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# Relations Between *Betula pendula* Roth. (Betulaceae) Leaf Morphology and Environmental Factors in Five Regions of Croatia

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In this research we used numerical analysis of environmental and morphometric data sets to study the possibility of environmental control of leaf morphology in *Betula pendula* stands from five regions of Croatia. The correlations were poor between leaf variables and the ecological gradients of the stands, as well as between the ecological, vegetational and biometric characteristics of the two morphologically most similar populations. This being so, we viewed the populations in the historical context. As the two morphologically closest *B. pendula* populations grow in disjoined natural marshland vegetation with different environmental features, their similarity might be found in the genetic background, which should be further investigated. Possibly, at least in these two areas of its Croatian distribution range, *B. pendula* grows in its primary habitats from preglacial times, and is of older (relict) origin than in the rest of its recent Croatian (secondary) area of distribution, where it recolonized after the Ice Ages.

**Key words**: *Betula pendula*, morphometry, leaf morphology, ecology, clinal variability, Croatia.

## INTRODUCTION

In Croatia, calcifuge silver birch (*Betula pendula* Roth., Betulaceae) forest, characteristic of Central and Western Europe (Mayer, 1986; Trinajstić, 1995), approaches the eastern limits of its climatic range. Silver birch is known for its broad ecological amplitude of light, water and nutrient requirements, but fertile, firm, mineral soils and ample water supply are its best prerequisites for good development. Silver birch is on the southernmost frontier of its European range of distribution in Croatia (Jalas and Suominen, 1976), where it is considered to be a pioneer forest species, absent from the primary habitats of the lowest (oak) area. Croatian silver birches are generally linked to secondary stands, highly affected by human activity (Vukelić and Španjol, 1990; Ilijanić, 1998), and are hardly ever to be found deeper in the woods.

As the physiology of each individual dictates the variability between the leaves of fertile and sterile annual shoots, at least some of the phenotypic differences observed in various *Betula* populations are also due to environmental rather than genetic differences (Lewontin, 1974; Stern and Roche, 1974; Thomas and Kenworthy, 1980; Coyle et al., 1982; Nygren and Kellomäki, 1983). In our previous papers (Kovačić and Šimić, 2001; Trinajstić et al., 2001) we discussed intra- and interpopulational variability of silver birch on the basis of seven measured morphological leaf traits, represented by population samples from five bioclimatically different regions in Croatia.

Even though the results have not pointed to differentiation of the local *B. pendula* populations in Croatia, significant differences between and within the studied populations have been determined, as seen in studies by Kovačić and Šimić (2001) and Trinajstić et al. (2001). The characteristics of the vegetation indicate that three populations (Krndija, Moslavina, Lika) are secondary, growing in simple *Pteridio aquilini-Betuletum pendulae* communities, while the two morphologically closest ones (Papuk and Gorski kotar) grow in the perimeter of wetland silver fir (*Abies alba* Mill.) forests with woody horsetail (*Equisetum sylvaticum* L.), which may have preserved some preglacial ecological characteristics unusual in Southeastern Europe today (Trinajstić, 1974; Trinajstić et al., 1997). This study was intended to examine two questions. First, do the localities with the biometrically most similar *B. pendula* populations also show strong ecological similarities

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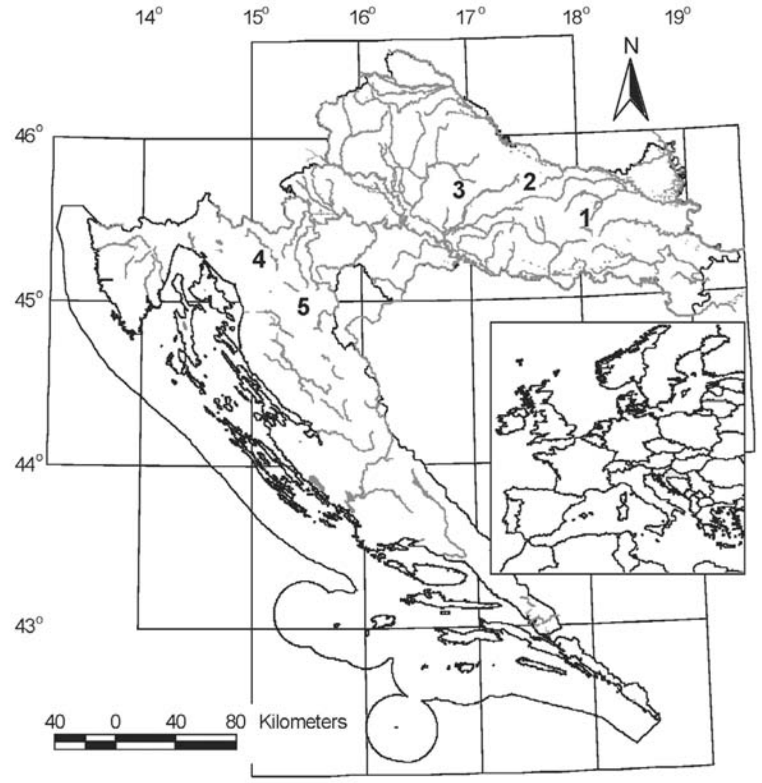

