

Distribution patterns, history, and dynamics of peatland vascular plants in Pomerania (NW Poland)

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Abstract: Pomerania is rich in various peatlands (fens, transitional bogs, raised bogs, spring-water mires, etc.), which support many rare and threatened plant species. This study was aimed: (1) to determine the phytogeographic diversity of Pomeranian peatland vascular plants associated with the classes *Oxycocco-Sphagnetea* and *Scheuchzerio-Caricetea nigrae*; (2) to attempt a reconstruction of the history of their postglacial migrations; and (3) to assess the dynamic trends of selected species. A database of records of 83 Pomeranian peatland plants was created, and cartograms of their distribution in Pomerania were made. Each taxon was briefly described, considering its distribution, phytocoenotic spectrum, and biological properties (e.g. pollination mode, diaspores dispersal). The phytogeographic analysis took into account geographic and directional elements, as well as mountain species found in Pomeranian peatlands. The plants' potential for colonization of new sites was assessed on the basis of Raunkiaer's life forms, modes of pollination and seed dispersal, and types of life strategies. As a result of numerical analysis and visual comparison of cartograms, 5 regional distributional types were distinguished: western, northern, eastern, all-Pomeranian, and disjunct. Within the eastern and all-Pomeranian types, which showed internal variation, several subtypes were distinguished. Most of the considered climatic variables (growing season length, temperature, and precipitation variables) were found to affect significantly the floristic variation of Pomeranian peatlands. The available palaeobotanical, palaeoclimatic, palaeoecological, and phytogeographic data, as well as original field research on the distribution of the taxa, allowed the formulation of hypotheses on the time and directions of their migration into Pomerania. Moreover, dynamic trends of selected species are analysed, and the decline of many peatland plant species in Pomerania is discussed.

Key words: flora, *Oxycocco-Sphagnetea*, *Scheuchzerio-Caricetea nigrae*, peatland, phytogeographic elements, chorotypes, pollination mode, diaspores dispersal, migration

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1. Introduction

The vegetation of Pomerania is exceptionally rich. This results from the great variety of habitats, reflected in the diversity of aquatic and terrestrial ecosystems. The most valuable ecosystems include peatlands, which create suitable living conditions for many endangered, vulnerable, rare, and protected plant species. Refugia of plant species of the cold climatic zone are found in this region. Their development there is possible thanks to the wet and cold substrate and the limited competition from trees and shrubs (or their complete absence), which allows them full access to light. The location of Pomerania close to the Baltic Sea, as well as the hydrographic and climatic conditions and the early post-glacial landscape, have all contributed to the concentration in this region of all possible types of peatlands characteristic for lowlands of Central Europe. These include extensive fens, transitional bogs, and raised bogs (e.g. small kettle-hole mires and, the largest in Poland, raised bogs located at drainage divides), as well as spring-water mires and calcareous fens, which are rare in other parts of Poland (Jasnowski *et al.* 1968; Sienkiewicz & Kloss 1995; Wołejko 2000).

The vegetation of Pomeranian peatlands, particularly of those located in the coastal belt, is particularly intere-

sting in respect of phytogeography. This area is affected by both the oceanic and continental climate. Consequently, this region is penetrated by species and communities whose centre of distribution is located in western or Boreal continental Europe (e.g. Czubiński 1950; Jasnowski *et al.* 1968; Jasnowski 1975; Jasnowski & Pałczyński 1976; Herbichowa 1979, 1998a; Herbich & Herbichowa 2002). Moreover, many species of peatland plants reach in this area (or its vicinity) some limits of their ranges.

Peatland ecosystems are subject to natural transformation. This is usually a very slow process, caused by plant succession or climatic changes. However, under the influence of various kinds of human activity, these ecosystems easily and quickly can be strongly and often irreversibly transformed or can even disappear together with their characteristic vegetation (e.g. Jasnowski *et al.* 1968; Herbichowa 1976; Wassen *et al.* 1989; Kooijman 1992; Fojt & Harding 1995; Joosten 1995; Rydin *et al.* 1999; Succow & Joosten 2001; Herbich & Herbichowa 2002; Kotowski 2002; Wołejko 2002; Paulissen *et al.* 2004; Prajs *et al.* 2006; Budyś 2008). This phenomenon is common not only in Poland. For example, in Denmark, Switzerland, large parts of Austria, Germany, and Great Britain, nearly all mires are damaged (Moen 1995, and references cited there). In Finland, wetlands

in the past covered about 10 million hectares, but 70% underwent various types of human transformation (Aapala *et al.* 1995). In Poland, about 80% of wetland ecosystems have been disturbed by human impact (Sienkiewicz & Kloss 1995). Due to the human degradation of peatlands their characteristic flora is impoverished.

Peatlands are natural archives of the vegetation history of the given area. Plant and animal remains preserved in peat deposits are indicators of climatic, palaeontological, and successional changes that took place in the postglacial period (Żurek 2001). The accumulated palaeobotanical data make it possible to construct isopol maps of individual species of trees, shrubs, and some herbs (Huntley & Birks 1983; Ralska-Jasiewiczowa 1983; Ralska-Jasiewiczowa *et al.* 2004). On this basis, the time and direction of their migration into the given area can be estimated. In spite of the rapid progress in palaeobotanical research, so far we have not accumulated a sufficient amount of direct evidence for all groups of plants. For this reason, in attempts to determine the hypothetical routes and time of migrations of species or groups of species, not only direct but also indirect evidence is used. When formulating hypotheses about the time of migration of mountain plant species that are found in the lowlands, the relationship of the given taxon with vegetation changes in the late glacial period and the Holocene has been taken into account (Zajac M. 1996). Earlier on, Czubiński (1950) estimated the time when plant species appeared in Pomerania on the basis of palaeobotanical data and current distribution of individual species or groups of species. The most probable direction of migration and the time of colonization of Pomerania by lichens in the postglacial period was determined by Fałtynowicz (1991), whereas Popiela (2004) provided similar data on forest plants.

Another question is the distribution of peatland plant species in a specified area. It may be considered on a local or national or global scale. The general distribution range of a given taxon forms the basis for assigning it to a proper geographic element. On the basis of the patterns of distribution of taxa, it is possible to distinguish and classify various distributional types. Attempts to classify regional ranges of plants in Poland were made, e.g., for forest species in Pomerania (Popiela 2004), species of the Kraków-Częstochowa Upland in southern Poland (Urbisz 2008), species whose range limits (general or local) run along the Vistula in the Lublin region (Kucharczyk 2003), and invasive species in Poland (Tokarska-Guzik 2005). Various types of local ranges of plant species were determined in some cities, e.g. Stuttgart (Kunick 1984), and Poznań (Jackowiak 1998). Regional distributional types have been used, e.g., for phytogeographic classification of study areas

(Zemanek 1991; Zajac M. & Zajac A. 1999, 2001; Urbisz 2008), reconstruction of the routes of species migrations (Kucharczyk 2003; Tokarska-Guzik 2005), and for formulation of hypotheses about directions and time of Holocene migrations of taxa associated with a given type of plant communities in Poland (Zajac M. & Zajac A. 2000). In contrast, local distributional types served to assess the impact of urbanization on the natural environment (Jackowiak 1994, 1998). Some of the species included in a given distributional type may have similar general distribution ranges and environmental requirements. Moreover, sometimes they have a similar history of colonization of the given area (Popiela 2004). Besides, it cannot be excluded that some similarities observed at the level of local or regional ranges may apply also to other macroscales.

The distribution of peatland plant species in Poland is shown in cartograms presented in the *Atlas of Distribution of Vascular Plants in Poland* (Zajac A. & Zajac M. 2001). Additionally, separate maps of distribution have been published for several species of this group. These maps cover the whole country (Żukowski 1965, 1969; Kuta 1991; Kucharski & Grzyl 1993; Sotek 2006a) or are limited to its lowland or northern part (e.g. Żukowski 1976; Sotek 2006b). Some regional maps are concerned only with Pomerania (Czubiński 1950; Jasnowska & Jasnowski 1979; Wołejko 1983; Popiela 2004; Sotek in print).

