

HABITAT PREFERENCE OF *PRIMULA* × *BREVISTYLA* IN THE CUHA VALLEY (BAKONY MOUNTAINS, HUNGARY)

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Habitat characteristics of the *Primula* × *brevistyla* hybrid zone developed in the Zörög Hill (Bakony Mts, Transdanubian Middle Range) containing even backcrossed individuals uniquely in Hungary – and we might say that uniquely even in Europe – are presented here applying Borhidi's ecological indicator values. The intermediate feature of the relatively narrow (some ten metres wide) zone rich in hybrids is well represented by the obtained light-, humidity- and temperature spectra comparing to those of the adjacent areas. The habitat most favourable for the hybrids can be found in a nudum like hornbeam-oak wood association developed on a steep western slope. Beyond the assessment of ecological indicator values we also tried to reveal other factors playing role in the long-term survival of the hybrid population, from which by our studies a community structural factor, the low ground coverage and therefore the resulting weak competition proved to be the most significant.

Key words: competition, ecological indicator values, habitat preference, hybrids, *Primula* × *brevistyla*

INTRODUCTION AND OBJECTIVES

Studies of population structure and hybrid zones have indicated that natural hybridisation is often found in tracts of intermediate habitats, or where conditions favouring both taxa are found in proximity and at the ecological limits of their distribution range (Arnold 1997, Huxel 1999). The phenomenon of hybridisation between *Primula veris* L. and *P. vulgaris* Huds. has attracted the attention of several researchers but only a few of them have dealt with the examination of the habitat characteristics of the hybrids. In this paper therefore we focused on the ecological examination of the habitat of the largest hybrid population known in Hungary, on the Zörög Hill, Bakony Mts which is part of the Transdanubian Middle Range.

The *Primula veris* L. (cowslip) and the *P. vulgaris* Huds. (primrose) have large overlapping areas in Europe (Meusel *et al.* 1978) and the result of hybridisation of the two species in some locations is the *Primula* × *brevistyla* DC. (= *Primula veris* × *P. vulgaris*). The phenomenon of hybridisation is however rela-

tively rare, hybrids have been reported from England (Clifford 1958, Woodell 1965), Scotland (Mowat 1961), Austria (Lüdi 1926) and Hungary. In Hungary interspecific *Primula veris* × *P. vulgaris* hybrid plants are only known from the wider region of the Bakony Mts. Hybrids established between *Primula veris* subsp. *canescens* (*syn.*: subsp. *inflata*) and *P. vulgaris* were reported first in Polgár's work (1935) who found them during the phytocoenological exploration of the Bakony Mts. He noted that the *P. vulgaris* occurred in the valley and the *P. veris* could be found in more sunny spots and when "moving upward from the valley on the slope we can frequently meet the hybrid of the two species". The occurrence of the hybrid has been reported from the Keszthely Mts by Nagy and Dános (1979) and Szabó (1987), from the northern Bakony and the Bakonyalja in the studies of Polgár (1935), Rédl (1942), Nagy and Dános (1979), Mészáros and Simon (1999), Cservenka *et al.* (2000) and Bauer (2001).

The spreading circumstances of the *Primula* species occurring in Hungary were examined by Nagy (1978); his study covers the pharmacobotanical comparison of the species beside their botanical description (spreading circumstances, taxonomy). He examined several *P. veris* subsp. *inflata* × *P. vulgaris* hybrid individuals occurring at different locations (Eplény, Keszthely Mts, Tapolcafő, Zörög Hill, Magszeg); his work drew the attention of the authors to the phenotypic variability of the protected hybrid occurring in large number in the area.