**Fig. 1.** Sampled *Betula pendula* populations on map of Croatia with MTB grid and unit denotations (insert: location of Croatia in Europe). 1 – Krndija; 2 – Papuk; 3 – Moslavina; 4 – Gorski kotar; 5 – Lika.

and vegetation characteristics? Second, is it possible to relate the variability of silver birch leaf characteristics generally to the ecological gradients of the habitat? Answers to these questions should provide better insight into the detailed relations between leaf morphology and environmental factors for disjunctive Southeast European *B. pendula* populations.

## MATERIALS AND METHODS

The material used in this research represented five disjunctive and bioclimatically diverse regions of the natural distribution of silver birch in Croatia. The studied localities were marked as in Figure 1, on a map of Croatia with an MTB grid and unit denotation (Nikolić et al., 1998). A total of 5000 leaves were investigated (5 populations, 10 trees per population, 50 fertile and 50 sterile shoot leaves per tree). Field sampling was described in Kovačić and Šimić (2001).

The first set of variables included seven morphological traits (Fig. 2) measured for each leaf with standard utensils (1 mm and 5° precision), grouped into leaves of fertile and sterile shoots. The biometric variables of the leaf measurements are presented in Table 1.

The second set of variables represented the ecological characteristics of the sampled localities. The climatological features of the sites included mean annual precipitation (mm/m$^2$), mean annual temperature (Tmean, °C), minimum annual temperature (Tmin, °C) and maximum annual temperature (Tmax, °C). The data covered 1961–1999 and came from the Croatian Meteorological and Hydrological Service (unpublished). The altitudes (m a.s.l.) and geographic coordinates of the localities were taken from 1:100,000 topographic maps. For statistical analysis, the geographical coordinates were converted from degrees, minutes and seconds to a decimal system of north and east coordinates. Each site was also characterized by the data on the type of vegetation (according to Trinajstić, 1974; Vukelić and Španjol, 1990; Pernar and Vranković, 1996; Trinajstić et al., 1997; present authors) and soil type (Martinović, 1997). Types of human impacts were classed as primary (climazonal forest vegetation with low human impact) or secondary (degraded vegetation with high human impact). The ecological characteristics of the investigated localities are shown in Table 2.

In our previous research, canonical discriminant analysis pointed to a high correlation for both types of leaves between the investigated populations, but the

TABLE 1. Biometrical variables of leaf measurements presented as arithmetical means (x) and standard deviations (in parentheses). Prefix F – fertile shoots, prefix S – sterile shoots. Fig. 2 explains leaf variable abbreviations