However, plant ranges are not static. Maps showing the distribution of a species in a dynamic way make it possible to illustrate its expansion or disappearance. Moreover, published records of many species were mostly historical, so it was necessary to check if the species can still be found there. All this has inspired me to start research on the distribution of vascular plant species of peatlands in Pomerania. The objectives of this study were: (1) to determine the phytogeographic diversity of Pomeranian peatland plants; (2) to reconstruct the history of migrations of peatland plant species into the study area during the postglacial period, on the basis of available palaeobotanical, palaeoclimatic, palaeoecological, and phytogeographic data, as well as original field research on the distribution of these species; and (3) to assess the dynamic trends of the studied species, on the basis of historical and current data. To reach these objectives, it was necessary to carry out the following research tasks:

- assessment of the distribution of vascular plant species associated with the classes *Oxycocco-Sphagnetum* and *Scheuchzerio-Caricetea nigrae* in Pomerania,
- analysis of the phytogeographic and ecological structure of the flora of Pomeranian peatlands,
- attempt to distinguish groups of peatland plant species with similar patterns of geographic distribution in the study area,

- assessment of the impact of selected climatic factors on the diversity of the peatland flora of the study area,
- formulation of hypotheses about the time of arrival and direction of migration of peatland plant species into the study area,
- attempt to present dynamic trends in the distribution of selected peatland plant species in Pomerania, and to discuss the processes of decline of peatland plant species in the study area.

2. General characteristics of the classes *Oxycocco-Sphagneteta* and *Scheuchzerio-Caricetea nigrae*

There is a need for a new synthetic approach and critical revision of the current classification of plant communities of mires in Poland (Jasnowska & Jasnowski 1983a; Kucharski *et al.* 2001; Matuszkiewicz 2001; Herbichowa 2004a; Herbichowa & Wołejko 2004a). The syntaxonomic classification used in this section is consistent with the traditional system given in the review of plant communities of Poland (Matuszkiewicz 1981, 2001). It supplements an earlier classification, included in the second edition of the monumental work *Szata roślinna Polski/Vegetation Cover of Poland* (Szafer & Zarzycki 1972), which describes the plant cover of Poland. According to the present, still provisional classification, plant communities of peatlands are mostly included in 2 classes: *Oxycocco-Sphagneteta* Br.-Bl. et R.Tx. 1943 and *Scheuchzerio-Caricetea nigrae* (Nordh. 1937) R.Tx. 1937.

The class *Oxycocco-Sphagneteta* includes the vegetation of wet heaths and raised bogs, fed exclusively or nearly exclusively by precipitation. It is strongly associated with the specific water regime where annual precipitation exceeds evaporation. Communities of this class are distributed in the Sub-Arctic-Boreal and Boreal zones of the Holarctic region, on acidic sites poor in nutrients. In Poland they are located mostly in the north. They are also found, although rarely, in central and southern Poland (mostly in the Sudetes and Carpathians) – outside their main distribution range. They develop in raised bogs, which are formed at drainage divides and river valleys and proglacial valleys, as well as in local depressions without outflow. A dominant role in their structure is played by dwarf shrubs and *Sphagnum* moss. Some trees may also be present. These habitats are characterized by a low number of plant species.

Communities of the class *Oxycocco-Sphagneteta* are grouped into 2 orders: *Sphagno-Ericetalia* Br.-Bl. 1948 em. Moore (1964) 1968, and *Sphagnetalia magellanici* (Pawl. 1928) Moore (1964) 1968. The first order, *Sphagno-Ericetalia*, consists of communities of wet heaths of the alliance *Ericion tetralicis* Schwick. 1933. Their main range of distribution covers the north-

-western part of Europe influenced by oceanic climate. They are distinguished by a large number of Atlantic species and a lack of Boreal (continental) species. In Poland they reach the eastern limit of their distribution ranges. The second order, *Sphagnetalia magellanici*, includes ombrotrophic moss communities of central and Sub-Arctic-Boreal parts of Europe. They are dominated by plants that form hummocks in raised bogs. The bogs are distributed in the lowlands and mountains, with a main distribution range in central Europe, and represent the alliance *Sphagnion magellanici* Kästner et Flössner 1933 em. Dierss. 1975. It can be divided into 2 groups: (1) communities of open raised bogs; and (2) communities of raised bogs with a loose layer of low trees or shrubs. The order *Sphagnetalia magellanici* includes also the alliance *Oxycocco-Empetrion hermaphroditi* (Nordh. 1936) R.Tx. 1937. It is composed of bogs of the Sub-Arctic-Boreal zone and is distinguished by the presence of species with a northern distribution. In Poland it is represented only by the association *Empetro-Trichophoretum austriaci* in blanket bogs of the Karkonosze Mts. (Zlatn. 1928) Jenik 1961 em. W.Mat. 1974 (Dierssen 1982; Matuszkiewicz 2001; Herbichowa 2004a; Kucharski & Kopeć 2007).

The class *Scheuchzerio-Caricetea nigrae* is composed of communities of fens, transitional bogs, and bog hollows. The class is divided into 3 orders: *Scheuchzerietalia palustris* Nordh. 1937, *Caricetalia nigrae* Koch 1926 em. Nordh. 1937, and *Caricetalia davallianae* Br.-Bl. 1949. The order *Scheuchzerietalia palustris* consists of communities of acidic dystrophic transitional bogs, as well as bog hollows. Its distribution range is Sub-Boreal and Boreal. The vegetation of the waterlogged bog hollows and erosional gaps in raised bogs and transitional bogs, or forming floating mats of *Sphagnum* moss and sedges in dystrophic lakes and in peaty pools, is grouped in one alliance, *Rhynchosporion albae* Koch 1926. By contrast, swampy sedge beds developing in dystrophic-mesotrophic habitats are included in the alliance *Caricion lasiocarpae* Vanden Bergh. ap. Lebrun et al. 1949. The second order, *Caricetalia nigrae*, groups acid low sedge mires of the alliance *Caricion nigrae* Koch 1926 em. Klika 1934. They are widespread in the temperate and Boreal zones of the Holarctic region. In Poland they are found in the lowlands and mountains, up to the subalpine line. In respect of flora and site conditions, they are closely related to both tall sedge communities (*Magnocaricion*) and wet meadows (*Molinietalia*), into which they can be easily transformed. Their sites are characterized by a moderate level of nutrients and low pH. They are fed by spring water or groundwater. Within the order *Caricetalia nigrae*, sometimes one more alliance is distinguished: *Calamagrostion neglectae* Pałcz. 1975 (Pałczyński 1975, 1983). The order *Caricetalia*

davallianae is composed of communities of spring-water mires, and fens, developing on substrates that are alkaline or neutral, rarely slightly acidic. In the synthetic work including detailed descriptions of plant communities in Poland (Matuszkiewicz 2001) they form the alliance *Caricion davallianae*. However, some authors distinguish 2 additional alliances: *Caricion demissae* Rybnicek 1964 (Pałczyński 1975, 1983), and *Sphagnowarnstorfiani-Tomenthypnion* Dahl 1957 (Herbichowa & Wołejko 2004a), which in the past was included in the order *Caricetalia nigrae* (Jasnowska *et al.* 1993; Kucharski *et al.* 2001). These communities develop on substrates fed by spring water or groundwater, rich in mineral salts, often particularly rich in calcium. In Poland, communities of this group are found at lower altitudes in the mountains and uplands, while in the lowlands mostly in the north. Because of the specific habitat requirements they are rare (Dierssen 1982; Jasnowska & Jasnowski 1983b, 1983c, 1983d; Kucharski *et al.* 2001; Matuszkiewicz 2001; Herbichowa 2004b; Herbichowa & Wołejko 2004a).

3. Study area

3.1. Location and limits

Pomerania (Polish: Pomorze) is a historical region including parts of northern Poland and Germany. In Germany, it includes Vorpommern and Rugia. In Poland,

it encompasses the Szczecin Coast (Pobrzeże Szczecińskie), Koszalin Coast (Pobrzeże Koszalińskie), Pomerelia (Pomorze Gdańskie), Kashubia (Kaszuby), Pomeranian Lakeland (Pojezierze Pomorskie) and Krajna. This study covered the part of Pomerania located in Poland. It is bordered in the north by the Baltic Sea; in the west by the Polish-German border between Kostrzyn to Gryfino, along the river Oder (Odra); in the east by the river Vistula between the Noteć Channel and the mouth of the Vistula at Mikoszewo; and in the south by the rivers Warta and Noteć, as well as the Noteć Channel (Fig. 1). The study area covers about 52 000 km². Further down in this article, the word *Pomerania* and the expression *all-Pomeranian* are used only in relation to the study area.