Our research area, the western slope of the Zörög Hill faces Porva-Csesznek and Vinye railway stations in the Cuha Valley. On this slope, up to the plateau of the Zörög Hill the *Primula vulgaris* Huds. occurs with high frequency, while the *Primula veris* Huds. subsp. *inflata* (Lehm) Dom. is frequent near the plateau. The weightpoint of occurrence of their interspecific hybrid falls on the upper section of the slope but many can be found on the chine, too. On the plateau, on the upper and middle section of the slope and at the bottom of the valley three, remarkably different forest associations have developed. On the basis of the results of the predictive mapping performed in the recent years (Cservenka *et al.* 2000) we assumed that among environmental factors the light seems to have the most definitive role in the habitat preference of *Primula veris* subsp. *inflata* × *P. vulgaris* hybrids. Partly for supporting this assumption, partly for revealing other environmental factors determining the establishment and conservational possibilities of these hybrid forms a detailed habitat indication study has been performed.

RESEARCH ON HYBRIDISATION BETWEEN PRIMULA VERIS L. (COWSLIP) AND P. VULGARIS HUDS. (PRIMROSE)

The first articles on reproduction biology of these hybrids had appeared from the second half of the 19th century. Darwin (1868) was the first who made a few reciprocal crosses; he gained some good seed with either *Primula veris* or *P. vulgaris* as a seed parent (seed-bearing partner), however in the *vulgaris* × *veris* crosses, some of the plants used as pollen parents were *Polyanthus* (we can frequently meet this name in the literature, which means typical F₁ *veris* × *vulgaris* plants), which Darwin considered to be a variety of *P. veris*.

Based on his field observations Miller Christy (1922) assumed that both species might be seed parents, but the *P. vulgaris* is probably more frequently. He found more hybrid individuals among primroses in forests than near to cowslips in meadows. Ernst (1925) found that in case of *veris* × *vulgaris* cross both the seed and capsule yield were as good as in case of intraspecific crosses. He could grow "hybrid families" from these seeds. Harrison (1931) stated that he could easily establish first generation hybrids originated from reciprocal crosses between *P. veris* and *P. vulgaris*. This is inconsistent with later studies in which no viable offsprings could be established for 5 years with different parental lines each time where the *P. vulgaris* was the seed parent (Valentine 1955). Harrison (1931) merely published his results and gave no experimental details.

Detailed reproduction biological examinations were performed by Valentine (1955) in cold house, who observed the fruit yield of parent species and the hybrids, capsule length and seed number per capsule without recognising significant differences between inter- and intraspecific crosses. However, significant differences were found in seed weight and in length of seed maturing. Seeds originating from interspecific crosses differ in size, content and weight from those of seeds of intraspecific crosses. He found that seeds originating from *veris* × *vulgaris* cross were filled, and contained matured endosperm and embryo, but their germination is significantly weaker than those of cowslip seeds. On the other hand the *vulgaris* × *veris* hybrid seeds are about the same length or a little longer than primrose seeds but do not contain matured endosperm. Half of the seeds participating in the experiment were completely empty while in other cases the endosperm could not be developed and sometimes very tiny unmaturing embryo initiatives were found. Among the 230 seeds constituting the sample only one contained a matured embryo and more or less developed endosperm. The content of seeds died in early stage of development shortly after fertilisation. Seeds established from *vulgaris* × *veris* cross did not germinate at all.

Woodell (1959) studied also the processes taken place after fertilisation both in case of intra- and interspecific crosses. Due to seed incompatibility has been shown by Valentine (1955) and Woodell (1959) the cross between the parent species is only successful when the *P. veris* is the seed parent. Relatively slow germination of hybrid seeds and the smallness of seedlings act against the survival of hybrids. However if the hybrids reach the stage of generative maturing they will (usually) grow sturdier. Literature data and field observations show that where the species come into contact in most populations hybrids form only a minute percentage of the populations. F₁ hybrids rather appear sporadically than in mass, and generally occur in habitats more like those of cowslip.

