Potamogeton ×fluitans (*P. natans* × *P. lucens*) in the Czech Republic. II. Isozyme analysis

***Potamogeton ×fluitans* (*P. natans* × *P. lucens*) v České republice. II. Analýza isozymů**

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Kaplan Z., Plačková I. & Štěpánek J. (2002): *Potamogeton ×fluitans* (*P. natans* × *P. lucens*) in the Czech Republic. II. Isozyme analysis. – Preslia, Praha, 74: 187–195.

Evidence from isozyme electrophoresis confirmed previous hypothesis on the occurrence of interspecific hybridization between *Potamogeton natans* L. and *P. lucens* L. formulated on the basis of morphology and stem anatomy. Isozyme phenotypes of the morphologically intermediate plants were compared with those obtained from the putative parents growing in the same locality. *P. natans* and *P. lucens* differed consistently in at least 12 loci and possessed different alleles at 7 loci. The hybrid had no unique alleles and exhibited an additive "hybrid" isozyme pattern for all 7 loci that could be reliably analysed and where the parents displayed different enzyme patterns. Both true parental genotypes were detected among samples of plants of *P. lucens* and *P. natans* from the same locality. The hybrid plants represent a recent F_1 hybrid generation resulting from a single hybridization event. Consistent differences in enzyme activity between submerged and floating leaves of *P. natans* and *P. ×fluitans* were observed in all interpretable enzyme systems.

K e y w o r d s : *Potamogeton*, hybridization, isozymes, electrophoresis, enzyme activity

Introduction

Potamogeton ×fluitans Roth (*P. natans* L. × *P. lucens* L.) was recently discovered in NE Bohemia, as a new taxon for the Czech Republic (Kaplan 2001). Its identification was based on the study of its morphology and stem anatomy. *P. ×fluitans* differs from *P. natans* especially in having submerged leaves with a distinct lamina and petioles of floating leaves without a flexible section at the junction with the lamina. From *P. lucens*, it is distinguished by the capacity to develop floating leaves and by forming long, narrowly oblong submerged leaves. Stem anatomical pattern of *P. ×fluitans* is intermediate between those of its parents. In contrast, it is easily distinguishable from that of the morphologically most similar *P. nodosus* Poir.

To test the hypothesis of interspecific hybridization and the identity of the plants of intermediate morphology, fresh samples of each taxon from the site were examined by isozyme electrophoresis. Results of the isozyme analysis of the hybrid and its putative parental taxa are presented and discussed here.

Material a methods

Plant material

Both putative parental taxa belong to an informal group of broad-leaved pondweeds. *Potamogeton natans* is characterized by floating leaves with a large, coriaceous lamina and petioles with a discoloured section, and all submerged leaves with a lamina reduced to linear phyllodes. The species has a circumpolar distribution and occurs in boreal and temperate regions of the Northern Hemisphere. In contrast, *P. lucens* never produces floating leaves and its submerged leaves have mostly well developed narrowly oblong to broadly elliptical lamina. The species occurs in Europe and the adjacent parts of north Africa, and in most of Asia (Wiegleb & Kaplan 1998). Both species are considered to be tetraploids with the chromosome number 2n = 52 (Hollingsworth et al. 1998, Preston et al. 1998a).

Potamogeton ×*fluitans* was found accompanied with both its putative parents in a fishpond at the WSW margin of the Arnoštice settlement near Žehrov village in the Český ráj Landscape Area, NE Bohemia, Czech Republic. All three taxa were extremely poor in individuals, with most stems growing from a few systems of rhizomes. Samples of each shoot complex were collected. Four plants of intermediate morphology were taken from the mixed population of both species, together with four and five samples of *P. lucens* and *P. natans*, respectively. Fresh plant material was taken for cultivation in the experimental garden at the Institute of Botany, Průhonice, Czech Republic, in 1997 and 1999. Leaf material from each plant was sampled for isozyme analyses in summer 1999 and immediately used for enzyme extraction. Of the two taxa with the capacity to produce floating leaves, *P. natans* and *P.* ×*fluitans*, both submerged and floating leaves were included in analyses. Voucher herbarium specimens from both field and cultivation are preserved at PRA.