In the physical-geographic division of Poland (Kondracki 2002), this area is located within the province of Central European Lowland, 2 subprovinces of the South Baltic Coast (Pobrzeże Południowobałtyckie) and the South Baltic Lakeland (Pojezierze Południowobałtyckie) and 8 macroregions: the Szczecin Coast, the Koszalin Coast, the Gdańsk Coast (Pobrzeże Gdańskie), West Pomeranian Lakeland (Pojezierze Zachodniopomorskie), East Pomeranian Lakeland (Pojezierze Wschodniopomorskie), South Pomeranian Lakeland (Pojezierze Południowopomorskie), Lower Vistula Valley (Dolina Dolnej Wisły), and Toruń-Eberswalde Proglacial Valley (Pradolina Toruńsko-Eberswaldzka).

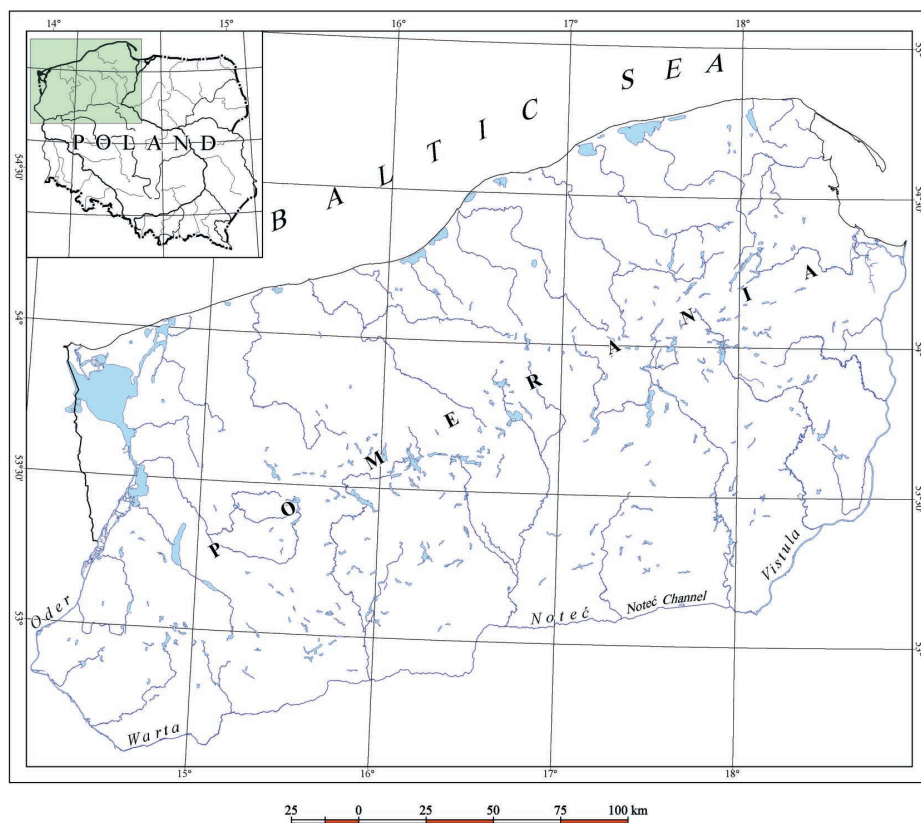


Fig. 1. Location of the study area (map by J. Prajs, on the basis of numerous resources)

According to an earlier geobotanical division of Poland (Szafer & Pawłowski 1972), Pomerania belongs to the Lowland-Upland Central European Province (Prowincja Niżowo-Wyżynna Środkowoeuropejska), Baltic Division (Dział Bałtycki), nearly completely within the subdivision Belt of Coastal Plains and Pomeranian Highlands, only its southern margins are within the subdivision Belt of Large Valleys. However, in the new geobotanical division of Poland (Matuszkiewicz 2008) the study area lies within the Central European Province (Prowincja Środkowoeuropejska), 2 Subprovinces (South Baltic and Central European Proper), and 3 Divisions (Pomeranian, Brandenburg-Wielkopolska, and Masovia-Polesie).

3.2. Climate

The climate of Pomerania is affected by penetrating moist masses of oceanic air and dry masses of continental air, as well as by land relief. Parts of Pomerania differ in the degree of pluvial continentalism, assessed on the basis of precipitation indices. Oceanic climate, with high precipitation, affects mostly the northern and western parts of the region. By contrast, the eastern and south-eastern parts are influenced by continental climate. Annual mean precipitation ranges from 525 to 750 mm. The highest precipitation (over 700 mm) is recorded in the central part of Pomeranian Lakeland. This is conditioned by land relief. Morainic hills, locally reaching over 200 m a.s.l., block polar-marine air masses, causing the relatively high precipitation. The lowest precipitation is recorded in the south and south-

west (locally, under 550 mm). The annual mean air temperature is the highest in the west (over 8.5°C), and the lowest in the east (under 7.5°C). The warmest month is July. The mean July air temperature is the highest (over 18.0°C) at the south-western margins of the region, while the lowest (under 17.0°C) in the central and northern parts of Pomerania. In the coldest month, January, temperature is the highest in the coastal region (mean air temperature over -1.0°C), and the lowest in the Tuchola Forest (Bory Tucholskie) and Kashubian Lakeland (about -3.0°C). The growing season is the longest at the western margins of the region (220-230 days), and the shortest near Gdańsk (about 180 days) as well as in the Polanów Plateau (Wysoczyzna Polanowska), Bytów Lakeland (Pojezierze Bytowskie), Kashubian Lakeland, and Tuchola Forest (about 190 days). In Pomerania the winds are mostly south-westerly and westerly and in the colder seasons also southerly (Woś 1999; Borówka 2002; Koźmiński *et al.* 2007).

3.3. Geology, land relief, and soils

The present landscape of Pomerania started to be shaped in the Quaternary and is associated chiefly with the last glacial period, known in this region as Vistulian (Weichselian). It was formed mostly in the period when the ice sheet started to melt down and retreat to the north. The Quaternary glacial sediments left in this area are dominated by boulder clay, which have formed belts of terminal moraines and extensive areas of ground moraine (Fig. 2). They are associated by fluvioglacial deposits, e.g. sandur sands, as well as sands and gravels

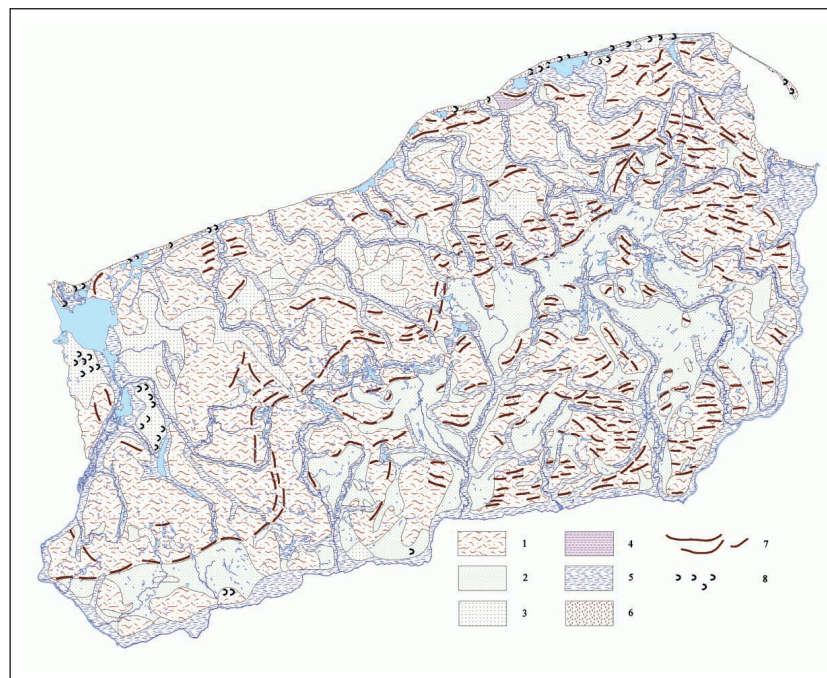


Fig. 2. Geomorphological map of Pomerania (after Kondracki 1988)

Explanations: 1 – ground moraine, 2 – outwash plains (sandurs), 3 – sandy terraces, 4 – periglacial lake basins filled with clays, dusts, and sands, 5 – valley floors and lower terraces, 6 – sandspits, 7 – terminal moraines, 8 – dunes