Mowat (1961) examined a "mixed" population near Fife (Scotland), in which the *P. veris* was less frequent than the *P. vulgaris*. In her research area of 10 km diameter the *P. vulgaris* was uniform while the *P. veris* seemed to be more variable. Some phenotypically *P. veris* looking individuals showed *P. vulgaris* characteristics. Clifford (1958) also assumed that introgression might take place, however he could not prove it statistically, while he pooled his samples from different localities, thus masking seasonal and environmental differences. Literature records indicate that backcrosses are very rare and their establishment requires very exceptional habitat conditions. The presence of a number of individuals that are either second generation segregates or backcrosses indicates that introgression is in progress. In the Zörög Hill even scapeless hybrid individuals showing *P. veris* flower characteristics also can be found in about 5–8% (Cservenka and Mihalik 2001). The presence of backcrossed plants supports Valentine's (1955) results, who found better germination (up to 75%) of seeds developed, while crossing *P. veris* with *P. veris* × *vulgaris* than of seeds originating from *P. vulgaris* (seed parent) × *P. veris* × *vulgaris* cross (up to 41%). It might be the reason of the appearance of primrose characteristics in cowslip populations that pollen from *P. veris* × *vulgaris* gets onto cowslip individuals through a pollen vector. The *P. vulgaris* populations are homogeneous not only due their distance from the mixed population but due the *P. vulgaris* × *P. veris* seed incompatibility.

A population comprising *P. vulgaris*, *P. veris* and hybrids between them has been found in a wood near Oxford (Boarstall Wood) by Woodell (1965). Similarly to the Zörög Hill, in this population not only first generation, but second generation hybrids and later segregates including backcrosses to each species have been found.

We agree with Woodell (1965) who assumed that habitat difference is the most important isolating factor. In England and (like in Hungary) the *P. veris* is a plant of unshaded or lightly shaded habitats, rarely found in woodlands, though often along the margins of woods. The *P. vulgaris* is a plant of more me-

sic environments, and either can be found in open conditions or in forests. On the basis of personal observations (Cservenka, in 1998, near of Aberdeen, Scotland) the moisture demand of *P. vulgaris* should be outlined; it also can be found in huge numbers in some locations along the open eastern coast of Scotland like in close proximity of waterfalls and creeks in forests and in shaded groves. Normally the species only meet along wood margins, in hedgerows, along woodland rides and paths. As Clifford (1958) pointed out, these meeting places are often disturbed, and in disturbed habitats introgression is favoured (Anderson 1949). Very often the disturbance is short-lived, and here lies one possible reason for such limited hybridisation.

Where the species occur together their flowering periods overlap. The flowering time of *P. vulgaris* lasts for about 6–8 weeks, the joint flowering period is usually 2–3 weeks. The lack of pollinators could only be a reason of the failure of fertilisation in case of long-lasting, continuous bad weather, but this practically cannot happen because of the long flowering period. As we mentioned before, fairly strong genetic barriers operate after fertilisation. From a consideration of these isolating factors, one could perhaps forecast that the most important factor leading to an extension of hybridisation would be a breakdown of the ecological isolation.

If a species cross takes place, and the *P. veris* thus pollinated sets seed, it is unlikely that the plants resulting from such seed will flower before their second year, even under very favourable conditions. In many areas, where F_1 plants occur, such as woodland rides after clearance has taken place, hedgerow after ditching, etc., the ground usually becomes rapidly grassed over a couple of years, and the establishment of any new plants, either of the species or of hybrids, will be greatly reduced. Hybrids are likely to be ill-adapted and at a great selective disadvantage. The fact that the F_1 plants rather appear in the near of cowslip, i.e. in grassy areas, will increase this effect. In meadows which are grazed, and therefore subject to some disturbance, backcross or F_2 plants are very rare, indicating that even here the hybrids are ill-adapted (Woodell 1965).