Electrophoresis

Freshly collected leaves were dabbed of water, marl and algae. Approximately 60 mg of leaf tissue was mechanically ground with Dowex-Cl (1-X8) and quartz sand and homogenized on ice in 0.75 ml tris-HCl extraction buffer. Two different extraction buffer systems were used: (a) "viola" (0.1 M tris-HCl pH 8.0, 70 mM 2-mercaptoethanol, 26 mM sodium metabisulfite, 11 mM ascorbic acid, 4% polyvinylpyrrolidon) was used to separate isozymes of PGI, PGM, AAT, ADH, EST, G6PDH, LAP, GDH, and 6PGDH, and (b) "luzula" (75 mM tris-H_3PO_4 pH 7.5, 13 mM 2-mercaptoethanol, 7.8 mM dithioerythritol, 2.8 mM L-ascorbic acid, 4% polyvinylpyrrolidon) for samples later stained for AAT, LAP, SOD, and PGI. The extracts were centrifuged for 10 min at 13,000 rpm and clear supernatants were stored at –75 °C for up to 16 months until investigated in electrophoresis.

Electrophoresis on non-denaturing polyacrylamide gels in a Hoeffer vertical electrophoresis unit was carried out. The gels consisted of separating gel (8% acrylamide, buffer of 1.82 M tris-HCl, pH 8.9) and stacking gel (4% acrylamide, buffer of 0.069 M tris-HCl, pH 6.9). The electrode buffer consisted of 0.02 M tris and 0.24 M glycine, pH 8.3.

The following ten enzymes were analysed: aspartate aminotransferase (AAT, EC 2.6.1.1), alcohol dehydrogenase (ADH, EC 1.1.1.1), esterase (EST, EC 3.1.1.-), glutamate dehydrogenase (GDH, EC 1.4.1.2), glucose-6-phosphate dehydrogenase (G6PDH, EC 1.1.1.49), leucine aminopeptidase (LAP, EC 3.4.11.1), phosphoglucoisomerase (PGI, EC

5.3.1.9), phosphoglucomutase (PGM, EC 2.7.5.1), superoxide dismutase (SOD, EC 1.15.1.1), 6-phosphogluconate dehydrogenase (6PGDH, EC 1.1.1.44). The staining procedures followed Vallejos (1983) to visualize ADH and 6PGDH, and Wendel & Weeden (1989) for PGM, PGI, EST, SOD, GDH, and G6PDH, with the following modifications: ADH (20 ml ethanol), 6PGDH (0.1 M tris-HCl pH 8.4, 30 mg 6-phosphogluconic acid), PGM (24 mg $MgCl_2$, 50 mg glucose-1-phosphate, 10 mg NADP), PGI (10 mg NADP, 24 mg $MgCl_2$), EST (Na-phosphate buffer pH 6.45; 25 mg β-naphthylphosphate, 50 mg Fast Blue BB), SOD (0.05 M tris-HCl pH 8.2, 4.5 mg EDTA, 5 mg NBT), G6PDH (30 mg NADP, 24 mg $MgCl_2$).

Enzyme systems AAT and LAP were stained using the following methods. Two staining solutions were prepared for AAT : A (20 ml 0.1 M tris-HCl pH 8.4, 240 mg aspartic acid, 40 mg α-ketoglutaric acid) and B (20 ml 0.1 M tris-HCl pH 8.4, 50 mg Fast Blue BB Salt, 50 mg Fast Violet B). The solution A was prepared at least 15 min before the application. Gel was rinsed in water and then in buffer tris-HCl pH 7. Solutions A and B were mixed and poured on gel. Gel was incubated in the dark at 32 °C until bands appeared. Then it was rinsed and fixed (1:1:3:5, glycerine, acetic acid, H_2O, methanol). The gel stained for LAP was rinsed in buffer 60 ml 0.2 M tris-maleate pH 6 and incubated 10 min with 40 mg L-leucyl-α-naphthylamide-HCl in 50% acetone and 60 mg $MgCl_2$ (both solved in 30 ml buffer). Afterwards solution of 25 mg Fast Black K Salt in 30 ml buffer was added and gel was incubated in the dark at 32 °C until bands appeared.

Results

Ten enzyme systems analysed represented 20–21 isozyme loci. Twelve loci enabled the interpretation of variation within samples studied; eleven of them were variable (Fig. 1). Others could not have been analysed mostly because of low enzyme activity in some or all samples.

