

Tetraploid populations of *Luzula multiflora* subsp. *multiflora* (*Juncaceae*) in Europe

Tetraploidní populace *Luzula multiflora* subsp. *multiflora* (*Juncaceae*) v Evropě

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Two cytotypes are found within *L. multiflora* subsp. *multiflora*, the hexaploids being widely distributed throughout Europe while tetraploids rarely scattered in several relatively restricted areas in the mountains. Distribution of the tetraploids of *L. multiflora* subsp. *multiflora* in Europe is summarized; they are found in the Pyrenees, the Alps, the Massif Central and the Tatra Mts. The tetraploids are analysed morphologically and compared with other allied taxa and populations of the group by means of cluster analysis. The tetraploids are grouped according to their localities, and form a cluster of its own. Pattern of variation in the *L. multiflora* s. l. and geographical origin of the tetraploids are discussed.

Key words: *Luzula* sect. *Luzula*, *Juncaceae*, taxonomy, biosystematics, karyology, Europe

Introduction

The section *Luzula* is a most diverse group of the genus in Europe (Kirschner 1993). The major feature of its differentiation involves several modes of karyotype evolution: true agmatoploidy, allopolyploid partial agmatoploidy, true allopolyploidy and (probably) autopolyploidy (Kirschner 1992). Morphologically, the differentiation manifests itself in a series of quantitative traits with minor overlaps; very few quantitative characters are found in the group.

Luzula multiflora represents the most complicated taxon in the section. In addition to a complex morphological differentiation on geographical and local ecological gradients, relic local populations and presence of several karyotypes within the species make the situation even more intricate. Even after exclusion of the most distinct infraspecific taxa (see Table 1), the rest is an assemblage of diverse forms.

Infraspecific taxa recognized within *Luzula multiflora* are listed below; it is obvious that morphological complexity makes it necessary to include a number of types of diverse origin in the species. Not only true polyploids (tetra- and hexaploids) are included in it but also a partial agmatoploid at the tetraploid level and, most surprisingly, also a diploid (agmatoploid) with 24 BL chromosomes. The type subspecies is the most widespread taxon of the section in Europe. Most of its geographical range is dominated by the hexaploid cytotype. It occupies a series of habitats, from lowlands to the secondary subalpine meadows, from meadows to damp woodlands, from early stages of succession to closed dense vegetation. On the other hand, the tetraploid cytotype is confined to

Table 1. – A survey of subspecies included in *L. multiflora* in Europe

Name	Karyotype	Distribution
<i>L. m.</i> subsp. <i>multiflora</i>	2n=24AL, 36AL	most of Europe, common
<i>L. m.</i> subsp. <i>frigida</i> (Buch.) V.Krecz.	2n=36AL	northern Europe
<i>L. m.</i> subsp. <i>hibernica</i> Kirschner & Rich	2n=24AL	Ireland
<i>L. m.</i> subsp. <i>snogerupii</i> Kirschner	2n=12AL+24BL	the Balcan Peninsula
<i>L. m.</i> subsp. <i>sibirica</i> V.Krecz.	2n=36AL	the N. Urals
<i>L. m.</i> subsp. <i>monticola</i> Kirschner	2n=24BL	the Pyrenees

Karyotype formulae introduced by Nordenskiöld (1951) are used. AL chromosomes are those of normal size, BL chromosomes are half-sized (due to simultaneous fragmentation), CL chromosomes are quarter-sized. In the subsp. *snogerupii*, therefore, chromosomes of two size categories are found.

limited areas in the mountains. The nature of this phenomenon is studied in the present contribution.

Material and methods

Material used in the present study includes samples from natural populations transferred to cultivation, and accessions of seeds cultivated in the Experimental garden of Institute of Botany, Průhonice. Detailed localities and other data are found in Kirschner (1992, 1996). Methods follow those employed in Kirschner (1991). Nomenclature used was discussed in considerable detail in Kirschner (1990).

Distribution of the tetraploid cytotype of *L. multiflora* subsp. *multiflora* in Europe

As stated above, the tetraploid populations of the subsp. *multiflora* are confined to relatively restricted areas in the mountains in continental Europe. Up to now, tetraploids have been detected in the Alps (Nordenskiöld 1951, 1956, Kirschner 1992), the Pyrenees (Kirschner 1995), the Massif Central (Nordenskiöld 1956) and the Belianske Tatry Mts., NE. Slovakia. Localities are summarized in Table 2.