There are fairly strong genetic barriers operate between these species after fertilisation as we described earlier; there is also some temporal isolation, and there is very considerable ecological isolation. From the consideration of these isolating factors one could perhaps forecast that the most important factor leading to an extension of hybridisation would be a breakdown of the ecological isolation. If one considers a mixed population in grassland, where the primrose has emerged from its usual shaded habitat, the establishment of hybrids would be inhibited in the manner suggested above. On the other hand, if cowslips occurred in woodland, then the hybrid seed would be given a greater chance of establishment, since ground cover in woodland is less complete.

Moreover in that woodland the proximity of the parent species together with regular disturbance might favour hybridisation. The situation observed by the authors in the Zörög Hill, Bakony Mts clearly strengthens the above theory of Woodell (1965). Both in Boarstall Wood and in the Zörög Hill the cowslip was found in atypical habitat, and its establishment might correlate with earlier complete clearance. F₁ hybrids generally occur in habitats more like those of cowslip than those of primrose. One would expect selection to favour backcrosses to cowslip, if anything.

MATERIALS AND METHODS

The size of the experimental area proved to be adequate to the phytocoenological survey performed for the examination of the habitat preferences of the above *Primula* species. With the survey of the three different forest associations and through the analysis of the relative ecological indices of the taxa of the selected quadrates habitat variables, ecological background factors being important in the establishment and survival of the hybrids tried to be revealed.

5–5 phytocoenological surveys were prepared in the three association types (dolomite detrital slope forest near the top: A1–5; hornbeam-oak forest on the upper part of the slope: B1–5; and submontane beech wood on the lower part of the slope: C1–5) with the method of Braun-Blanquet using 20 m × 20 m quadrates. The coverage percent values were estimated in the field instead of recording AD values. The cluster analysis of the surveys was performed with Statistica 6.0 software (StatSoft 1987). The samples were evaluated either individually or assembled on the basis of the relative ecological indicator values [light- (LB), temperature- (TB) and water (WB) indices] given by Borhidi (1993, 1995) in order to reveal the most characteristic differences among the examined habitats.

For the comparison of habitats (A, B, C) ecological value spectra were prepared. The joint occurrence of the parent species generally growing in different habitats indicates the special, intermediate feature of the upper section of the western slope of the Zörög Hill. Borhidi *et al.* (2000) draw the attention that in intermediate habitats, near to boundary of tolerance, the indicator values of certain species may increase. The ecological value spectra of the surveys were prepared only for the herb layer either with calculating percent contribution or mass. The reason for this that the herb layer reacts in a short time to the change of the ecological factors and it is not exposed to direct human effects regarding the canopy (selective cutting of trees, etc.). Nomenclature of taxa and syntaxa: Simon (2000) and Borhidi and Sánta (1999).

RESULTS

Contrary to Woodell (1965) we recognised obvious difference in the ground flora associated with the parent- and the hybrid species. The dendrogram (Fig. 2) construed on the basis of coenological surveys reflects that those two groups of samples which contain *Primula* hybrids (A1–5, B1–5) separate even on the first level of similarity from surveys of the bottom of the valley (C1–5) in which only *Primula vulgaris* appears. The primary reason of this that near the bottom of the valley predominantly zonal, mixed, submontane beech-grove (*Daphno laureolo-Fagetum* (Isépy 1970) Borhidi in Borhidi et Kevey 1996) can be found, in which the other parent species, the *P. veris* does not occur at all. On the other branch of the dendrogram surveys made on the chine (A) and on the steep western slope (B) separate from each other on the second similarity level. On the top a wood intermediate between detrital slope forest (*Primulo veris-Tilietum platyphyllae* (Isépy 1968) Borhidi 1996) and mullein oak-wood has developed and contains even xerothermic oakwood species in considerable number, while on the steep western slope a – nudum like – horn-beam-oak forest poor in species could be recognised.