AAT gave patterns consistent with 3 loci, of which *Aat-1* was insufficiently stained and could not be scored in all individuals. The slower products *Aat-2* and *Aat-3* were polymorphic. The uppermost band in *P. lucens* and *P.* ×*fluitans* of the *Aat-2* locus is considered as a secondary band. A single band of *P. lucens* at *Aat-2* presented a subset of the bands seen in *P. natans*. The putative hybrid displays banding pattern which was consistent with additive inheritance but which was also displayed by *P. natans*. *Aat-3* isozyme phenotype of the hybrid is identical to that of one of its parents, namely *P. natans*, but distinct from *P. lucens*.

The pattern of ADH consisted of a single visualized locus. Two isozyme phenotypes were detected among samples of *P. lucens*. One consisted of two bands, while the other one and those of all samples of *P. natans* and *P.* ×*fluitans* as well produced a single invariant band representing one homozygous allele.

Three loci were stained by EST. In *Est-1*, a single band of *P. natans* represented a subset of the bands seen in *P. natans* and *P.* ×*fluitans*. *P. natans* and *P. lucens* shared no alleles at *Est-2* and *P.* ×*fluitans* showed an additive banding pattern. *Est-3* was visualized only in some samples of *P. natans*, and therefore excluded from analysis.

GDH did not differentiate *P. lucens* from *P. natans*. All studied samples were monomorphic, although differences in enzyme activity among individual samples were observed. The complexity of the pattern is likely due to the post-translation modification

of a minority portion of molecules of the subunit. Five faint bands of heteromers indicated that GDH was hexameric in plants studied.

Some variation was detected by G6PDH but the patterns could not have been analysed with certainty because of a low enzyme activity.

The gel stained for LAP displayed one locus of more alleles. Two different isozyme phenotypes were detected among samples of *P. lucens*, one of which was possessed by plants of *P.* ×*fluitans* but distinct from that of *P. natans*.

It was not possible to interpret PGI because also 6PGDH was indeliberately stained in the same place on the gel.

Two loci were stained for PGM but for low enzyme activity of *Pgm-1* only *Pgm-2* could be interpreted. This locus distinguished both parents with the hybrid displaying an additive profile.

Three loci of SOD were found which clearly distinguished the parents from each other but unfortunately enzymes of the hybrid showed low or no activity.

Two loci were detected in 6PGDH, both variable and distinguished parents which were homozygous in *6pgdh-1* as well as in *6pgdh-2*. Isozymes of the two loci formed intergenic heterodimers giving rise to multibanded isozyme patterns, apparently complicated especially in *P.* ×*fluitans* (Fig. 2). The symmetrical position of homodimeric bands of both *6pgdh-1* and *6pgdh-2* loci in plants of *P. lucens* and *P. natans* most likely brought about the lower number of bands of intergenic heterodimers (expected 4, stained 3). At any case, 6PGDH represented the most useful isozyme marker for detection of putative parental plants.

Potamogeton natans and *P. lucens* differed consistently in at least 13 loci. Each species possessed unique enzyme bands at *Est-2*, *Pgm-2*, *6pgdh-1*, and *6pgdh-2*. The hybrid combined the enzyme bands of *P. lucens* and *P. natans* at all of these loci, as well as at *Aat-2*, *Est-1*, and *Lap-1*. Both species differed consistently also in three loci of SOD for which data of *P.* ×*fluitans* were not available (see above).

Two genotypes were detected among plants of *P. lucens* at *Adh-1* and *Lap-1*, possibly also at *G6pdh-1*, and of *P. natans* at *Aat-1*, *Aat-2* and *Sod-1*. In contrast, *P.* ×*fluitans* was found to be invariable in all observed loci.

No true differences were found between isozyme banding patterns of submerged and floating leaves within individuals of *P. natans* and *P.* ×*fluitans*. However, the leaf types mostly differed significantly in enzyme activity. In all enzyme systems the bands representing submerged leaves were generally fainter than those of floating leaves.

