenon are reflected in various biochemical processes and the potential presence of genes that increase trees' defense reactions (Hückelhoven and Pillen 2024). Larger leaves showed greater resistance compared to smaller leaves. This larger leaf size influences goat willow's preexisting defense mechanisms, which include features such as thicker cell walls, a larger surface area for wax secretion, a greater number and size of leaf hairs, and variations in the shape and arrangement of stomata. These structural differences effectively hinder the pathogen's ability to establish an infection (Hückelhoven and Schouten 2024). The growth of goat willow is hindered in unfavorable conditions, but these plants can rapidly change their growth dynamics when conditions improve (Dušek and Květ 2006). Soil moisture is essential for germination in the first year, and prolonged three-week droughts can result in seedling mortality (Tiebel et al. 2023). According to the above-mentioned, planting and restoring goat willows in high-quality habitats is expected to reduce the occurrence of *Melampsora caprearum*. On the other hand, in lower-quality habitats with decreased productivity, especially in places prone to drought, soil fertilization measures are necessary to promote the growth of goat willow, i.e., to reduce the incidence of *Melampsora caprearum*.

This study also showed that the goat willow genotype influences the abundance of uredinia on leaves, while leaf dimensions did not show a significant effect. Similar to the influence of the genotype on the uredinia occurrence, several mechanisms existed within the goat willow trees, primarily different defense reactions, which contributed to the slow development of the pathogen (Hückelhoven and Schouten 2024). These findings are partially in agreement with a similar study by Toome et al. (2010a, 2010b), which demonstrated that leaf area and clones of *Salix viminalis* L. and *Salix gmelinii* Pall. (*S. dasyclados* Wimm.) impacted the abundance of *Melampsora epitea* rust pustules. Research on the rotting of goat willow branches showed that the branch dimensions did not affect the rot's intensity; rather, the number of microorganisms played a more critical role. This suggests that the size of the branches has limited importance in mitigating rot (Angst et al. 2018). Similar to the aforementioned research, the leaf dimensions had no significance in the abundance of the *Melampsora caprearum* uredinia, i.e., the intensity of leaf destruction. However, in the case of *Melampsora caprearum* rust, it is possible to directly reduce the damage intensity to individual trees by preventing the infection of specific leaves. Pruning can effectively shape the canopy to consist mainly of less sensitive leaves.

Damage to trees caused by *Melampsora caprearum* can potentially reduce the genetic diversity of goat willow. Research on the decline of genetic diversity in goat willow within fragmented habitats has led to recommendations for preserving populations with various genetic diversity (Tokdemir et al. 2024). In the case of *Melampsora caprearum*, it was found that the genotype and the leaf dimensions of goat willow independently influence the occurrence of infection. In this way, in addition to utilizing and restoring resistant trees, it is possible to encourage the development of large leaves on more susceptible trees. This approach can preserve the stability of various willow stands and create conditions for conserving particularly endangered habitats.

Goat willow is an important component in species succession, where competition on different floors affects species distribution and herbaceous plants' biomass in the understory (Mudrák et al. 2016a). Also, active measures are needed in damaged habitats, where restoration is complex, to enable vegetation succession (Mantero et al. 2023). The lifespan of goat willow seeds is expected to shorten due to global climate change (Tiebel et al. 2024). The germination of goat willow seed depends on whether it is protected within the soil or located on the soil surface (Tiebel et al. 2018). As such, the mechanical removal of weeds in the vicinity of the goat willow trees is recommended, especially in poor habitats, to enhance the nutrient uptake from the soil. Early stimulation of goat willow tree growth is necessary to limit competition from other plants for space and nutrients. Therefore, we suggest that promoting the development of trees with larger leaves is particularly important in endangered habitats where rapid vegetation recovery is needed. The goat willow genotypes were grown under the same environmental conditions, indicating a direct relationship between leaf size and resistance. The development of goat willow leaves can be stimulated by applying various forestry sylvicultural measures. These include reduction in competition from other vegetation (Mudrák et al. 2016ab) and thinning (Leonardsson and Götmark 2015), which will contribute to better growth of goat willow, positively impacting leaf development. Another way is to plant seedlings that have larger leaves. Moreover, since certain goat willow genotypes show greater resistance to the occurrence of *Melampsora caprearum*, they should be used where selecting seedlings with larger leaves is not possible.