Starting from the – generally characteristic – habitat preference of the two parent species in the Bakony Mts the evaluation of light-, temperature- and water demand spectra seemed to be the most reasonable, however the other

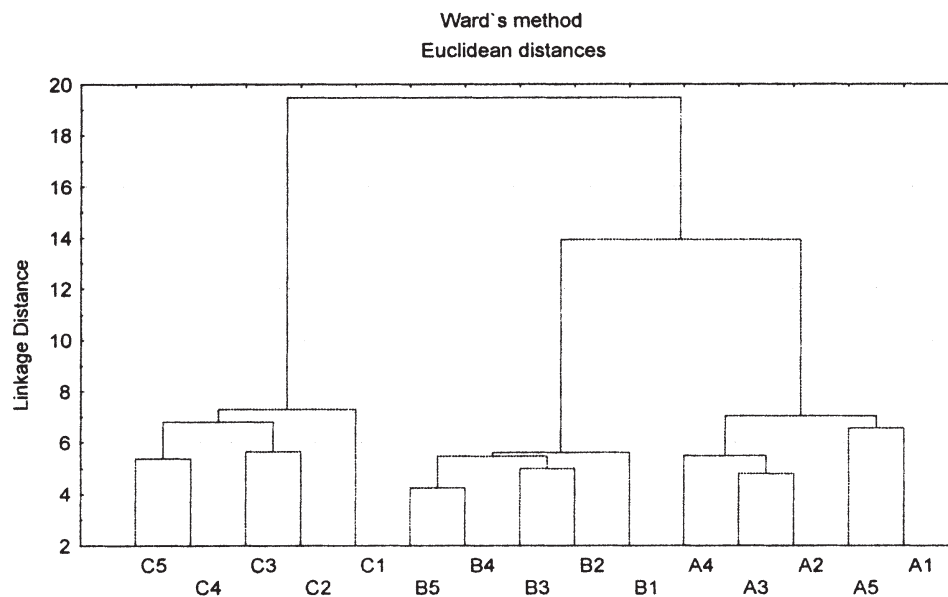


Fig. 1. Dendrogram showing the relation among the studied quadrats

relative ecological indices were also involved in our examinations. During the calculations performed either based on percent contribution or mass similar tendencies were experienced in each case, however considering percent mass the degree of differences among groups (from surveys A1–C5) became more conspicuous. Nevertheless, we present here the results of calculations performed on the basis of percent contribution while the standard deviation between surveys belonging to each type is smaller. Though Borhidi *et al.* (2000) calculate with percent mass in their work when evaluates ecological indices – here, in the turistically favoured Cuha Valley which is also considerably disturbed by game – the calculation of percent contribution seemed also appropriate for the evaluation of the selected parameters (light- (LB), temperature- (TB) and water (WB) indices). When calculating with percent contribution, taxa being outstandingly abundant – often only due degradation – do not alter the value spectra of the survey in such extent. For the calculation of indices rather influenced by degradational effects (N-value, value of naturalness (SBT) obviously the consideration of percent mass gives more objective and realistic picture.

Regarding the light spectra (Fig. 2) among the surveys of the chine (A), the western slope of the hill (B) and the bottom of the valley (C) an unambiguously descending light degree series can be recognised. In samples A1–5 the contribution of halfflight (L7) and halfshadow-halfflight (L6) plants are characteristic but the representatives of light plants and full light plants of open habitats (L8, L9) are also present. In the B and C surveys the percentages of L6, L7 decrease and the shadow and shadow-halfshadow plants (L4, L5) become more significant. In surveys made on the bottom of the valley (A1–5) the percent contribution of shadow plants (L3) exceeds 10%. On the basis of the light as an environmental variable comparing the spectra graduation can be recog-