Discussion

Isozyme data confirmed the hybridization between *P. lucens* and *P. natans* suggested on the basis of morphology and stem anatomy (Kaplan 2001). All isozyme phenotypes of *P.* ×*fluitans* that could have been reliably interpreted in terms of alleles can be explained as a result of inheritance from these species. The hybrid has no unique alleles and exhibits an additive "hybrid" isozyme pattern for those loci where the parental alleles are different. Both parental genotypes were detected among samples of plants of *P. lucens* and *P. natans* from the same locality.

Most Central-European lowland and shallow water reservoirs filled for many years and exhibiting eutrophic conditions are relatively poor in species of water macrophytes. The

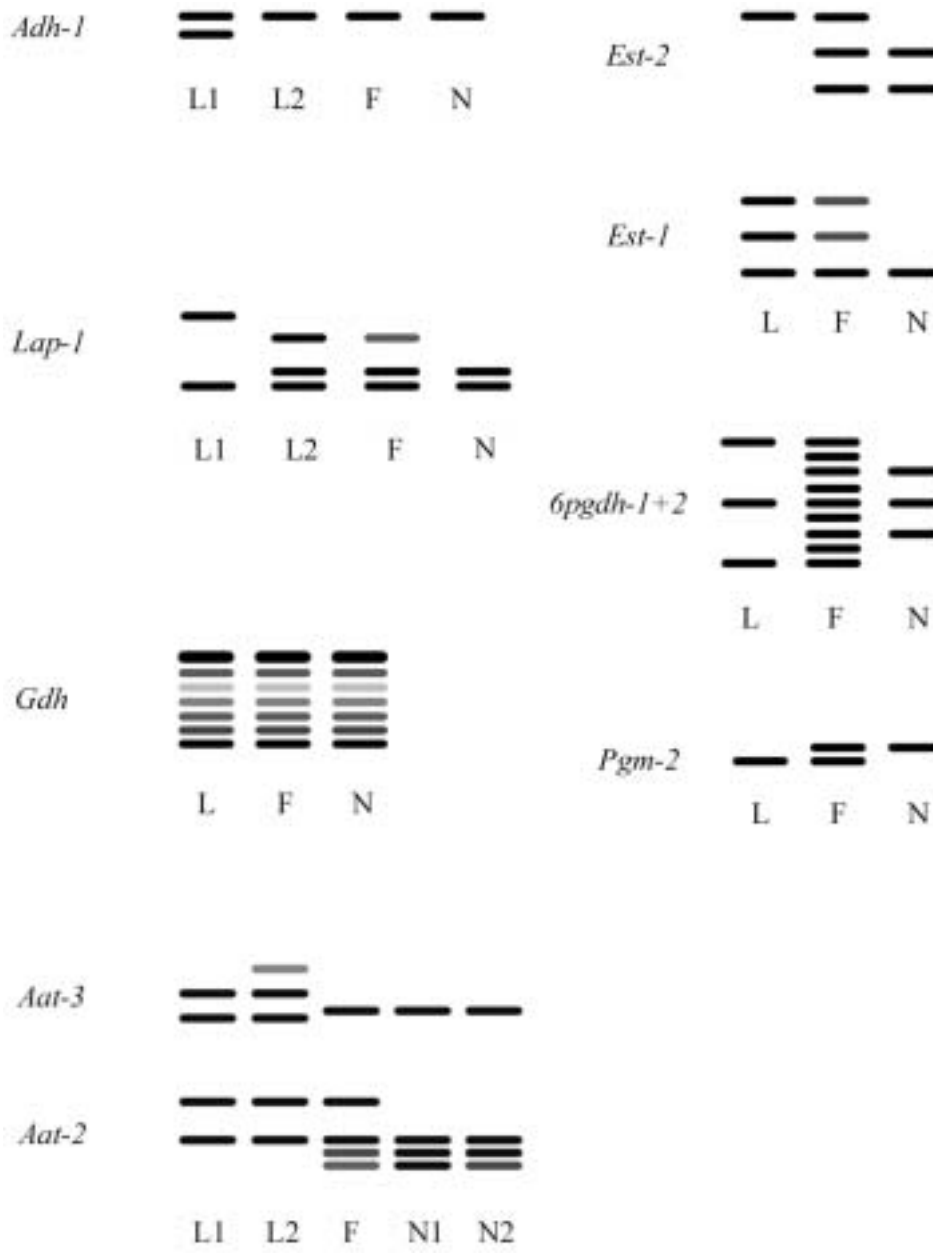

Fig. 1. – Observed isozyme phenotypes of selected isozyme loci of *Potamogeton lucens* (L), *P.* ×*fluitans* (F) and *P. natans* (N). Numbered symbols (e.g. L1, L2) correspond to different single-enzyme phenotypes. Grey bands denote less intensively stained bands in a gel. Size of bands and distances between them within a locus are printed in 135% of actual size as appeared on the gel.

