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Phytogeographical aspects of the West European soft-water macrophyte flora

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SUMMARY

A literature study on the plant geography of West European soft-water macrophyte species was carried out. The purpose of this study was to find an explanation for the specific composition of the Dutch soft-water flora. In The Netherlands, soft-water macrophyte species with very different geographical ranges coexist. With respect to species distribution, four geographical groups could be distinguished: (1) a group with a boreal distribution; (2) a group with an atlantic distribution; (3) a group with a distribution that extends over the boreal and the atlantic area; and (4) a group with a wider distribution. Boreal and atlantic species favour different soft-water microhabitats and are ecologically not similar. *Littorella uniflora* (L.) Aschers., both boreal and atlantic, combines the ecological characteristics of both groups of species.

Key-words: atlantic, boreal, ecology, plant geography, soft-water macrophyte species.

INTRODUCTION

The soft waters of the West European lowland are characterized by a highly exclusive macrophyte flora which is, however, not rich in species. During our research over the past decade it became apparent that the soft waters in The Netherlands generally have a richer flora than those in the surrounding countries. In this paper an analysis is given of the biogeography of the soft-water macrophytes in order to explain this relative richness in species from the species distribution patterns and to arrive at phytogeographical groups of West European soft-water species.

Parallel with this biogeographical study, ecological data were collected to find support for our hypothesis that an interconnection exists between geographical distribution and the ecology of the species. This may have consequences for the phytosociological classification of the soft-water plant communities. The present paper provides an answer to the formulated hypothesis and discusses the phytosociological aspects.

METHODS AND TERMINOLOGY

The analysis of the distribution areas of the species was based on the works of various authors.The atlantic flora has been studied in detail by Dupont (1962) and Roisin (1969).

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Hultén has dealt with the amphi-atlantic (Hultén 1958) and boreal species (Hultén 1950), and Meusel *et al.* (1965, 1978) considered the central European flora. Apart from these general books we also consulted specialized works on aquatic plants (Donat 1926–1928a,b; Samuelsson 1934; Sculthorpe 1967; Casper & Krausch 1980, 1981) and various flora atlases such as Perring & Walters (1962) for Great Britain, Van Rompaey & Delvosalle (1972) for Belgium, Mennema *et al.* (1980, 1985) and van der Meijden *et al.* (1989) for The Netherlands, Haeupler & Schönfelder (1989) for Germany and Jalas & Suominen (1989) for Europe.

The term atlantic species is used in the broad sense, including all species that are restricted in their occurrence to the atlantic 'coastal' areas, from Portugal northward to southern Norway, and which extend at most 500–1000 km inland. A distinction between 'eu-atlantic' and 'subatlantic' was not made, as these terms cannot be sharply defined and are applied inconsistently by various researchers (Dupont 1962; Roisin 1969). Thus the term atlantic covers both the eu-atlantic and subatlantic regions. In accordance with Hultén (1958), the term amphi-atlantic is applied to boreal plant species occurring on both sides of the Atlantic Ocean.

RESULTS AND DISCUSSION

Phytogeographical groups

The results of the biogeographical analysis are shown in Table 1. The Table contains all soft-water species of Western Europe, as well as a number of species commonly found in soft waters, but which have a much wider ecological range. It is obvious that the soft-water flora is rather heterogeneous. Four biogeographical groups can be distinguished.

(1) Boreal species that have their main distribution in the northernmost parts of the northern temperate zone, with some relic stations in France and the mountainous areas of Central Europe.
(2) Atlantic species that occur only in atlantic 'coastal' areas. A few species extend among the western Mediterranean and are distinguished as atlantic–mediterranean.
(3) Species that have a combined boreal and atlantic distribution.
(4) Species that have a much wider and generally a more continental distribution.