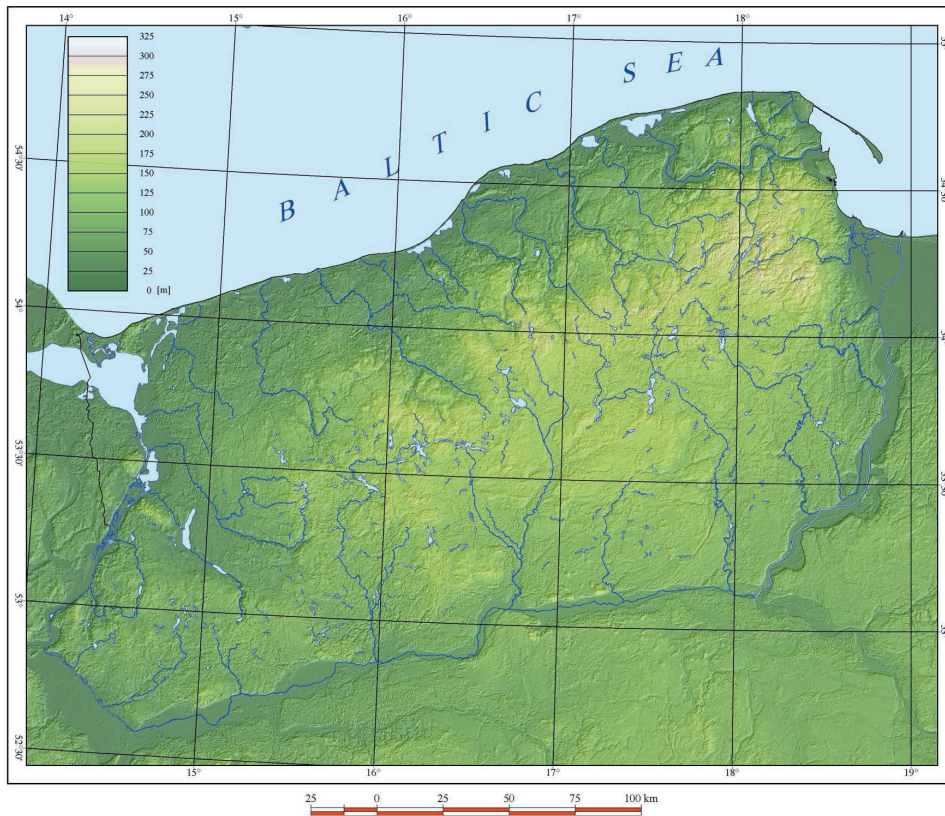


Fig. 3. Hypsometric map of Pomerania (map by J. Prajs, on the basis of numerous resources)

forming eskers and kames. In this region, interglacial deposits include peats and other bog deposits. Like sands, they were accumulated in the later stages of the Holocene (Alexandrowicz 1999; Gilewska 1999; Borówka 2002).

In the young glacial part of Pomerania, land relief forms well-defined belts, resulting from the gradual retreat of the ice sheet (Fig. 3). Exceptions include the azonal bottoms of proglacial valleys and river valleys, e.g. of the Vistula, Oder (Odra), and the proglacial valley of Łeba and Reda, which result from the action of meltwater from the melting ice sheet. At the edges of the valleys, terraces have formed. At the higher terraces, as a result of lowering of the water level, numerous inland dunes have appeared, e.g. in the Goleniów Plain (Równina Goleniowska) or in the Tuchola Forest.

Three latitudinal belts can be distinguished in the young glacial area: (1) lake-rich plateaus, (2) a hilly zone, and (3) coastal lowlands. The lake-rich plateaus are found in the southern part of the region. This belt includes extensive outwash plains, dissected by river valleys, and groups of hills and moraine ridges, corresponding to stages of ice sheet retreat. Some glacial troughs with ribbon lakes are also present there. The lake-rich plateaus are bordered in the north by the hilly zone. The Pomeranian part of this zone is limited by 2 large lobes: of the lower Odra (in the west) and of the lower Vistula (in the east). Moreover, along the axes of

old river valleys, smaller lobes have been formed: of the Rega, Parsęta, Wieprza, and Stupia. The hilly zone includes chains of terminal moraines with numerous basins and lakes. It is dissected by numerous glacial troughs. In the west-east direction, its mean altitude increases, reaching the highest elevation in the Kashubian Lakeland (Wieżyca, 329 m a.s.l.). The belt of coastal lowlands is located at the back of terminal moraines of the Pomeranian phase. Its edges cover the lowest parts of 2 large valleys: of the Odra and of the Vistula. Between them, the belt is much narrower. It is characterized by the shallow or wavy deposits of ground moraine, alternating with terminal moraines. The area is diversified by the presence of kames (hills) and numerous local depressions without outflow. It is obliquely dissected (in the east-west direction) by Pomeranian proglacial valleys that lead to the Baltic. The system of these valleys, which channelled meltwater, resulted in the development of outwash plains (sandurs). The narrow coastal zone has a younger land relief, shaped in the Holocene. It is dominated by sandspits with dunes, while cliffs are rare. In the depressions among dunes, peat is accumulated. Also currently, some processes cause changes in the shoreline, e.g. as a result of cliff abrasion; or influence land relief, e.g. due to marine accumulation and wind action (Alexandrowicz 1999; Gilewska 1999; Kostrzewski 1999; Borówka 2002).

Nearly throughout Pomerania, zonal soils have developed. Most of them are podzols and brown-earth soils. Only small areas are covered by intrazonal soils: alluvial, peaty or other waterlogged soils, and chernozems near Pyrzyce (Prusinkiewicz & Bednarek 1999).

3.4. Hydrological conditions

Pomerania has a well-developed hydrographic network. The eastern part of the region lies in the catchment of the lower Vistula, while the western part in the catchment of the lower Odra. The drainage divide runs along the hilly zone and determines the direction of water flow: northwards, to the Baltic (catchments of coastal rivers), or southwards, to the Toruń-Eberswalde Proglacial Valley (catchments of the Noteć and Warta). Catchments of the rivers that flow directly into the sea are mostly composed of morainic plateaus. Some sections of the rivers on the northern slopes of Pomeranian hills resemble mountain streams, because of the large slope angle (2-3‰, sometimes up to 5‰). Most of the rivers that flow southwards, cross outwash plain terraces. Many of them, especially in their upper sections, flow through numerous lakes.

Pomerania is rich in natural lakes. There are 3385 lakes with an area of over 1 ha in this region. Most of them are of glacial origin. Renewable resources of groundwater in Pomerania are some of the richest in Poland. The greatest supply of groundwater is recorded in outwash plains, which are composed of permeable de-

posits of sand or sand with gravel. By contrast, in the morainic plateaus covered by the hardly permeable boulder clay, the supply of groundwater is usually very limited (Dynowska & Pociask-Karteczka 1999; Borówka 2002).

3.5. Peatlands

In Pomerania, peatlands cover a total area of 381 052 ha, including 19 000 ha of raised bogs, 36 144 ha of transitional bogs, and 325 908 ha of fens (IMUZ 2006). From 25 to 50 peatlands are found per 100 km² there. Most of Polish raised bogs are located in Pomerania. They are completely dependent on water supply from precipitation, which is poor in nutrients. They develop at drainage divides as well as in river valleys and proglacial valleys, at the sites that are free from the influence of groundwater or floods. They are concentrated mostly in the eastern and central parts of the West Pomeranian Lakeland and in the Kashubian Lakeland, as well as along the Baltic coast (Fig. 4). In the coastal belt there are some large raised bogs of the Baltic type, which reach there a regional southern limit of their main distribution range. The postglacial landscape is also associated with kettle-hole mires. They develop in usually small kettle holes. They are common in the Bytów Lakeland. The fens, formed in former lake basins and in valleys of slow-flowing rivers, depend on the presence of groundwater and surface water. They are more or less rich in organic compounds. The largest among them are in this region the peatlands in valleys