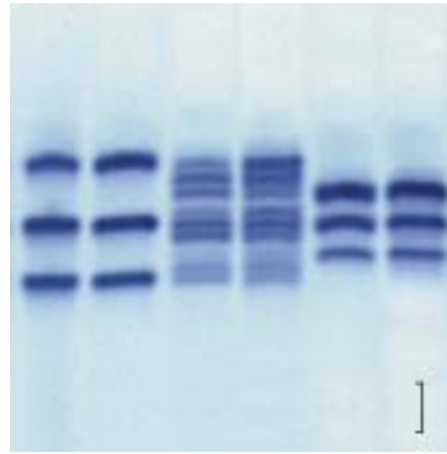

Fig. 2. – A part of the polyacrylamide gel stained for 6PGDH showing isozyme phenotypes with intergenic heterodimers of two samples of each of *Potamogeton lucens*, *P.* × *fluitans* and *P. natans*. Scale bar = 5 mm.

bottom is usually covered by thick organic-rich sediment (sapropel) which is often toxic because of anaerobic conditions. Water transparency is generally low and seed germination is inhibited. Populations of colonized plants are relatively stabilized. If present, species of *Potamogeton* mostly persist vegetatively. In contrast, new standing-water habitats exhibit rapid and considerable changes of plant communities. High concentration of nutrients is released from flooded soil while water transparency is still high. This enables explosive development of macrophyte vegetation. Seedling recruitment is possible, limited only by germination from seed bank.

These features of the early stage of succession were observed also in the fishpond near Žehrov. According to Rydlo (1999), the pond was reconstructed only a few years ago. The bottom was seasonally exposed and the sediment oxidized and mineralized. Soon after the filling of the pond, many species of water macrophytes, such as five species of *Potamogeton* L., three of *Ranunculus* subg. *Batrachium* (DC.) Peterm., *Sagittaria sagittifolia* L., *Oenanthe aquatica* (L.) Poir., *Lemna minor* L., *Schoenoplectus lacustris* (L.) Palla, *Chara vulgaris* L. etc., were reported (Rydlo 1999, Kaplan 2001). Most *Potamogeton* species were found in flower. Their populations were rather poor in individuals, forming spatially restricted small colonies of stems, each growing from a single or a few systems of rhizomes. Rapid changes of water vegetation between two visits of the pond in 1997 and 1999 corresponded to quite an initial stage of succession.

From these field observations and from the results of isozyme analysis it may be concluded that hybridization between the parental taxa took place in the locality quite recently. Seeds of *P. natans* and *P. lucens* survived in a drying sediment and germinated during the period with comparatively high water transparency after the pond bottom had been flooded again. Another possibility is that plants of the parental species were introduced by waterfowl. Regardless of how these species had colonized the newly established habitat, according to this hypothesis they hybridized short after the pond was filled.

Potamogeton ×*fluitans* is considered to be a sterile hybrid. Although it has been known that fruit production is extremely rare in this taxon (Preston 1995, Hollingsworth et al. 1995, Wiegleb & Kaplan 1998), seed viability has never been confirmed nor even studied so far. No trace of developed fruits has been found among the Czech material (Kaplan 2001). All information available suggests that the hybrid plant found near Žehrov represents a recent F_1 hybrid generation resulting from a single hybridization event.