Figure 1 shows the geographical area in Europe where the species classified as boreal and those classified as atlantic are to be found, while Fig. 2 presents the distribution of the species that have a combined boreal and atlantic distribution. The map in Fig. 1 clearly shows that The Netherlands is in the region where the distribution areas of boreal and atlantic species overlap. Among the boreal species, *Lobelia dortmanna* L. reaches the southern limit of its continuous area of distribution in the 'Kempen' district in Belgium. Further southward there are some isolated populations in Brittany and southwestern France. The two *Isoetes* species are already outside their main area of distribution in The Netherlands. They did occur in a few scattered localities. *Isoetes echinospora* Durieu was also found in Belgium. Further southward they occur only in isolated mountainous stations. The same is true for *Subularia aquatica* L., which has been recorded in The Netherlands once and was known to occur in various localities in the 'Kempen' district in Belgium.

The atlantic floral element dwindles out towards the north, no doubt as a consequence of gradually decreasing winter temperatures; however, almost all species do reach The Netherlands. In the case of *Ranunculus omiophyllus* Ten., which is common in the UK and

Table 1. Phytogeographical groups in the West European soft-water flora

Boreal species	
**Isoetes lacustris* L. s.l.	Incompletely circumboreal, montane
**Isoetes echinospora* Durieu s.l.	Circumboreal, montane
**Lobelia dortmanna* L.	Amphi-atlantic, boreal
*(†)*Subularia aquatica* L.	Circumboreal
*†*Eriocaulon aquaticum* (Hill) Druce	Amphi-atlantic, boreal; in Europe only in Ireland, Skye and Mull
*†*Ranunculus reptans* L.	Circumboreal, montane
*†*Potamogeton epihydrus* Raf.	Amphi-atlantic, boreal; in Europe only in the Hebrides
Species which are boreal as well as atlantic	
**Myriophyllum alterniflorum* DC.	Atlantic, boreal, amphi-atlantic
**Littorella uniflora* (L.) Aschers.	Atlantic, boreal
Atlantic species	
(a) Not reaching Denmark:	
Hypericum elodes L.	Atlantic
Echinodorus repens (Lamk.) Kern & Reichgelt	Atlantic
Ranunculus ololeucos Lloyd	Atlantic, radiating to the Mediterranean
(†)*Ranunculus omiophyllus* Ten.	Atlantic
(†)*Ranunculus tripartitus* DC.	Atlantic
(b) Extending into southern Norway and Sweden:	
Pilularia globulifera L.	Atlantic
**Scirpus fluitans* L.	Atlantic
Luronium natans (L.) Raf.	Atlantic
(*)*Potamogeton polygonifolius* Pourret s.s.	Atlantic
Echinodorus ranunculoides (L.) Engelm. ex Aschers.	Atlantic–mediterarrean
**Apium inundatum* (L.) Rchb.	Atlantic–mediterranean
Elatine hexandra (Lapierre) DC.	Atlantic, extending into central Europe
Eleocharis multicaulis (Sm.) Sm.	Atlantic
Deschampsia setacea (Huds.) Hack.	Atlantic
Species with a wider distribution	
**Utricularia australis* R.Br.	Atlantic–mediterranean and central European
Nitella flexilis (L.) J. Agardh	Atlantic and central Europe; world-wide
Chara globularis Thuill. var. *globularis*	Atlantic, boreal and central European; world-wide
Callitriche hamulata Kütz. ex Koch	Mediterranean–atlantic, boreal and central European
(*)*Juncus bulbosus* L.	Europe
**Potamogeton obtusifolius* Mert. & Koch	Temperate–boreal, central European, extending into Russia
Lythrum portula (L.) D.A. Webb	Atlantic–mediterranean and central European
**Potamogeton gramineus* L.	Europe
**Eleocharis acicularis* (L.) R. et Sch.	Temperate–boreal
**Sparganium minimum* Wallr.	Temperate–boreal (extending southward and there montane)
(*)*Ranunculus flammula* L.	Europe
Ranunculus peltatus Schrank	Europe
*†*Eleocharis parvula* (R. et Sch.) Link ex Bluff, Nees et Schauer	Atlantic and Baltic shores

*On other continents as well; (*)on other continents, but very few localities.
†Not in The Netherlands; (†)probably extinct in The Netherlands.