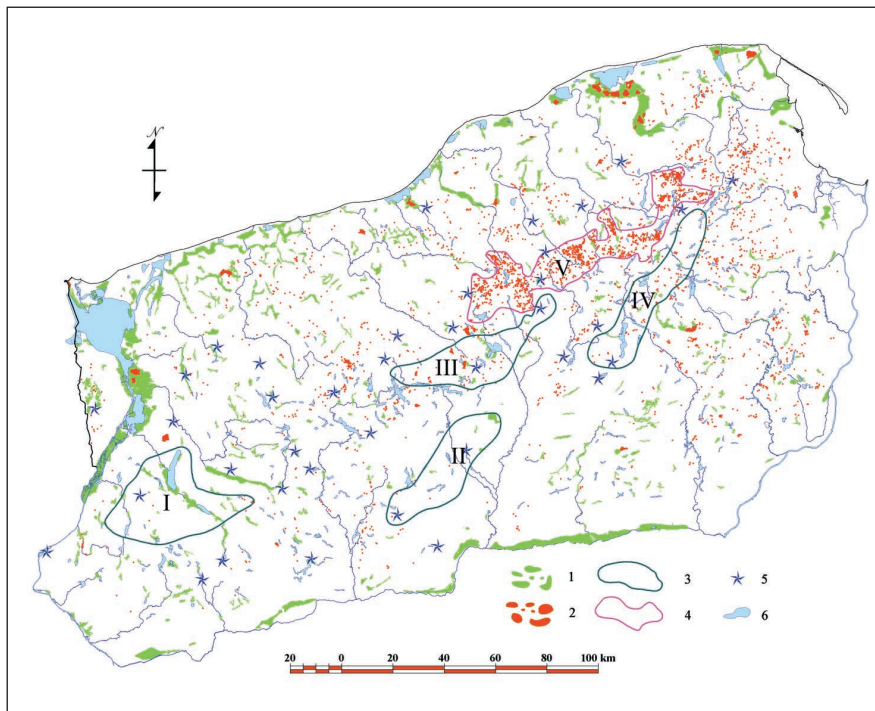


Fig. 4. Distribution of peatlands in Pomerania (after Jasnowski *et al.* 1994)

Explanations: 1 – fens and transitional bogs, 2 – kettle-hole mires and raised bogs, 3 – areas of calcareous fens, 4 – areas of moss bogs, 5 – clusters of spring-water mires, 6 – lake; areas of calcareous fens, I – Myślubórz district, II – Wałcz district, III – Drawsko district, IV – Kashubian district; areas of moss bogs, V – Bytów district

of the Noteć (50 000 ha) and Odra (25 000 ha). Oligodystrophic transitional bogs are found both in outwash plains and on moraines. They are fed by groundwater and surface water as well as by precipitation. They are often formed as a result of plant succession in water bodies. They may be an intermediate stage between fens and raised bogs. Relatively rare elements of landscape are calcareous fens, developed on calcareous gyttja and marl (calcareous lake sediments). The largest aggregations of peatlands of this type are located in the Myślubórz, Wałcz, Drawsko, and Kashubian Lakelands (Fig. 4). Pomerania is also rich in spring-water mires, which are dome-shaped or hanging on morainic slopes (Jasnowski *et al.* 1968, 1972; Jasnowski 1975, 1990; Herbichowa 1979, 1998a, 1998b, 2004a, 2004b; Jasnowska & Jasnowski 1981; Wołejko 2000; Pawlaczyk *et al.* 2001; Ilnicki 2002; Tobolski 2003; Herbichowa & Potocka 2004; Herbichowa & Wołejko 2004b; Herbich & Ciechanowski 2009).

3.6. Transformations of Pomeranian vegetation in the late glacial period and the Holocene

In the late glacial period, the first warmer phase, termed the Bølling, took place around 12 400-12 000 ¹⁴C BP. In central Poland, mean July temperature was then about 15-16°C (Wasylikowa 1964; Tobolski 1998). In northern Poland, park tundra with juniper bushes developed then (Latałowa 2003a, 2004). In the Older Dryas (12 000-11 800 years ¹⁴C BP), the climate became cooler and more continental. Mean July temperature decreased to 10-12°C (Wasylikowa 1964). Large parts of Pomerania were then covered by steppe-tundra with shrubs. It was composed mostly of shrubby *Salix*, *Betula*, and *Hippophaë rhamnoides* (Latałowa 2003a). Climatic conditions improved again in the Allerød (11 800-10 700 years ¹⁴C BP), when mean July temperature in central Poland rose to 13-16°C (Wasylikowa 1964). In Pomerania, various forest communities dominated by *Betula* and *Pinus* gradually developed then. The forest stands were not dense, so they created favourable conditions for light-demanding plants (heliophytes), e.g. *Empetrum nigrum*, *Juniperus*, and *Hippophaë rhamnoides*. On wet sites, patches of tundra were preserved. At that time, wetland vegetation, including communities with *Sphagnum* also developed there, particularly in the areas where the process of ice melting was slower (Tobolski 1975/1976; Okuniewska-Nowaczyk 1992; Latałowa 2003a, 2004; Latałowa *et al.* 2004). In the last cooler phase, the Younger Dryas (10 700-10 000 years ¹⁴C BP), mean July temperature in central and northern Poland fell to 10°C, whereas later it was not lower than 12°C, and westerly winds prevailed (Wasylikowa 1964; Nowaczyk 1986; Tobolski 1998; Latałowa 1999). Heliophilous communities were then formed along the Baltic coast. On drier sites, plants

typical of cold steppes were abundant, while on wet sites, species characteristic of tundra appeared. In that phase, a frequent component of the flora of Pomerania was *Juniperus* (Latałowa 2003a; Milecka 2005).

A relatively fast climatic warming initiated the last interglacial – the Holocene. In the Pre-Boreal period (10 000-9000 years ¹⁴C BP), the climate of central Europe was continental, with cold winters, hot summers and low precipitation (Ralska-Jasiewiczowa & Starkel 1999). In the early Pre-Boreal period, dwarf *Betula* were still frequent components of the flora of northern Poland. This was followed by a fast development of forests codominated by *Betula* and *Pinus*, with low contributions of *Populus tremula*, *Sorbus*, and *Salix*. The ground layer included light-demanding species. In Pomerania, from the west, *Corylus* started to spread, and *Ulmus* also appeared. Shallow water bodies were gradually transformed into peatlands, with communities dominated by mosses and low sedges (Ralska-Jasiewiczowa & Starkel 1999; Latałowa 2003b).

In the Boreal period (9000-8000 years ¹⁴C BP), humidity gradually increased. Some wetlands became lakes (Latałowa *et al.* 2004). The whole period was characterized by dynamic migrations of successive species of deciduous trees, and transformations of forest communities. At the beginning of this period, *Corylus* was very expansive. Also *Ulmus* expanded its range then. *Quercus* and *Alnus* spread from the west. Moreover, *Tilia* appeared in this area. Light-demanding herbaceous plants gradually declined. At the end of the Boreal period, the role of *Corylus* was smaller (Latałowa 2003b). The telmatic (i.e. periodically flooded) zone of water bodies was overgrown by emergent vegetation (rushes, etc.). At their edges, in limited areas, sometimes peatlands were developed (Milecka 2005).

Westerly winds and humid air masses from the Atlantic still prevailed over Europe. Air temperature increased, so that in the Atlantic period (8000-5000 years ¹⁴C BP) it was on average about 2-3°C higher than at present. Mean January temperature was about 2°C and precipitation was also higher than now (Nowaczyk 1986; Starkel *et al.* 1998; Bradley *et al.* 2003). Such conditions allowed the spread of *Hedera helix* and *Viscum album*. Simultaneously, they contributed to the disappearance of many sites of bog plant species. In Pomerania, all components of temperate mixed deciduous forests were already present. Climax communities developed then. Dense deciduous forests, composed mostly of *Quercus*, *Tilia*, and *Ulmus*, covered extensive areas then. *Fraxinus* was less common, as it only started to spread in this region. Frequencies of light-demanding species (e.g. *Betula* and *Corylus*) decreased then. In the Baltic coastal zone, the frequency of *Pinus* slowly declined (Latałowa 1982, 1992). Its sandy parts were covered by deciduous forests dominated by *Quercus*

(Tobolski 1975). Forests of the Atlantic period reached their optimum on morainic soils of northern Poland in 6500-6000 years ¹⁴C BP (Latałowa 1982). Some forest patches were regularly burnt by Mesolithic tribes. In some areas, forest communities were gradually degenerated and turned into open habitats. These included glades and patches of nitrophilous vegetation (Ralska-Jasiewiczowa 1999; Latałowa 2003b; Milecka 2005). At the end of the Atlantic period, the frequency of *Ulmus* decreased. The climate became cooler and precipitation increased, so soils were more prone to leaching. The gradual leaching of calcium and increasing acidity lead to podzolization. As a result, soil fertility was progressively reduced. In mixed deciduous forests, the frequency of *Quercus* rose gradually. The raised bog Słowińskie Błoto (of the Baltic type) started to be formed then (Herbichowa 1998a).