Rise of *P.* ×*fluitans* and its successful growth to an adult plant must be considered a rare event. The hybrid has been detected in only 9 countries so far (Kaplan 2001) despite the fact that both parental species are sympatric in a large range from Western Europe through much of Eurasia to Japan. Even though both *P. lucens* and *P. natans* have shared many localities in the Czech Republic and the field survey has been extensive especially during the past 50 years, morphologically remarkable *P.* ×*fluitans* has never been found until now. The explanation of this fact should be looked for in the biology of *Potamogeton* species. In established populations, vegetative reproduction is perhaps much more important than reproduction by seeds. Brux et al. (1987) noted rare establishment of plants of *P. alpinus* Balb. from seed in the wild despite a rich seed bank. Van Wijk (1989) concluded that maintenance of populations of *P. pectinatus* L. was almost entirely due to vegetative persistence and reproduction while the main function of fruits was in dispersal and long-term survival during unfavourable periods. Hollingsworth et al. (1996a) reported that although fruits may be produced in quantity by large populations of *P. pectinatus*, seedling recruitment was rare. Field observations and isozyme analyses of the partitioning of variability within and between populations of *P. pusillus* L. and *P. berchtoldii* Fieber confirmed prevailing clonal persisting by means of turions (Kaplan & Štěpánek, unpubl.). Even if plants in some populations of *Potamogeton* species flower and fruit freely, seedling recruitment in stabilized populations is generally rare. Faster growth of new stems from rhizomes or turions causes the seedlings to fail in competition for light. In waters with very low light transparency the seedlings die soon after germination from seeds.

It may be assumed that pollination and crossing between *P. lucens* and *P. natans* is more frequent in sites of their joint occurrence but the germinating seedlings are mostly unsuccessful in competition with adult perennial plants, regrowing in spring from underground rhizomes or axillary short leafy shoots. Once established, *P.* ×*fluitans* is usually restricted to the pond where it rose. However, according to field observations made in Germany and Austria, the hybrid growing in running waters can propagate vegetatively by uprooted plants and stem fragments.

So far, four hybrids were investigated in detail using isozyme electrophoresis to verify putative parentage in *Potamogeton*, namely *P.* ×*schreberi* G. Fisch [= *P. natans* L. × *P. nodosus* Poir.] by Hollingsworth et al. (1995), *P.* ×*suecicus* K. Richt. [= *P. filiformis* Pers. × *P. pectinatus* L.] by Hollingsworth et al. (1996b), *P.* ×*bottnicus* Hagstr. [= *P. pectinatus* L. × *P. vaginatus* Turcz.] by Preston et al. (1998b), and *P.* ×*sudermanicus* Hagstr. [= *P. acutifolius* Link × *P. berchtoldii* Fieber] by Fant et al. (2001). To test the hypothesis that a newly discovered population of *P.* ×*schreberi* is distinct from the morphologically similar *P.* ×*fluitans*, isozyme phenotypes of this latter hybrid were used for comparison in the first named study, too[1]. A comparison of the isozyme banding patterns of floating and

[1] When the present paper was in the proof stage, a detailed study on *P.* ×*fluitans* in Great Britain by Fant et al. was published in Pl. Syst. Evol. 229: 45-57, 2001.

submerged leaves of *P. natans* and *P.* ×*fluitans* was also made by Hollingsworth et al. (1995) to check for intra-individual variation but none were found. Although no true differences in banding pattern were found in the present study either, consistent differences in enzyme activity between submerged and floating leaves within a single individual of *P. natans* and *P.* ×*fluitans* were observed. Bands of enzymes from submerged leaves were almost always fainter. It was not explicitly stated in the former study whether the leaves differed in enzyme activity or not, but the fact that different sampling methods were employed by the two research teams may have caused differences in observations. Single leaves were collected in the field, placed in plastic bags and transported to the laboratory by Hollingsworth et al. (1995). All leaves were probably preserved under uniform conditions which may have caused equalization of differences in enzyme activity between submerged and floating leaves. In the present study, the leaves were collected early in the morning from plants growing in cultivation tanks of the experimental garden and processed immediately for enzyme extraction whereby the physiological differences between the two types of leaves could have remained almost unchanged.

Acknowledgements

We are especially grateful to K. Kottová for considerable help with laboratory work. We thank Š. Bercha and I. Kaplanová for taking care of the cultivated *Potamogeton* material. We are also grateful to J. Kirschner for reading and commenting the manuscript. The research was supported by grants no. 206/98/1539 from the Grant Agency of the Czech Republic and no. AV0Z6005908 from the Academy of Sciences of the Czech Republic. Print costs were partly covered by grant no. 206/02/0773 from the Grant Agency of the Czech Republic.