Fig. 1. The geographical area in Europe where the species classified as boreal and those classified as atlantic are distributed. Outlying records are not presented. (———), boreal species; (– – – –), atlantic species.

western France, the occurrence is marginal, as it has been found only once. *Ranunculus ololeucos* Lloyd, *R. tripartitus* DC. and *Hypericum elodes* L. extend northward into north-western Germany. *Echinodorus repens* (Lamk.) Kern & Reichgelt reaches the northern limit of its area in the 'Kempen' district in The Netherlands (Kern & Reichgelt 1950). The second author could not confirm the occurrence of this species in north-western Germany. Most atlantic species reach southern Norway and Sweden; *Luronium natans* (L.) Raf. is, however, extremely rare in the northern part of its area of distribution (Samuelsson 1934; Nilsson & Gustafsson 1978).

The relative richness of the soft-water flora of The Netherlands is thus a consequence of its geographical position, just within the area of the boreal species and just within the area where the atlantic flora is still fairly well represented.

Fig. 2. The geographical area in Europe of the species which have a combined boreal and atlantic distribution. Outlying records are not presented. (———), *Littorella uniflora*; (– – – –), *Myriophyllum alterniflorum*.

Ecological aspects

Autecology of the species in relation to biogeographical groups. **The group of boreal species.** In western Europe the boreal group consists of seven species, which are all amphi-atlantic. This means that the taxa are morphologically very similar on both sides of the Atlantic, but it does not imply that they are genetically identical.

Both *Isoetes* species are polymorphic, i.e. they have developed a number of more or less differentiated races in Europe and North America, which are considered by some authors to constitute separate species, but are treated collectively by others (Hultén 1958; Kott & Britton 1983). Taxonomic controversies concerning the taxon *Isoetes* have not been fully resolved to this day. Recently, Kott & Britton (1983) published a taxonomic revision of

the genus in northeastern North America, which was based on a wide range of criteria. It was found that the European *Isoetes echinospora* Durieu and the North American *I. braunii* Durieu and *I. muricata* Durieu are very similar in most characteristics. Together they are named *I. echinospora* sensu lato. *I. braunii* and *I. muricata* have also been treated as varieties and subspecies of *I. echinospora*. A complete list of synonyms is given by Kott & Britton (1983). These authors also suggest that the European *I. lacustris* L. and the American *I. macrospora* Durieu are in fact the same species. To prove the latter statement, however, further work would be required. Polymorphism in *Isoetes* may have been stimulated by the complex reproduction of this cryptogam, causing inbreeding and local variations between populations.

In contrast, *Lobelia dortmanna* shows very little variability over its geographical range. With respect to *Eriocaulon aquaticum* (Hill) Druce, it can be remarked that the chromosome number of the European population differs from that in North America ($2n=64$ versus $2n=32$) (Löve & Löve 1958). Mulligan & Calder (1964) claim that the European and the North American populations of *Subularia aquatica* can be regarded as subspecies on morphological grounds. The native British populations of *Potamogeton epihydrus* Raf. have not been studied in this respect, but Sculthorpe (1967) expects them to consist of genetically impoverished clones.

Of the two species in Europe that have a combined boreal and atlantic distribution, *Myriophyllum alterniflorum* DC. is also amphi-atlantic. Its variety *americanum* Pugsl. has also been recorded from the UK.

There are differences of opinion about the taxonomic status of the vicarious species *Littorella uniflora* and *L. americana* Fernald. The latter was described by Fernald (1918), but is considered by some authors as a variety of the former species or even as conspecific with it. Although further study will be necessary to settle the taxonomy of *Littorella*, it is clear that the North American taxon and the European one are morphologically very similar (Dietrich 1971). The differences described by Fernald (1918) seem to be within the range of variation shown by the European species.