On the other hand, the excessive spread of willows must be addressed in productive habitats, as this negatively impacts vegetation change (Cannone et al. 2022). Since these habitats enable the natural tendency for larger leaves to develop (Dušek and Květ 2006), we suggest that less susceptible genotypes should be prioritized. In this way, adequate protection is provided without the danger of changing the vegetation.

Defoliation of goat willow trees caused by *Melampsora caprearum* can have indirect negative consequences on the development of subsequent vegetation. The fallen leaves of goat willow can hinder the seed germination of other species in vegetation succession (Mudrák and Frouz 2012). Species diversity at the beginning of vegetation indicates its further development (Mudrak et al. 2016b). On the other hand, disturbances during succession affect the resumption of vegetation growth (Gustafsson et al. 2021). Also, goat willows have lower shoot vigor than other tree species in these habitats. Therefore, the thinning measures can be planned to follow the needs of the field (Leonardsson and Götmark 2015).

The length and width of goat willow leaves are proven parameters for distinguishing *Salix caprea* from *Salix gracilistyla* Miq. and their hybrids (Seo et al. 2021). Accordingly, balancing the cultivation of trees with different leaf morphologies is necessary to preserve the natural goat willow gene pool and phenotype. Also, *Salix caprea* has slightly lower photosynthesis parameters than green alder (*Alnus alnobetula* (Ehrh.) K.Koch) and aspen (*Populus tremula* L.) as other pioneer species (Popa and Popa 2021). Regulating the diversity of other woody species that share a habitat with willow can contribute to forming different habitus of willow and improve the effect of photosynthesis in a specific habitat.

The ectomycorrhiza of goat willow consists of the species *Hebeloma populinum, Cortinarius atrocoerulaeus, Inocybe hirtella, Laccaria cf. ochropurpurea, Tuber maculatum, Cenococcum geophilum* and *Phialophora finlandia* (Hrynkiewicz et al. 2023). In addition, endophytic fungi in the roots improve the physiology of goat willow (Likar and Regvar 2013). Biotization of goat willow seedlings gives these fungi the possibility of better growth, and further research should explore the potential use of some of these fungal species to protect goat willows from the rust fungus *Melampsora caprearum*. Currently, it is known that the level of soil salinity and the season influence the development of different genera of ectomycorrhizal fungi (Hrynkiewicz et al. 2015).

Producing reproductive material, as well as the natural regeneration of more resistant goat willow trees or genotypes with large leaves, also indirectly suppress *Melampsora caprearum* rust. Goat willow seeds are dispersed over long distances from the parent trees (Tiebel et al. 2019). Therefore, goat willow genotypes with a higher degree of resistance, i.e., with larger leaves, have the potential to intensively spread to other localities; they provide the basis for creating goat willow stands less susceptible to damage from this rust.

Finally, it should be noted that the findings on the host–rust interaction contribute to a better understanding of how climate change impacts these pathogens (Helfer 2014). There were several historical periods of the spread of different willow species into new areas, so it is necessary to conduct ecological studies to extend knowledge of habitat differentiation for different willow species (Wagner et al. 2021). Therefore, we believe that findings on the influence of the goat willow leaf morphology on the development of *Melampsora caprearum* can be used to predict the future distribution of this rust due to the expected impact of climate change on tree development.

ACKNOWLEDGMENTS

This study was supported by the Ministry of Education, Science and Technological Development of the Republic of Serbia, grant number: 451-03-66/2024-03/200027.

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