In the later Holocene, under the influence of favourable moisture conditions, fens and transitional bogs gradually turned into raised bogs (Latałowa *et al.* 2004). In the Sub-Boreal period (5000-2500 years ¹⁴C BP), forests were greatly transformed. The composition of communities became more and more similar to their present composition. Human impact on vegetation was growing. In northern Poland, farming was initiated (about 5000 years ¹⁴C BP). Neolithic economy led to creation of coppiced forests. In the Bronze Age, the role of cultivation and animal husbandry increased. The first open pastures were formed then. In the Sub-Boreal period, environmental conditions were most strongly transformed by the Lusatian culture (3300-2400 years ¹⁴C BP). In large parts of the region, human settlement contributed to irreversible changes. Cattle grazing, plant cultivation, deforestation, and burning, lead to great transformations, so that even when human activity ceased, forest communities did not regenerate to their original form. The role of *Ulmus*, *Tilia*, *Fraxinus*, and *Corylus* was limited. Disturbed sites were gradually covered by forests composed of *Pinus*, *Quercus*, and the last forest-forming species that appeared in the Holocene: *Carpinus* and *Fagus*. Both *Carpinus* and *Fagus* appeared in the area of Central European Lowland as so-called "late immigrants" (Birks 1986; Huntley 1988). In Pomerania, *Carpinus* was very expansive, while *Fagus*, migrating from the west, spread slower (Ralska-Jasiewiczowa 1999, 2004; Latałowa 2003b).

In the early Sub-Atlantic period (2500 years ¹⁴C BP) the climate became cooler, more humid, and less stable. Two warmer periods can be distinguished (early and late medieval) and the so-called Little Ice Age in the 17th-19th centuries (Ralska-Jasiewiczowa & Starkel 1999). In Pomerania, the process of formation of raised bogs was intensified. On the morainic deposits, forest communities were formed, dominated by *Carpinus* or *Fagus*. Less fertile soils were colonized by *Pinus*. In the west-

ern part of the region, forests were dominated by *Fagus*, while in central and eastern parts of the Baltic coast, by *Carpinus*, which was later outcompeted by *Fagus*. The decline in economic activity during the Migration Period (375-550 AD) allowed forest regeneration in large parts of Pomerania. An important component of the forests was *Carpinus*, which easily adapts to disturbed sites. However, in the late Sub-Atlantic period, the frequency of *Pinus* increased again. Also herbaceous species became more common, because the area of open habitats increased dramatically due to farming activity (Ralska-Jasiewiczowa 1999; Latałowa 2003b; Milecka 2005).

4. Methods

4.1. Selection criteria and list of peatland plant species

For the analysis of distribution of vascular plant species of bogs and fens in Pomerania, taxa associated with the classes *Oxycocco-Sphagnetea* and *Scheuchzerio-Caricetea nigrae* were selected. These include the species found in communities assigned to any of these classes, although not always being their characteristic (Ch.) or differential (D) species.

Initially, a draft list of 110 species was compiled, mostly based on numerous reports about peatland vegetation in Pomerania (e.g. Kępczyński 1960; Jasnowski 1962; Jasnowski *et al.* 1968; Herbichowa 1979; Jasnowska & Jasnowski 1983a, 1983b, 1983 c, 1983d, 1983e; Gos & Herbichowa 1991; Boińska & Boiński 2002). Works from other parts of Poland (e.g. Fijałkowski 1959; Polakowski 1963; Pałczyński 1975) and synthetic works about plant communities in Poland (Matuszkiewicz 1981), Polish vegetation (Szafer & Zarzycki 1972), plant communities of central and north-eastern Germany (Schubert *et al.* 1995), as well as vegetation of NW European mires (Dierssen 1982) were also taken into account.

The next stage was a revision of this list, by elimination of the taxa that do not reach Pomerania, e.g. *Carex capillaris*, *C. magellanica*, *C. microglochis*, *Juncus stygius*, and *Sedum villosum*. This was done on the basis of available published data: mostly general distribution maps of individual species (see Zając M. 1992) and data from the ATPOL database (*Distribution Atlas of Vascular Plants in Poland*). From this list, I excluded also the frequently misidentified species: *Dactylorhiza traunsteineri* and *Oxycoccus microcarpus* (*Vaccinium microcarpum*), because the existent data would wrongly reflect their range. By contrast, *Carex buxbaumii* (a species frequently identified as *C. hartmanii*) was taken into account because its localities could be verified on the basis of specimens from Polish herbaria. Other excluded species require in Poland further taxonomic research (e.g. *Dactylorhiza russowii* and *Carex*

demissa). Subspecies were not considered separately because the available data did not allow me to do so.

A final stage of list verification was the exclusion of eurytopic species, i.e. those that are found in communities of other classes and reach their optimum there. It was assessed on the basis of numerous phytosociological publications, particularly from Pomerania, but also unpublished data and my own observations. Exceptions were the species that play an important role in communities of the classes *Oxycocco-Sphagnetea* or *Scheuchzerio-Caricetea nigrae*, e.g. *Carex rostrata*, *Empetrum nigrum*.

The final list includes 83 species, and their distribution was analysed in detail (Table 1).

Species names follow Mirek *et al.* (2002), while the classification and names of syntaxonomic units mostly follow those of Matuszkiewicz (2001). If another name

or syntaxonomic unit was used, the author's name is given in the text. The distribution of species in Poland was assessed on the basis of Zajac A. & Zajac M. (2001). Characteristics of the 83 analysed species, in alphabetic order, are included in Annex.

4.2. Sources of floristic data and mapping method

The analysis is based on both my own floristic records and all available data about records of peatland plant species in Pomerania since the early 19th century. In total, 30 952 floristic records were collected, including published records (61.6%), unpublished records (33.3%), and herbarium specimens (5.1%). Unpublished records mostly originated from the ATPOL database (Zajac A. & Zajac M. 2001) or from my field research, as well as information kindly provided by botanists working in Pomerania. The small contribution of herbarium data results mostly from their limited collections. Moreover, in historical specimens, it was often difficult to decipher the handwritten labels in German. Many labels contained only very general or no information about location, and/or lacked the date of collection.

To supplement the data, particularly from the areas that were less explored by botanists, as well as to verify the records of rare and endangered species, I did field research in Pomerania in 1999-2008, and collected in total 1108 floristic records. I also verified published and herbarium data for rare taxa, e.g. *Carex buxbaumii*, as well as for those reaching in Pomerania a limit of distribution or having a disjunct distribution.

To reconstruct the changes in species distribution, special attention was paid to historical records from the 19th and early 20th century. They account for 26.4% of all the analysed records. Most of them were made by German botanists, who explored Pomerania at that time. The records were localized on the map of Pomerania on the basis of translations of German place names by using special dictionaries (e.g. Rospond 1951; Bialecki 2001, 2002), or the place names were searched for on old German maps from the early 20th century and next compared to post-war Polish maps.

The collected database on peatland plant species of Pomerania has been deposited at the Laboratory of Computer Chorology, Institute of Botany, Jagiellonian University, Kraków, and at present it is an integral part of the continuously updated ATPOL database.

The resultant maps of species distribution are cartograms made according to the ATPOL methods (Zajac A. 1978). The basic unit was a square of 5 km × 5 km, so Pomerania was divided into 2090 such squares. A filled square denotes the presence of the species in that area. It is treated as a single locality irrespective of the number of sites of the species within this square.