According to the definition by Den Hartog & van der Velde (1988), all boreal and atlantic–boreal soft-water species are, with one exception, true aquatic plants, i.e. they can achieve their generative reproduction with all vegetative parts submerged. Furthermore, it is striking that with the exception of *Potamogeton epihydrus* and *Myriophyllum alterniflorum* all species are isoetids, i.e. species with a contracted stem and a rosette of stiff, compact, radical leaves with large air lacunae. The isoetid growth form can be considered the most efficient growth form for aquatic plants under the circumstances prevailing in oligotrophic soft waters, where hardly any inorganic carbon is available. The surface–volume ratio is reduced, and the large air lacunae favour internal transport of gases. Refixation of respired CO_2 occurs, and O_2 produced during photosynthesis can be transported to the roots, where it can be released into the substratum, aiding the oxidation of organic material which provides them with CO_2 (Søndergaard 1979; Søndergaard & Sand-Jensen 1979; Roelofs *et al.* 1984). Furthermore, several species use CAM photosynthesis, which is a clear adaptation to aquatic environments where CO_2 availability is limited (Madsen 1985). There is a clear relationship between the development of undergound biomass and the nutrient content of the environment; the root system is very well developed in oligotrophic substrates, which at the same time secures excellent anchoring.

As these plants are all true aquatics, they abound in permanently submerged waters. *I. lacustris* can descend down to 4 m depth and cannot stand emersion. *I. echinospora* and

L. dortmanna occur in shallower waters and can tolerate short periods of immersion. This is also true for *E. aquaticum* and *S. aquatica*. *L. uniflora* occupies a special position, as it can descend to considerable depths, but is only able to reproduce generatively in very shallow waters or when the plants are emerged. The species is able to develop a special terrestrial form with flattened leaves (Casper & Krausch 1981). The sterile aquatic form of *R. reptans* L. exhibits an isoetid growth form.

The boreal isoetids in particular have their habitat in the very soft waters. These aquatic systems are characterized by a very low alkalinity (< 1 meq l^{-1}) and are the least buffered of the soft waters. This type of water was very common in The Netherlands and Belgium in the first half of this century. Its flora comprised *I. lacustris*, *L. dortmanna*, *L. uniflora* and a few atlantic species, all of them tolerant to acid conditions (Arts *et al.* 1990). The more widely distributed soft-water species were absent from these very soft waters. They were inhabitants of the soft waters, which had a higher acid-neutralizing capacity (alkalinity up to 2 meq l^{-1}) and whose richer flora also comprised a higher number of atlantic species.

The group of atlantic species. The atlantic soft-water species are for the larger part not true aquatic plants, but amphiphytes, which are able to tolerate inundation for a considerable time, but which can only reproduce in the short period when they are emerged. They are restricted to the banks of water systems with fluctuating water levels. Due to the shallowness of the Dutch soft-water habitats these plants may form a quite extensive vegetation.

Among the atlantic soft-water species are only five true aquatics, namely, *R. ololeucos*, *R. omiophyllus*, *R. tripartitus*, *P. polygonifolius* Pourret and *Luronium natans*. *R. ololeucos* and *R. tripartitus* are batrachiids, i.e. heterophyllous species with finely divided submerged leaves and floating leaves; the other three species only have floating leaves and are mini-nymphaeids. It is obvious that the floating leaves of these species provide them with sufficient inorganic carbon from the air and enable them to live in soft water. However, the petioles and stems cannot be too long as the production of the necessary structural carbohydrates is a costly investment in a carbon-stressed environment. Thus these species are restricted to shallow water. Another factor that may restrict their occurrence is that the plants are fully submerged before they develop floating leaves, and then are completely dependent on the inorganic carbon available in the water itself or the bottom substrate. How *P. polygonifolius* and the *Ranunculus* species deal with this problem is still unknown; in the juvenile stages under submerged and oligotrophic conditions, plants of *L. natans* are often isoetid. When submerged, the two amphiphyte *Echinodorus* species can also adopt an isoetid growth form. Most atlantic species are generally found under conditions of less extreme alkalinity than the boreal species.

Species with a wider distribution. This is in fact a residual group. It contains mainly species which are frequently found in soft waters, but which also occur in waters with a higher content of inorganic carbon, and with higher nutrient concentrations. They are less exacting in their ecological requirements than the species of the other groups and thus by no means characteristic. However, some of these species may be dominant, e.g. *P. gramineus* L. and *E. acicularis* (L.) R. et Sch. The only species in this residual group with very special requirements is *E. parvula*, a small perennial with an isoetid growth form. This species is strictly bound to sites where oligotrophic soft water comes into contact with unpolluted brackish or sea water (tidal oscillations, temporary flooding, mixing).