Ecological data available allow to conclude that the tetraploid cytotype is generally confined to alpine or subalpine meadows. In this type of habitat, it is able to get in contact with other taxa or biotypes of the section: *L. sudetica* (2n = 48CL), *L. alpina* (2n = 12AL+24BL) and, rarely, with the hexaploid cytotype of the type subspecies. The latter two forms are likely to hybridize with the tetraploid cytotype. A hybrid between the tetraploid cytotype and *L. alpina* has been collected by Nordenskiöld in the Grossglockner region (cf. Kirschner 1991: 109); the plant is sterile and has 2n = 28 = 20AL+8BL chromosomes. Hybrids between the tetraploid and the hexaploid cytotypes can be expected to exhibit higher fertility (a similar situation was described by Nordenskiöld 1956, from N. America).

Morphology of the tetraploids

The tetraploid samples of the subsp. *multiflora* do not share any more conspicuous character. They are usually smaller, more slender, often dark-flowered; their floral parts are of slightly smaller size. On the other hand, almost each population is characterized by

Table 2. – Localities of the subsp. *multiflora* tetraploids (2n=24AL)

Sample number/source	Locality	Locality
Kirschner 1992		Austria, Osttirol, Praegraten, Eisseehütte, ca 2500 m a. s. l. (leg. Albertshofer, 1987)
L124 (Kirschner et al. 1988)		Austria, Oberösterreich, Dachstein-Gruppe, N. of Schladming, Lackenmoosalm, ca 2000 m (Bastl 1985, seeds from GZU cultivated, 2n=24 counted under no. KI66/86)
Nordenskiöld 1956		Austria, Styria, Koralpe, ca 1800 m (Widder 6)
Nordenskiöld 1956		Austria, the Gross Glockner Massive
Nordenskiöld 1951		Austria, Styria, Glashütten (non vidi)
L266 (Kirschner 1995)		Spain, León, Santa Maria de Valdeon, Vega del Liordes, 1860–1880 m (Montserrat et al. 1988)
Nordenskiöld 1956		France, Massif Central (seeds from Bot. Gard.)
L258 (Kirschner 1992)		Slovakia, the Belianske Tatry Mts., Zadné Jatky, ca 2000 m
L259 (Kirschner 1992)		Slovakia, the Belianske Tatry Mts., Hlúpy, ca 2000 m
L260 (Kirschner 1992)		Slovakia, the Belianske Tatry Mts., Kopské sedlo, ca 1800 m

Note: The above records include only cases with voucher material available (material used by Hedda Nordenskiöld has been studied in UPS) or plants cultivated by the author.

some features of general habit. For instance, plants from the Tatra Mts. have congested inflorescence and are more robust than those from the other populations, plants from the Pyrenees, León, have very few clusters (usually one or two subsessile ones and one pedunculate). Plants from the Alps are typically dwarf but otherwise of normal multifloroid appearance.

Some floral features of selected tetraploids, typical subsp. *multiflora*, an aberrant Greek hexaploid (cf. Kirschner 1993: 161) and typical plants of subsp. *frigida*, have been measured and analysed by means of cluster analysis. Characters measured are given in Table 3, samples are listed in the caption to the Figure 1. The data were processed by programs of the NTSYS-PC package (Rohlf 1993) using STAND, SIMINT-DIST, SAHN and TREE programs. A cophenetic value matrix derived from the original distance matrix has been obtained by means of COPH program, and the goodness-of-fit test was carried out (MXCOMP), the cophenetic correlation showing very good fit degree ($r=0.928$).

Four more distinct clusters can be recognized in the phenogram corresponding to the basic units of the samples: hexaploid *multiflora* samples (HM), the subsp. *frigida* (FR), the aberrant Greek hexaploid (GH – superficially close to the subsp. *frigida*), and the cluster of the tetraploid subsp. *multiflora*. Within the latter, the samples are mostly, with one exception, grouped according to the original localities (the Alps – TA, the Tatra – TT and the Pyrenees – TP).

Discussion

The variation pattern observed in the whole *Luzula multiflora* subsp. *multiflora* is extremely complex. Even a small portion of the overall variation, a selection of tetraploid populations

Table 3. – Characters evaluated in the cluster analysis.

1.	Seed length (excluding caruncles)
2.	Seed width (dorsal view)
3.	Length of caruncles (appendages)
4.	Tepal length (outer tepals of basal florets measured)
5.	Length of capsule segments
6.	Length of style
7.	Length of stigma
8.	Shape of capsule segments (subacuminate or slightly subacuminate in subsp. <i>frigida</i> , obovate in the other strains).

compared with some hexaploid strains, shows relative distinctiveness of the local populations. On the other hand, great number of various hexaploid forms covers and blurs the more conspicuous gaps in the variation of the tetraploids. Thus, I do not consider it possible to treat the assemblage of the tetraploid populations as a separate taxonomic unit. General similarity between *L. m.* subsp. *frigida* and the tetraploids (and, as shown on the case of the Greek hexaploid sample, some hexaploid populations) may suggest that the evolution of mountain populations might have been temporally or spatially divided from the diversification of later, ecologically less specialized, hexaploid invaders in Europe.