| Leaf variable mean value | Population | | | | |
|---|---|---|---|---|---|
| | Krndija | Papuk | Moslavina | G. kotar | Lika |
| F*ptl* (mm) | 17.6 (3.2) | 18.5 (3.4) | 16.6 (3.7) | 18.0 (3,6) | 17.5 (3.8) |
| F*lbl* (mm) | 42.2 (4.9) | 43.9 (6.0) | 41.5 (6.6) | 44.2 (6.6) | 43.1 (6.8) |
| F*lbw* (mm) | 3.0 (4.4) | 32.3 (4.6) | 31.3 (4.8) | 31.4 (4.7) | 33.5 (5.9) |
| F*dlb* (mm) | 12.6 (2.2) | 14.4 (2.8) | 12.9 (2.3) | 14.5 (3.0) | 12.6 (2.9) |
| F*alb* (˚) | 134.0 (26.1) | 109.7 (15.1) | 123.1 (16.3) | 111.0 (10.4) | 125.3 (15.0) |
| F*nvr* | 7.3 (0.8) | 6.9 (0.8) | 7.2 (0.8) | 7.2 (0.8) | 6.9 (0.8) |
| F*ntr* | 3.3 (0.8) | 2.9 (0.7) | 3.0 (0.6) | 3.2 (0.8) | 3.2 (0.8) |
| S*ptl* (mm) | 16.9 (3.2) | 18.6 (3.3) | 17.1 (3,6) | 17.4 (3.2) | 18.1 (3.2) |
| S*lbl* (mm) | 44.6 (6.5) | 46.5 (6.3) | 43.5 (6.8) | 44.4 (6.7) | 44.9 (6.8) |
| S*lbw* (mm) | 36.2 (4.9) | 35.9 (4.9) | 34.3 (5.0) | 33.7 (5.0) | 36.5 (5.4) |
| S*dlb* (mm) | 11.5 (2.6) | 14.5 (2.9) | 12.7 (2.2) | 13.9 (2.9) | 13.1 (2.9) |
| S*alb* (˚) | 156.1 (17.3) | 125.4 (15.4) | 134.7 (19.3) | 124.6 (14.6) | 136.6 (18.9) |
| S*nvr* | 7.6 (0.8) | 7.2 (0.8) | 7.3 (0.7) | 7.2 (0.8) | 7.1 (0.8) |
| S*ntr* | 3.5 (1.0) | 3.2 (0.8) | 3.2 (0.7) | 3.3 (0.8) | 3.6 (0.9) |

TABLE 2. Ecological characteristics of 7 investigated localities. Type of vegetation: PB – *Pteridio aquilini-Betuletum pendulae*, AE – *Abies alba-Equisetum sylvaticum*. Type of soil: A – automorphic-cambic, H – hydromorphic-pseudogleic. Type of stand (human impact): 1 – primary, 2 – secondary (for further details see text)

| Ecological characteristic | Population | | | | |
|---|---|---|---|---|---|
| | Krndija | Papuk | Moslavina | G. kotar | Lika |
| Tmean (˚C) | 10.8 | 10.2 | 10.3 | 10.3 | 8.7 |
| Tmax (˚C) | 38.3 | 36.2 | 36.5 | 38.3 | 37.0 |
| Tmin (˚C) | –22.2 | –23.3 | –21.5 | –23.9 | –27.3 |
| Precipitation (mm/$m^2$) | 771.1 | 938.5 | 893.5 | 1236.3 | 1355.1 |
| Altitude (m a.s.l.) | 200 | 650 | 210 | 450 | 525 |
| Coord. N | 45.42 | 45.48 | 45.58 | 45.43 | 44.62 |
| Coord. E | 18.05 | 17.58 | 16.78 | 15.28 | 15.33 |
| Type of vegetation | PB | AE | PB | AE | PB |
| Type of soil | A | H | A | A | H |
| Type of stand | 2 | 1 | 2 | 1 | 2 |

correlation between the two geographically closest populations, Krndija Mt. and Papuk Mt., was surprisingly poor. To further explain that result, in this study we investigated the relations between the populations according to their leaf characteristics by calculating Euclidean distances (*D*). For scaling, an interpopulational matrix of variance-covariance was used, based on the investigated populations. Of the many different cluster analysis procedures, the UPGMA (average linkage between groups) agglomerative hierarchical procedure was used. The data were standardized by the *Z*–score method (Sneath and Sokal, 1973).

The relations between silver birch populations according to the ecological characteristics of the localities were investigated using cluster analysis in the same way as above. The results are presented in dendrograms (Fig. 3a,b).

The relationships between the characteristics of the leaves sampled from the birch population sites and the ecological features of those localities were investigated by comparing the two dendrograms. A cophenetic value matrix was produced for each dendrogram. The cophenetic correlations between two symmetric dissimilarity matrices were calculated using normalized Mantel statistics (*Z*) with 1000 random permutations to measure the degree of relationship between the two matrices (Legendre and Legendre, 1998). According to Rohlf (1990), the degree of fit can be interpreted subjectively as very good ($0.9 < r$), good ($0.8 < r < 0.9$), poor ($0.7 < r < 0.8$) or very poor ($r < 0.7$). The nonparametric Spearman's correlation coefficient (*R*) (Sokal and Rohlf, 1989) was employed to relate the variability of the biometric leaf variables to ecological gradients. Complete statistical