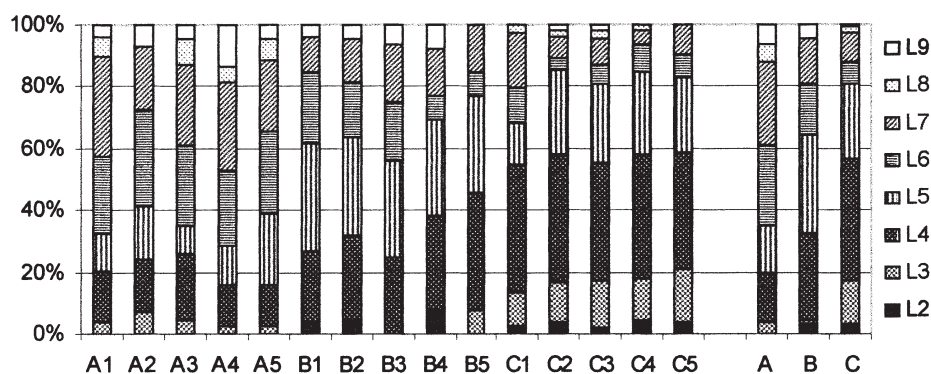


Fig. 2. Light spectra (LB) calculated by percent contribution in each quadrat and in their average

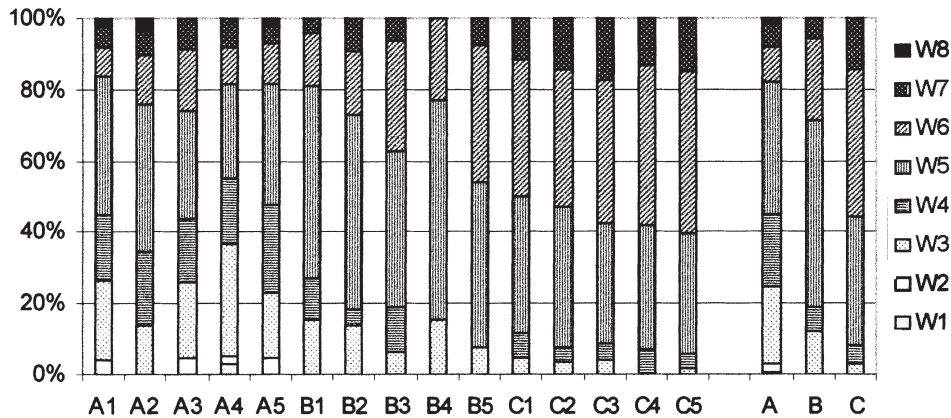


Fig. 3. Humidity spectra (WB) calculated by percent contribution in each quadrat and in their average

nised in solar radiation from A to C, but the difference between A and B samples is more conspicuous.

On the basis of the evaluation of the humidity requirement in samples A1–5 the contribution of plants of semi-dry habitats (W4), and plants of even drier habitats (W3, W2) is altogether about 40–50%, which is only 15–25% in B samples, and under 10% in C samples (Fig. 3). Representatives of semi-humid habitats (W5) reach their highest contribution in B samples, while contribution of plants of fresh soils (W6) is the highest at the bottom of the valley. The change of spectra between A and C can be considered almost completely gradatory while plants of different WB values show the highest contribution in each group of samples.

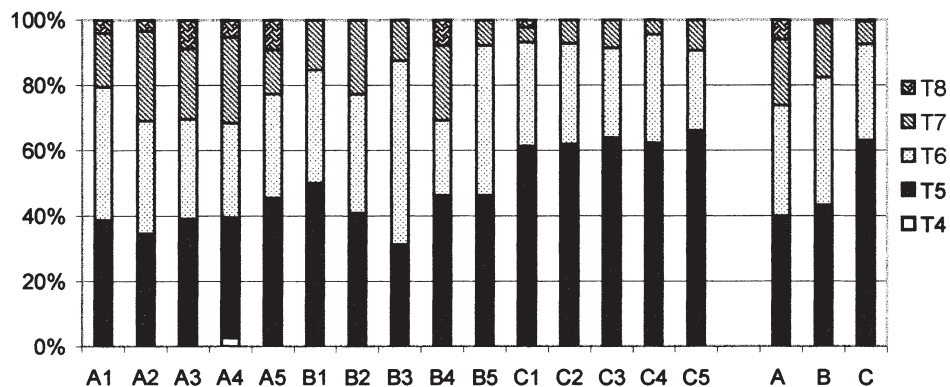


Fig. 4. Temperature spectra (TB) calculated by percent contribution in each quadrat and in their average