The cartograms showing the distribution of *Carex buxbaumii* and *Viola epipsila* are based exclusively on

Table 1. List of species selected for the analysis of distribution

Class <i>Oxycocco-Sphagnetea</i>	
<i>Andromeda polifolia</i>	<i>Erica tetralix</i>
<i>Baeothryon cespitosum</i>	<i>Eriophorum vaginatum</i>
<i>Carex pauciflora</i>	<i>Ledum palustre</i>
<i>Chamaedaphne calyculata</i>	<i>Oxycoccus palustris</i>
<i>Drosera rotundifolia</i>	<i>Rubus chamaemorus</i>
<i>Empetrum nigrum</i>	<i>Vaccinium uliginosum</i>
Class <i>Scheuchzerio-Caricetea nigrae</i>	
<i>Agrostis canina</i>	<i>Hermidium monorchis</i>
<i>Baeothryon alpinum</i>	<i>Hydrocotyle vulgaris</i>
<i>Blysmus compressus</i>	<i>Juncus acutiflorus</i>
<i>Calamagrostis stricta</i>	<i>Juncus alpino-articulatus</i>
<i>Carex brunnescens</i>	<i>Juncus filiformis</i>
<i>Carex buxbaumii</i>	<i>Juncus subnodulosus</i>
<i>Carex canescens</i>	<i>Liparis loeselii</i>
<i>Carex chordorrhiza</i>	<i>Lycopodiella inundata</i>
<i>Carex davalliana</i>	<i>Malaxis monophyllos</i>
<i>Carex diandra</i>	<i>Menyanthes trifoliata</i>
<i>Carex dioica</i>	<i>Orchis palustris</i>
<i>Carex distans</i>	<i>Parnassia palustris</i>
<i>Carex echinata</i>	<i>Pedicularis palustris</i>
<i>Carex flava</i>	<i>Pedicularis sceptrum-carolinum</i>
<i>Carex heleonastes</i>	<i>Pedicularis sylvatica</i>
<i>Carex hostiana</i>	<i>Pinguicula vulgaris</i>
<i>Carex lasiocarpa</i>	<i>Polygala amarilla</i>
<i>Carex lepidocarpa</i>	<i>Primula farinosa</i>
<i>Carex limosa</i>	<i>Ranunculus flammula</i>
<i>Carex nigra</i>	<i>Rhynchospora alba</i>
<i>Carex panicea</i>	<i>Rhynchospora fusca</i>
<i>Carex pulicaris</i>	<i>Salix myrtilloides</i>
<i>Carex rostrata</i>	<i>Saxifraga hirculus</i>
<i>Carex viridula</i>	<i>Scheuchzeria palustris</i>
<i>Comarum palustre</i>	<i>Schoenus ferrugineus</i>
<i>Dactylorhiza incarnata</i>	<i>Schoenus nigricans</i>
<i>Dactylorhiza maculata</i>	<i>Stellaria crassifolia</i>
<i>Drosera anglica</i>	<i>Stellaria palustris</i>
<i>Drosera intermedia</i>	<i>Swertia perennis</i>
<i>Eleocharis mamillata</i>	<i>Tofieldia calyculata</i>
<i>Eleocharis quinqueflora</i>	<i>Triglochin palustre</i>
<i>Epipactis palustris</i>	<i>Valeriana dioica</i>
<i>Eriophorum angustifolium</i>	<i>Veronica scutellata</i>
<i>Eriophorum gracile</i>	<i>Viola epipsila</i>
<i>Eriophorum latifolium</i>	<i>Viola palustris</i>
<i>Hammarbya paludosa</i>	

verified herbarium materials. A revision of herbarium specimens of *Viola epipsila* was made earlier by Kuta (1991). Its current cartogram corrects the location of one of its 3 Pomeranian sites, whose German name was earlier translated incorrectly.

The cartograms for individual species are included in Annex.

4.3. Methods of phytogeographic-ecological analysis

The phytogeographic analysis of peatland plant species of Pomerania was conducted in relation to geographic and directional elements as well as mountain species found in the lowlands.

The analysed taxa were assigned to geographic elements according to the latest classification of geographic elements among plant species native to Poland (Zajac M. & Zajac A. 2009), on the basis of principles proposed by Braun-Blanquet (1923), and supplemented by Pawłowska (1966, 1977). Mountain species recorded in lowlands were classified according to Zajac M. (1996).

Directional elements, i.e. species that in Poland reach limits of their ranges, were distinguished among the analysed plants on the basis of maps of their distribution in Poland (Zajac A. & Zajac M. 2001) and in Europe (Jalas & Suominen 1972, 1983, 1989; Jalas *et al.* 1999), as well as their general distribution ranges (Meusel *et al.* 1965, 1978; Hultén & Fries 1986; Meusel & Jäger 1992). To specify the limits of some of them, attention was paid also to their distribution in eastern Germany (Benkert *et al.* 1998) and in Scandinavia (Hultén 1950, 1964, 1971). I took into account also a work where peatland plant species were included in the western directional element of the Polish vascular flora (Zajac M. & Zajac A. 2006). Within the analysed group, some taxa have a well-defined limit of distribution in Pomerania. This applies also to those reaching their limit at the boundary of the region and only sporadically found outside Pomerania, in scattered, isolated localities. These species are included in the groups of taxa that constitute directional elements in the peatland flora of Poland within Pomerania.

To determine the potential of peatland plant species for spread and colonization of new sites, species descriptions in this study included also plant forms, mode of pollination and diaspore dispersal, as well as types of life strategies. These characteristics affect the shape and size of the species range. Depending on access to suitable habitats and climatic conditions, they may contribute to its expansion or disappearance.

Plant life-forms of individual taxa are associated with plant adaptation to unfavourable seasons according to the Raunkiaer system (1905), on the basis of available sources (e.g. Rothmaler 1990; Zarzycki *et al.* 2002; Rutkowski 2004).

Mode of pollination and diaspore dispersal was assessed on the basis of data by Pijl (1969), Frank & Klotz (1990) and Rothmaler (1990), and references therein, and my own observations. When showing graphically the contributions of life-forms as well as modes of diaspore dispersal to the total number of analysed peatland plant species, some species were counted twice or thrice, as some of them belong to more than one category.

The ecological analysis took into account Grime's (1977, 1979) classification of plant strategies, known as the C-S-R Triangle theory. He distinguished 3 primary categories: C (competitors) – relatively long-lived plants that easily outcompete others; S (stress tolerators) – plants that are resistant to stress; R (ruderals) – short-lived pioneer plants; and 4 secondary (mixed) categories: C-R, S-R, C-S, and C-S-R.

This classification, although not perfect, has not been rejected (e.g. Falińska 2004). It enables characterization of life strategies of individual species and, consequently, prediction of its tendencies to disappear, expand or to persist at the same site. This method deserves to be used in phytogeography (Kornaś & Medwecka-Kornaś 2002).

For individual species, information on types of life strategies was extracted from a paper by Frank & Klotz (1990), and only for *Lycopodiella inundata* from the short note by Cieszko & Kucharczyk (1999a, 1999b), while for *Rubus chamaemorus* it was based on my own observations and available published data. The analysis did not include 10 species, because my own observations and published data are not sufficient to determine their life strategy.

Most of the conducted analyses concerned 83 species. However, in some cases, when some detailed data were missing, the number of species taken into account was smaller. Every time, this number is given in figures or tables.

The scope of distribution of each species was assessed on the basis of its frequency i.e. number of ATPOL squares where it has ever been recorded (Table 2).

In this scale, the category “common” is missing because the most frequent species was recorded in 630 squares on the cartogram, which account for only 30% of the total number of 2090 squares in Pomerania and

Table 2. Frequency of species

Frequency class	Number of ATPOL squares	Frequency description
I	1-10	extremely rare
II	11-50	very rare
III	51-100	rare
IV	101-200	infrequent
V	201-400	moderately frequent
VI	≥ 401	frequent

for about 45% of the 1402 squares where peatland plant species were recorded.

To determine the dynamic trends of selected species, for which sufficient documentation has been collected, their cartograms show separately the records made before 1901; in 1901-1950; in 1951-1970; in 1971-1990; and after 1990. These maps and the collected database were used for classification of the taxa in respect of their dynamics. In this classification, special attention was paid to a lack or dramatic decrease (to only several current localities) of the analysed species; gradual decline all over Pomerania or in some parts of the region, as well as appearance of new, earlier unknown local populations. On this basis, the following categories were distinguished:

- probably extinct species: no current records, none of the earlier localities in Pomerania was confirmed after the year 1950;
- endangered species: the number of localities has decreased to several or one;
- species disappearing quickly from Pomerania: in the past found in at least several dozen localities, but now recorded only in few localities;
- species disappearing from some parts of Pomerania;
- species relatively frequent in the past, now less frequent but also recorded at new sites
- rare species that have disappeared from some sites but are also recorded at new sites
- species that clearly tend to spread and colonize new sites.

A more detailed classification of the peatland plant species according to IUCN (2001) threat categories will be presented in a separate publication.

4.4. Classification of regional distributional types

Numerical methods are an effective tool for distinguishing geographic regions, i.e. areas that are homogeneous in respect of geomorphological, climatic, geological, pedological, and other environmental factors (Dufrene & Legendre 1991), as well as distributional types of individual species (e.g. Bolognini & Nimis 1993; Dzwonko & Kornaś 1994; Jackowiak 1998). Application of such methods to determine the relationships between the distribution of a species or group of species and distribution of an environmental factor was initiated by Haeupler (1974). On the basis of a statistical analysis of cartograms prepared for a floristic atlas of the southern part of Lower Saxony, that author compiled a list of environmental factors and species correlated with a given taxon.