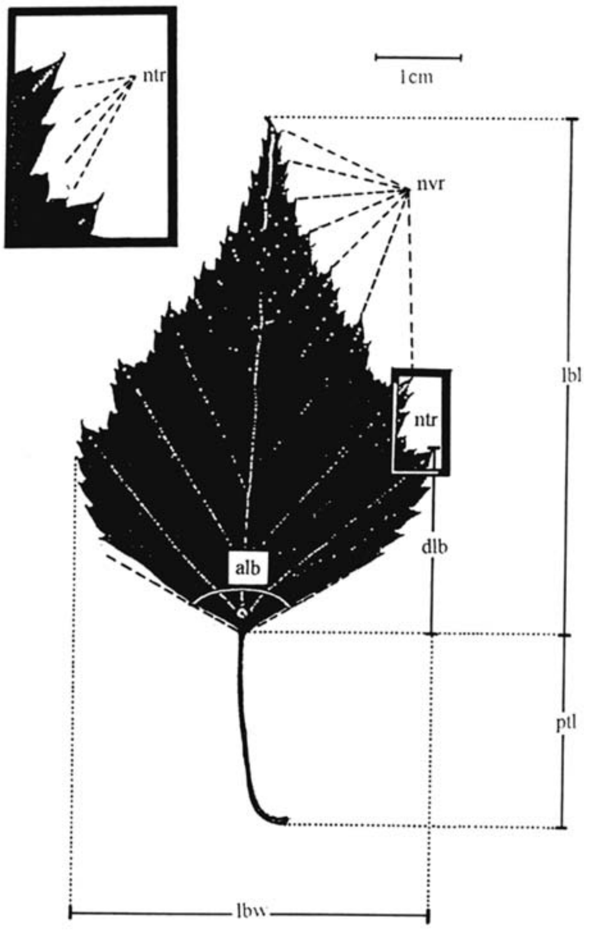

**Fig. 2.** Measured leaf variables. *ptl* – petiole length; *lbl* – lamina length; *lbw* – lamina width; *dlb* – distance from leaf base to widest point of lamina; *alb* – angle of leaf base; *nvr* – number of veins on right side of lamina; *ntr* – number of teeth between second and third vein on right side of lamina.

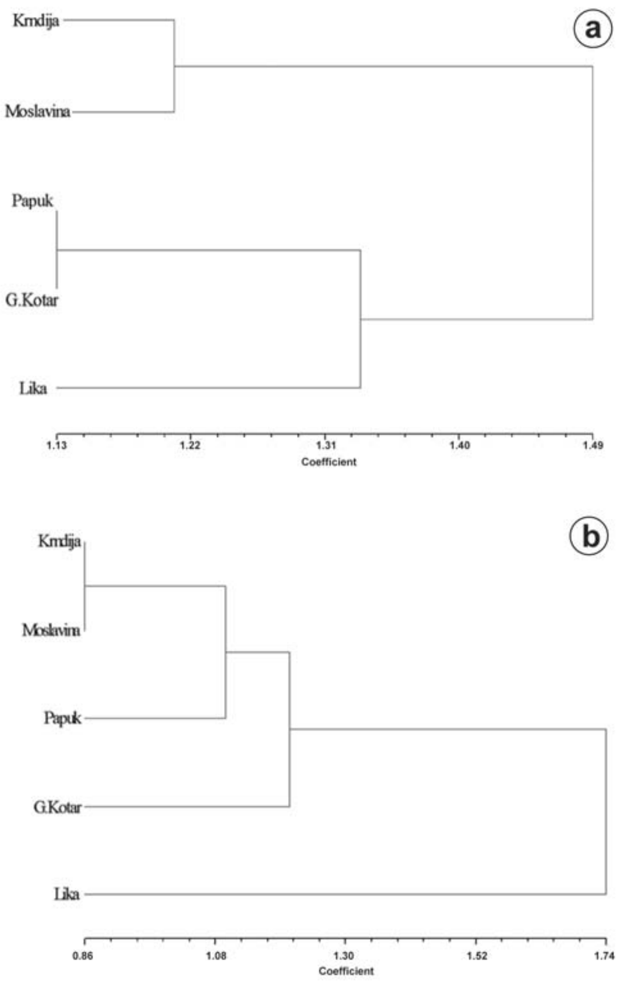

**Fig. 3.** Biometric variables. (**a**) Cophenetic correlation matrix: r = 0.55678, (**b**) Ecological variables. Cophenetic correlation matrix: r = 0.85898.

analyses were done using NTSYS and STATISTICA (StatSoft) packages (Rohlf, 1990).