Souhrn

Analýza isozymů potvrdila hypotézu o hybridizaci mezi druhy *Potamogeton natans* L. and *P. lucens* L., předtím formulovanou na základě morfologických znaků a znaků v anatomii lodyhy. Z porovnání isozymových fenotypů předpokládaných rodičů a intermediárních rostlin vyplývá, že se skutečně jedná o kříženec, který nemá žádný znak (alelu), který by se nevyskytoval u rodičovských rostlin, a že ve všech interpretovatelných lokusech vykazuje doplňkové hybridní uspořádání proužků. Oba genotypy skutečných přímých rodičů nalezeného kříženec byly detekovány. Nalezený kříženec představuje recentní F_1 generaci, vzniklou v důsledku jediné hybridizace. Aktivita enzymů se důsledně lišila mezi extraktem z ponořených a vzplývavých listů u *P. natans* and *P.* ×*fluitans*.

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Received 17 January 2001
Revision received 22 October 2001
Accepted 1 November 2001

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Distribution and phytocoenology of selected woody species of North Korea (D. P. R. K.)

Botanický ústav AV ČR, Průhonice 2001, 340 str. ISBN 80-86188-10-8.

Recenzovaná kniha navazuje na dvě předchozí publikace J. Kolbeka a M. Kučery z let 1989 a 1999, věnované stručné charakteristice a vyobrazení vybraných severokorejských dřevin. Shrnuje poznatky o rozšíření, fytocenologii a ekologii jednotlivých taxonů, získané během četných, především českých a slovenských expedic v letech 1969–1990 a doplněné údaji z dříve publikovaných zahraničních pramenů. Jsou zde shrnuta data o více než pěti stech dřevinách (stručný popis, rozšíření, ekologie). Při velkém bohatství severokorejské dendroflóry nebylo možné zahrnout do tohoto přehledu všechny její taxony. Autoři se proto soustředili především na vybrané druhy, u nichž mohli na základě vlastních terénních výzkumů předložit dosud neznámé údaje o výškovém a plošném rozšíření, fytocenologii jednotlivých taxonů s vazbou na základní vegetační typy a ekologii.

Schematická mapka Severní Koreje zpřístupňuje čtenáři orientaci v území. Z přehledu syntaxonů severokorejské dendroflóry je možné získat představu o vegetační diverzitě a současném stavu fytocenologického výzkumu tohoto botanicky velmi zajímavého území.

Jednotlivé taxony, jimž je v publikaci zpravidla věnována samostatná stránka, jsou abecedně uspořádány. Jejich základní taxonomickou charakteristiku doplňují často též údaje o celkovém areálu, černobílé kresby M. Kučery nebo černobílé fotografie. V zelených sloupcích jsou zpracována základní data o výškovém rozšíření jednotlivých taxonů ve studovaných pohořích a jejich fytocenotické vazbě. Přiložené mapky u každého taxonu v některých případech nezachycují jeho celkové známé rozšíření v Severní Koreji, neboť údaje v místních flórách poskytují pouze obecné informace o výskytu taxonů v tomto území. Jsou v nich zaznamenány pouze ty lokality, u nichž bylo doloženo jejich výškové rozšíření, především na základě údajů z expedic. Proto tyto mapky často zůstávají zcela prázdné, což na první pohled zamlžuje představu o dosud známém celkovém rozšíření některých taxonů.

Kromě podrobného textu k téměř 400 taxonům, doloženým kresbou nebo fotografií, obsahuje recenzovaná kniha stručnou charakteristiku dalších více než sta dřevin bez vyobrazení, převážně s údaji o výškovém rozšíření v jednotlivých pohořích a jejich fytocenotické vazbě. Knihu uzavírá výstižný souhrn a 48 názorných barevných fotografií jednotlivých taxonů nebo vegetačních jednotek (asociací nebo svazů).

Tato přehledně zpracovaná kniha vhodně doplňuje dosavadní sporé znalosti o severokorejské dendroflóře. Je prvním pokusem o zachycení vazby jednotlivých druhů dendroflóry na dosud uváděné vegetační jednotky ze Severní Koreje. Bude jistě cennou příručkou pro všechny botaniky, studující východoasijskou flóru a vegetaci, i pro zahrádkáře, toužící obohatit svůj sortiment východoasijskými dřevinami, z nichž se již některé velmi dobře aklimatizovaly v našich podmínkách.

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