The type of variability observed among the tetraploids allows to conclude that the tetraploid cytotype is composed of more or less relic populations that diverged and can be characterized morphologically on the basis of minor quantitative differences.

Character of distribution of the tetraploids suggests that the tetraploids are of glacial age, and might have been relatively widely distributed in Europe. High level of variation of the *L. multiflora* group in Spain, and absolute lack of tetraploids in N. Europe indicate that the source of the migration of tetraploids might have been in the Iberian Peninsula.

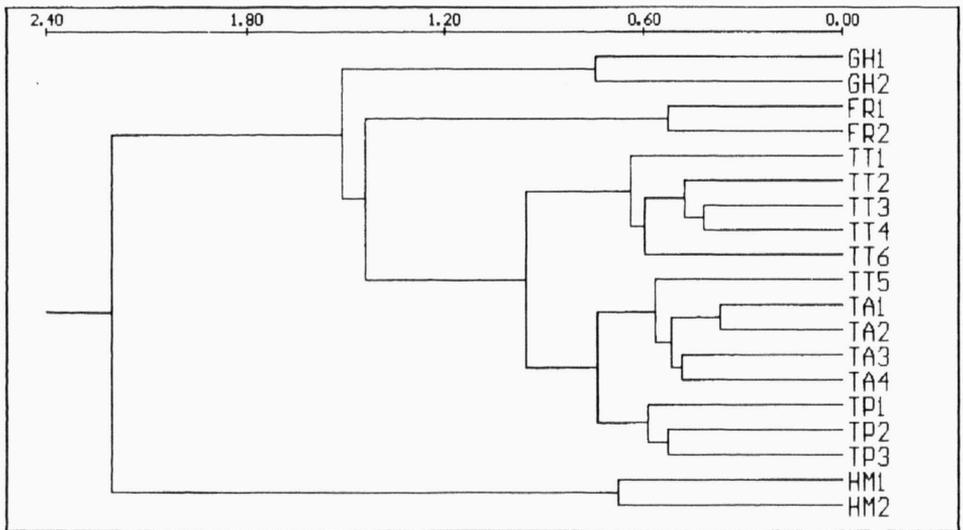


Fig. 1. – Results of cluster analysis of selected populations of the *Luzula multiflora* group. HM: hexaploid *L. multiflora* subsp. *multiflora*. TP: tetraploids from the Pyrenees. TA: tetraploids from the Alps. TT: tetraploids from the Tatra Mts. FR: *L. multiflora* subsp. *frigida*. GH: an aberrant hexaploid population from Greece.

As proposed above, the European hexaploids were spreading during a later period, probably together with some open communities of \pm damp forests, as indicated by the ecological amplitude of the hexaploids nowadays.

It should be added that there are other tetraploids (either true ones or partial agmatoploids at the tetraploid level) in Europe and the north, occupying geographically or ecologically marginal areas: It is *L. groenlandica* Böcher (Greenland and N. America), *L. multiflora* subsp. *hibernica* (Ireland), *L. divulgata* Kirschner (semixerophilous forest habitats in E.C. Europe), *L. multiflora* subsp. *snogerupii* (Balcan Peninsula), and *L. alpina* Hoppe (the Alps). The subsp. *hibernica* and *L. alpina* probably are also of Iberian origin.

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Souhrn

V rámci poddruhu *Luzula multiflora* subsp. *multiflora* jsou známy dva cytotypy. Hexaploidní cytotyp ($2n=36$) je rozšířen prakticky v celé Evropě a dominuje na řadě stanovišť od nížiny do subalpínského stupně, zatímco tetraploidní cytotyp ($2n=24$) je znám z několika navzájem dosti vzdálených horských oblastí. V předloženém článku je shrnuto rozšíření tetraploidů v rámci subsp. *multiflora*: dosud byli nalezeni v Pyrenejích, v pohoří Massif Central, v centrálních Alpách a v Belianských Tatrách. Při podrobné morfologické analýze (pomocí shlukové analýzy zkoumáno 8 převážně kvantitativních znaků u 19 populací tetraploidů a jejich srovnání s hexaploidy a dalšími podobnými či příbuznými populacemi se ukázalo, že tetraploidi z jednotlivých území tvoří obvykle samostatné shluky, a současně tvoří shluk oddělený od hexaploidů. Charakter proměnlivosti subsp. *multiflora* a pravděpodobný vznik a časový sled šíření obou cytotypů jsou též obsahem diskuse.

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