## RESULTS

For the five investigated populations, cluster analysis applied to the biometric variables of fertile and sterile shoot leaves provided the dendrogram shown in Figure 3a. Papuk and Gorski kotar are linked to the first cluster at a Euclidean distance of D = 1.13, showing relatively high morphometric resemblance, to which is linked Lika (D = 1.33). The second cluster is composed of Krndija and Moslavina (at D = 1.21). The two clusters are linked together at D = 1.49.

Regarding the ecological variables of the five investigated populations (Fig. 3b), Krndija and Moslavina are linked at a distance of D = 0.86, depicting relatively high ecological resemblance. That cluster is joined with Papuk (D = 1.09), Gorski kotar (D = 1.21) and (most distant) Lika (D = 1.74).

The cophenetic correlations between the two symmetric dissimilarity matrices total 0.19399 by Mantel test statistics, which could be interpreted as a very poor fit. In other words, there is low congruence between the populations according to their biometric features and the related sites according to their ecological features. The nonparametric Spearman's correlation coefficient (*R*) also generally indicates a very low correlation between the biometric variables and the ecological characteristics. Table 3 presents all the correlations significant above $p < 0.005$. The number of veins (F*nvr*, S*nvr*) is positively correlated with mean annual temperature, and negatively with altitude and average annual precipitation. The number of teeth is positively correlated with annual temperature maximum (for F*ntr*) and negatively with northern latitude (for S*ntr*).

TABLE 3. Correlation between biometrical and ecological variables of 5 growing sites: selected Spearman *R* values significant at $p < 0.005$

| Biometry & ecology | Spearman R | t (N-2) | p |
|---|---|---|---|
| F*nvr* & altitude | –0.94868 | –5.19615 | 0.01385 |
| F*ntr* & Tmax | 0.92105 | 4.09644 | 0.02631 |
| S*nvr* & Tmean | 0.92105 | 4.09644 | 0.02631 |
| S*dlb* & altitude | 0.90000 | 3.57624 | 0.03739 |
| S*nvr* & precipitation | –0.97468 | –7.54983 | 0.00482 |
| S*ntr* & coord. N | –0.97468 | –7.54983 | 0.00482 |
| F*nvr* & Tmean | 0.97333 | 7.34847 | 0.00521 |

Of all the other measured variables describing leaf size and shape, only S*dlb* seems to have some positive correlation with altitude.

## DISCUSSION

The results of our previous morphometric studies contradicted expectations that silver birch populations would follow the annual precipitation regime in the Sava River basin, as some other communities do (Ilijanić, 1963; Franjić, 1996), clinally changing their morphological and physiological characteristics from east to west; the most prominent morphological resemblences were found to be between two disjoined populations from Papuk Mt. and Gorski kotar, 250 km apart. Since at that time we were interested in only the component of variability conditioned ontogenetically, of which the diversity of leaf shapes is representative, that result made us wonder about the component of variability that is conditioned by any modification of different aspects of the environment.

Since the development of every population should be based on diverse environmental influences as well as genetics, this time we put our morphometric data in the context of the ecological characteristics of each locality. Accordingly, the silver birch population from Lika, morphometrically clearly isolated from the other investigated populations, also seems ecologically remote from the rest. The Lika region has a montane climate, while the other investigated regions have a moderate continental climate (Bertović, 1975), so this result is not unexpected. Regional differences between populations of woody species can be connected to macroclimatic gradients (Dancik and Barnes, 1975; Pelham et al., 1988).