The spectra calculated from TB values (Fig. 4) also well reflect the difference among the three groups of samples. When calculating with percent contribution, the spectra of A and B groups are more similar to each other, the C samples visibly separate from them. It is a basic difference that in the samples of the bottom of the valley the contribution of taxa of “mesophilous broad-leaved forest belt” (T5) is over 60%, but near to the top of the hill – in the A and B group of samples – species of submontane broad-leaved forest belt (T6) and of thermophilous forest or woodland belt (T7) altogether reach contribution higher than 50%. Calculation performed with percent mass remarkably reflects the differences (Fig. 5). It is interesting to note, that samples of groups A and B how much differ from each other despite that they were considered similar by the previous method. In the spectrum of group A the T8 species while in that of group B the T6 species contribute with more than 30%. On the basis of percent mass a relatively smoothly descending temperature-graduation series can be recognised.

Our study supports the previous assumptions that the key factor of the occurrence of the *Primula* hybrids is the proximity of the *Primula veris*. (Samples A and B are much closer to each other even in space.) Regarding the spectra of the examined ecological scales, the three examined habitats remarkably differ from each other; moreover graduation in the contribution of ecological indicator values could be recognised.

The relative frequencies of the three *Primula* taxa compared to each other were also examined in the different habitats (A, B, C). The relative frequencies of *Primula* hybrids are the highest in samples B, which can be explained with the small number of species (14–27 species) in the herb layer. The cover of the

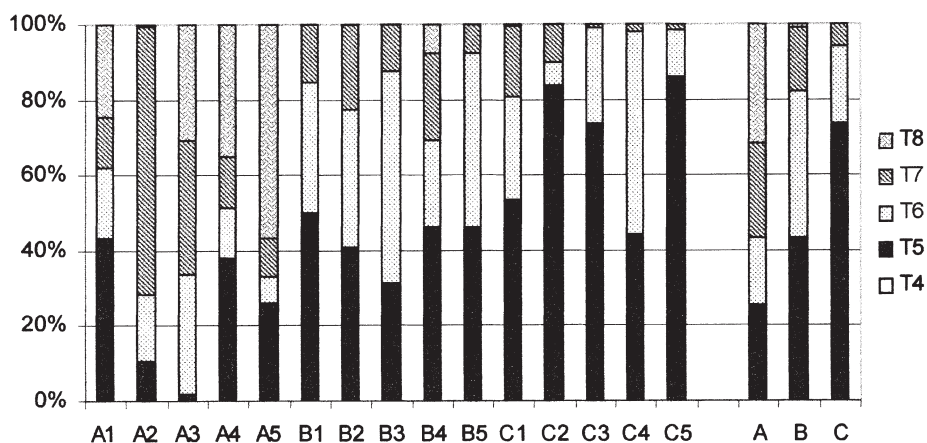


Fig. 5. Temperature spectra (TB) calculated by percent mass in each quadrat and in their average

herb layer in the B samples is the lowest, almost nudum-like as we mentioned before. In the early spring aspect the *Primula* hybrids occurring in smaller or larger spots are the most attractive elements of the understory of the wood. Visibly here manifest the effects of competition between species of the herb layer the least which may be favourable for the establishment and survival of hybrids usually being more sensitive for competition. For supporting our assumption we examined whether there was any relation between the relative frequency of the *Primula* hybrids and the total coverage of the herb layer in each survey. The statistical examination revealed that – on the basis of percent coverage of 15 coenological surveys – significant negative correlation exists between the relative frequency of the *Primula* hybrids and the total coverage of the herb layer (-0.725 ; $p = 0.002$).