Synecological aspects. The boreal and atlantic soft-water species generally occur spatially separated, as a consequence of differences in morphological and ecophysiological

properties of the species, and differences in their tolerance to the degree of harshness of the abiotic environment. The boreal soft-water plants (*I. lacustris, I. echinospora, L. dortmanna, E. aquaticum, S. aquatica*) are submerged isoetids which occur mainly in waters with an alkalinity of 1 meq l^{-1} or less. They tolerate acidification to some extent, except for *I. echinospora* (Arts *et al.* 1990). Their community has been described as Isoeto–Lobelietum, although other names have also been employed for some equivalent communities in restricted areas (Westhoff & Den Held 1969; Schoof-van Pelt 1973; Dierssen 1975; Pietsch 1977), and has been classified traditionally in the Littorellion alliance (order Littorelletalia) (Westhoff & Den Held 1969).

The atlantic soft-water communities are less homogeneous. One can distinguish a group of truly aquatic communities, which can be accommodated in the Potamion graminei (order Luronio–Potametalia), and a group of amphiphytic communities, which in the past have been classified in various ways. In the most recent phytosociological treatment (Schaminée *et al.* 1990) they have been placed in the Hydrocotylo–Baldellion and Samolo–Baldellion (order Littorelletalia).

In addition to *Juncus bulbosus* L., which has a wider range and thrives optimally in acidified waters, the only 'connecting species' between the submerged Littorellion alliance and the amphibious Hydrocotylo–Baldellion is *L. uniflora*. Not only does this aquatic macrophyte have a boreal–atlantic distribution, but it is also the least exacting species of the isoetids. Its tolerance to desiccation and to a higher trophic level and higher alkalinity enable it not only to grow in the submerged boreal community, but also to extend higher on the shore into amphibious communities of the atlantic Hydrocotylo–Baldellion. Consequently, the vegetation on exposed mineral bottoms in the sublittoral of soft-water bodies in the atlantic area of Western Europe, where the boreal species have dwindled out, generally consists of a dense unispecific sward of *L. uniflora*, which continues into the lower part of the littoral zone. The amphiphytic species of the Hydrocotylo–Baldellion are confined to the littoral zone, but also settle in the area occupied by the uppermost part of the *Littorella* sward. In shallow soft-water bodies, which are common in The Netherlands and Belgium, this zonation pattern is usually disguised. In the general geographical context, however, this situation in The Netherlands and Belgium can be considered atypical. It has complicated syntaxonomic classification. In the boreal regions of Europe, amphiphytic communities with *R. reptans* take the same zonational position as the Hydrocotylo–Baldellion communities.

Different views exist about the syntaxonomic position of boreal and atlantic soft-water communities. There is a consensus of opinion, however, that they must in any case be considered to belong to two different alliances. Den Hartog (1983) suggests that the aquatic and isoetid plant communities of the Littorellion are so different from the amphiphytic communities of the Hydrocotylo–Baldellion that they must be classified into different orders, but Dierssen (1975) and Schaminée *et al.* (1990), among others, place them in one and the same order.

From an ecological point of view it is interesting to compare the Hydrocotylo–Baldellion with more eutrophic vegetation units. Den Hartog & Segal (1964) suggested that the Hydrocotylo–Baldellion (then called Hypericion elodis) is in many respects the counterpart of the Lolio–Pontentillion anserinae (then called Agropyro–Rumicion; see Sykora (1983)) in the poor environments, because it occupies a transition between the contrasting regimes of the aquatic and the terrestrial environments and consequently is subjected to environmental fluctuations as a consequence of periodic (predictable) and episodic (unpredictable) fluctuations of the water level (flooding, drought).

CONCLUSIONS

In The Netherlands, soft-water species with very different geographical ranges coexist. This combination of species, some of which have a very limited distribution, contributes greatly to a characteristic, rare and relatively species-rich soft-water flora.

Within the Dutch soft-water flora, four main geographical groups can be distinguished. Boreal and atlantic species favour different soft-water microhabitats and are ecologically not similar. *Littorella uniflora* has geographical as well as ecological characteristics of both the atlantic and the boreal species.

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