On the other hand, the easternmost silver birch population, originating from Krndija Mt., both morphologically and ecologically was poorly correlated with the geographically closest population at nearby Papuk Mt., and seems closer to the central Croatian population at Moslavina Mt. Comparing the vegetation of those two stands, we established that the Krndija and Moslavina populations are secondary, as is usual in Croatia, growing in abandoned fields now overgrown by fern brakes [*Pteridium aquilinum* (L.) Kuhn] in similar soil. In contrast, the two remaining populations, which are biometrically most similar, grow at sites differing ecologically at Papuk and Gorski kotar. As for our morphometric investigations we chose solitary silver birch trees for sampling, or those growing on the very perimeter of the forest, we noticed that although the type of soil was different, the sampled trees were growing in the close vicinity of similar types of vegetation: wetland silver fir (*Abies alba* Mill.) forests rare for this part of Europe, which are also two of the few known woody horsetail (*Equisetum sylvaticum* L.) localities in Croatia (Trinajstić, 1974; Trinajstić et al., 1997). Previous authors recognized the vegetation of these disjoined regions to be similar in some respects, and speculated that at least some parts of Papuk Mt. and the Gorski kotar region preserved their unusual flora and vegetation due to their peculiar ecological characteristics from a time of much colder climate, when this part of Europe was covered with uniform forest vegetation which today is either much more to the north or else in mountains higher than our studied Croatian localities (Pernar and Vranković, 1996; Trinajstić et al., 1997). Both Papuk and Gorski kotar lost any contact with the Alps after the last Ice Age (during the Holocene, ~10,000 years ago), but *E. sylvaticum* remains associated with silicate series of the altimontane belt (Jalas and Suominen, 1972), represented by pure acidophilus marshland fir forests, as in the Alps, Papuk and Gorski kotar. Consequently, the related Croatian habitats are considered to be descendants of the large virgin forests of the pre-Holocene era. However, comparing the published phytocenological relevs from Papuk (Vukelić and Španjol, 1990; Trinajstić et al. 1997) and Gorski kotar (Trinajstić 1974), we found that these forests today are not very similar; there is only 16.48% similarity of floristic structure between these two marshland fir communities, though *E. sylvaticum* is part of them. As our present results show, Papuk and Gorski kotar are not highly related ecologically either; the two biometrically most similar silver birch populations are therefore both ecologically and vegetationally rather distant, although morphologically very similar.

Furthermore, the correlations between the measured *B. pendula* leaf variables and the ecological gradients of the habitat are found to be at best poor. The numbers of veins and teeth of the leaves (*nvr*, *ntr*), which seem to be best correlated with the ecological gradients, in fact do not affect the main features: leaf shape and size. The calculated relations between the main morphological variables (*ptl*, *lbl*, *lbw*, *dlb*, *alb*) and ecological characteristics are so inconsistent and poorly expressed that they represent barely any correlation between ecological traits and leaf size and shape.

This result is very similar to those of North American *Betula* studies (Sharik and Barnes, 1979). Messier and Puttonen (1995) also find that silver birch at the center of its distribution range does not appear to have much morphological plasticity in leaf display, considering the varied ecological characteristics of the locality.

If there is a poor ecological correlation among the morphologically most similar *B. pendula* populations, and if variability in mean leaf characteristics cannot be related to the ecological gradients, what is the main factor in the development of silver birch populations? The answer to this final question is not easy to give.

The *Betula* genus is a taxon of originally cold temperate hardwoods, also inhabiting warm temperate biomes during global climate changes (Eocene-Miocene) and then cold temperate communities again after a cooling period (Oligocene) (Tallis , 1991; Nikolov and Helmisaari, 1992). After the Ice Ages, *B. pendula* remained a member of warmer climate flora in the southernmost parts of Europe such as Croatia today, but never again continuously distributed as a true forest species as before: it remains secondary. Apparently the birches were never restricted far enough to the south for their refugia to be completely isolated, and also had a mainly continuous distribution across Europe during the glaciations (Huntley and Birks, 1983). However, some of the recently disjunctive and reproductively isolated populations, such as those from Papuk Mt. and Gorski kotar, may preserve a number of genetic characteristics of their former primary habitats from the time of much colder climate. There they might even have coexisted and hybridized with other *Betula* species. They may be of older origin than those in other parts of the recent (secondary) Croatian distribution range, as at Krndija or Moslavina Mt. The normal distribution of frequencies and relatively low variance among the measured *B. pendula* leaf variables, together with the inconsistency and low dependence between the morphological and ecological properties of the investigated populations and their habitats, indirectly point to strict genetic control of leaf development. Croatian silver birch populations have not yet been investigated on the molecular level. Here we note that recently the chloroplast and ribosomal DNA *ITS* regions have been found to be surprisingly invariant over many *Betula* species in Europe, a finding unexplained so far (Ferris et al., 1999). The Croatian silver birch populations, in which the possibility of introgression today can be ruled out almost entirely, should be compared to the *Betula* species of Central Europe. At this point, before further molecular investigations are completed, we can only hypothesize that the main reason for this peculiar morphological similarity of disjoined silver birch populations at the very frontier of the European *B. pendula* range of distribution lies purely in their genetics.

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