While no relative indicator value have been given for the hybrids till now, based on our experiences and habitat indicational examinations we recommend the following relative ecological indicator values, social behaviour type and coenoelement category for the *Primula* × *brevistyla*:

	WB	TB	RB	LB	NB	KB	(SBT)	Coenoelement category
<i>Primula vulgaris</i>	6	7	7	5	5	2	S	Aremonio-Fagion
<i>Primula veris</i>	4	6	7	7	3	3	G	Querco-Fagetea
<i>P. × brevistyla</i>	5*	6*	7*	6*	3*	3*	Sr*	Querco-Fagetea*

*(recommended values)

DISCUSSION

In the above paper the habitat characteristics of the *Primula* × *brevistyla* hybrid zone (Cservenka 2000) developed on the Zörög Hill are presented applying Borhidi's ecological indicator values. The intermediate feature of the relatively narrow (some ten metres wide) zone rich in hybrids can be characterised well by the shown light-, humidity- and temperature indicator spectra comparing to those of the adjacent areas. The habitat most favourable for the hybrids can be found in a nudum-like hornbeam-oak wood association developed on a steep western slope. Beyond the assessment of ecological indicator values we also tried to reveal other factors playing role in the long-term survival of the hybrid population, from which by our studies a community structural factor, the low ground coverage and therefore the resulting weak competition proved to be the most important.

Experiences of our examinations performed at the habitat of the hybrids are basically similar to those of earlier observations of Clifford (1958), Mowat (1961) and Woodell (1965) by which it is necessary for the establishment of hy-

brid populations that one of the parents move out from its typical habitat and move in such a place which lets the hybrid seedlings to grow up and bring flowers. It will only be possible if the *Primula veris* settles in the forest in such a habitat where the coverage of the herb layer is small for some reason. The steep, rocky dolomite slopes near to the plateau having frequently been disturbed by game are such places. In the detrital slope forest (A) developed on the dry chine the *P. veris* finds favourable conditions regarding temperature and light. In small number, but it also occurs on the steep western slopes, in the closed forest (B) some metres far from the chine. The Atlantic-Mediterranean *Primula vulgaris* (which probably had entered the area of the northern Bakony from the direction of the Bakonyalja through the Cuha Valley) being very frequent in the mesophilous forests (and clearances) of the northern Bakony, regarding its habitat preference here is a less specialised species which presence presumably is limited by the higher amount of precipitation in the northern Bakony. It is due to these factors that the two species meet with relatively high frequency on the upper third of the western slope of the Zörög Hill providing thus the possibility for hybridisation. The slow germination of hybrid seeds is against the survival of seedlings (Woodell 1959), so the joint occurrence of the parent species is not enough in itself for either the establishment or stable existence of hybrid populations. On the western slopes of the Zörög Hill however the seedlings can grow in such an environment, where the competition in the herb layer is low partly due to the steep, rocky surface partly due to the strong closure of the foliage (except early spring). Our observations also correspond with those of the previous researches (Clifford 1958, Woodell 1965) namely, that hybrids may be over-represented in hybrid zones by the virtue of living longer. This is shown by the highest relative frequencies of the *Primula* × *brevistyla* experienced on the western slopes of the Zörög Hill and the significant relative negative correlation found between these values and the cover of the herb layer. From an other approach, resulting from the relatively high hybrid fitness the ongoing introgression may produce a hybrid zone that expands as hybrids displace parental genotypes. According to the "Evolutionary novelty model" both the environmentally dependent and hybrid fitness components are important in hybrid zone dynamics (Arnold 1997). However our results support the assumptions by which the *Primula* hybrids are generally ill-adapted and at a great selective disadvantage; their appearance and survival depends on numerous ecological and community structural factors, it seems that they have been adapted well to the special circumstances described above.

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