In this study, numerical methods were used to distinguish distributional types (chorotypes) of peatland plants in Pomerania. A group of taxa with similar distribution patterns in Pomerania was defined here as a chorotype. Chorotypes were distinguished on the basis

of a matrix of Operational Geographic Units (OGUs) and species. OGUs are individual geographic units used for numerical analyses (Crovello 1981), in this case: squares of 5 km × 5 km each, generated on the basis of the ATPOL database (Zajac A. 1978).

At the first stage of numerical analysis, a matrix of ATPOL squares × species was generated from the database of peatland plants in Pomerania. For each species, its presence or absence in a given ATPOL square was recorded as binary data. To achieve a stable classification, extremely rare species (up to 10 localities) were excluded. The matrix prepared in this way was subjected to numerical classification by Unweighted Pair Group Method with Arithmetic Mean (UPGMA), with the use of the Jaccard similarity coefficient. For this purpose, MULVA-5 software (Wildi & Orlóci 1996) was applied.

The distinguished groups formed a basis for the classification of chorotypes. However, visual comparison of the groups revealed that small corrections are necessary, due to a lack of consistency between the true status and that assigned by the software. The corrections consisted in a different classification of 5 of the 69 species subjected to UPGMA, and additionally in separation of a group of species with south-eastern distribution, i.e. the *Salix myrtilloides* subtype (see section 5.2.2). In contrast, species with very similar distribution patterns were considered as one group.

In the final classification, to allow proper distinguishing and defining of chorotypes, the following additional ordering criteria were applied (apart from the concentration of localities in some parts of Pomerania): distribution pattern of other localities of the given species, its range in Poland, and general distribution. The number of groups (chorotypes) should not be excessive, so it was limited to basic types, covering large parts of Pomerania. Nonetheless, if remarkable variation in distribution patterns was noticed within a given type, some subtypes were distinguished. When separating the subtypes, attention was paid also to (1) a clear relationship with a given part of the range of the distributional type, reflected in a concentration of localities in this area; (2) avoidance of some areas within the range of the given distributional type. The final description of distributional types takes into account also the initially excluded extremely rare species (up to 10 localities) whose pattern of distribution corresponds to one of the distinguished chorotypes.

Names of distributional types include geographic directions, as they unambiguously indicate the parts of Pomerania that are preferred by plants of the given type. In contrast, the name of each subtype includes the scientific name of the plant whose distribution pattern is most representative of for the given subtype.

4.5. Numerical analyses

4.5.1. General remarks

The database for numerical analyses consists of 2 files: (1) species presence/absence in ATPOL squares; and (2) climatic variables, on the basis of available sources. The first file includes data for 69 taxa because extremely rare species (up to 10 localities) were excluded, to obtain more reliable results. The following climatic variables were taken into account:

(a) temperature (Michalska 2001):

- mean January temperature: ranges of 0 to -0.5; -0.6 to -1.0; -1.1 to -1.5; -1.6 to -2.0; and -2.1 to -2.5 [°C]
- mean July temperature: ranges of 16.5-17.0; 17.1-17.5; 17.6-18.0; and 18.0-18.5 [°C]
- mean daily maximum temperature in July: ranges of ≤ 29.5; 29.6-30.0; 30.1-30.5; 30.6-31.0; and 31.1-31.5 [°C]
- mean daily minimum temperature in January: ranges of ≥ -14; -14.1 to -15.0; -15.1 to -16.0; -16.1 to -17.0; -17.1 to -18.0; and -18.1 to -19.0 [°C]
- mean annual amplitude: ranges of ≤ 17.5; 17.6-18.0; 18.1-18.5; 18.6-19.0; 19.1-19.5; 19.6-20.0; and 20.1-20.5 [°C]

(b) precipitation:

- precipitation in April-September (Kozłowski 2001): ranges of ≤ 325; 325-350; 350-375; 375-400; and 400-450 [mm]
- mean annual precipitation (Kozłowski 2001): ranges of 525-550; 550-575; 575-600; 600-650; 650-700; and 700-750 [mm]

(c) mean areal evaporation (Gutry-Korycka 1994): ranges of ≤ 500; 500-550; 550-600; and 600-650

(d) growing season length (Kozłowski & Michalska 2001): ranges of ≤ 210; 210-215; 215-220; 220-225; 225-230; and ≥ 230 [days].

All data were encoded in binary form 0/1 (absence/presence of a species or factor). Climatic variables were recorded as nominal variables, i.e. in defined ranges. For example, mean July temperature was encoded in 4 ranges of 16.5-17.0°C, 17.1-17.5°C, 17.6-18.0°C, and 18.0-18.5°C (see above) as *dummy variables* (ter Braak & Šmilauer 2002).

Data on species occurrence and climatic variables were analysed jointly, to detect relationships between them by canonical correspondence analysis (CCA; ter Braak & Šmilauer 2002; Dzwonko 2007).

4.5.2. Significance of climatic variables

To determine the statistical significance of climatic variables in explaining the floristic composition of Pomeranian peatlands, a Monte Carlo permutation test was applied (Manly 1991), with the forward selection pro-

cedure in CANOCO for Windows software (ter Braak & Šmilauer 2002). The first selected variable was the one that best explained the overall variance, and the others were ranked according to their decreasing significance in explaining the overall variation of the dataset in association with the earlier selected variables. For this reason, the value of “extra fit” (Lambda A) was calculated. It shows the additional variance explained, i.e. the difference in the sum of all individual CCA values when the next variable is added. Moreover, statistical significance was calculated for individual variables individually (*P*).

4.5.3. Canonical correspondence analysis (CCA)

This method assumes non-linear, non-monotonous distribution of species along climatic gradients (ter Braak 1987). In this case, the best synthetic climatic gradients were generated as linear combinations of climatic variables, so as to maximize species niches, i.e. separation of species along the axes (ter Braak & Verdonschot 1995). For this purpose, CANOCO for Windows software was used (ter Braak & Šmilauer 2002). Statistical significance of the relationship between species and climatic variables was assessed by a global permutation test, reduced model. CCA does not require the assumption of normal error distribution. It is particularly useful for binary data with a large number of empty cells.

CCA of climatic variables was done twice. The first analysis included temperature variables, while the second one included precipitation variables. Additionally, mean areal evaporation and growing season length were taken into account in both analyses.

Results of the numerical analysis are presented graphically as biplots, generated by CanoDraw software (ter Braak & Šmilauer 2002). For each of the analysed groups of variables, the biplot includes species and climatic variables.

5. Results

5.1. Geographic and ecological structure of the flora of Pomeranian peatlands

5.1.1. Geographic elements

A vast majority of peatland plant species in Pomerania (about 87%, i.e. 72 species) are Holarctic (Table 3). Within the Holarctic element, most species are Circumboreal (58%), while other sub-elements are much smaller: European-temperate (16%), Euro-Siberian (8%), Amphi-Atlantic (4%), and Arctic-Alpine (1%). Out of the 83 studied species, 11 are connective elements:

- Holarctic-Mediterranean-Irano-Turanian, or more precisely: European-temperate-Mediterranean-

Table 3. Geographic elements represented by the studied vascular plant species associated with the classes *Oxycocco-Sphagnetea* and *Scheuchzerio-Caricetea nigrae*

Species	Geographic element	Species	Geographic element
<i>Agrostis canina</i>	sa-ES	<i>Eriophorum vaginatum</i>	CB
<i>Andromeda polifolia</i>	CB	<i>Hammarbya paludosa</i>	CE: ce-n
<i>Baeothryon alpinum</i>	CB(d)	<i>Hermium monorchis</i>	ES-Asiatic (m)
<i>Baeothryon cespitosum</i>	CB(d)	<i>Hydrocotyle vulgaris</i>	CE: sat
<i>Blysmus compressus</i>	CE-M(n)-IR(m)	<i>Juncus acutiflorus</i>	sa-CE: ce-b
<i>Calamagrostis stricta</i>	CB(n)	<i>Juncus alpino-articulatus</i>	CB
<i>Carex brunnescens</i>	CB	<i>Juncus filiformis</i>	CB
<i>Carex buxbaumii</i>	CB(d)	<i>Juncus subnodulosus</i>	sa-CE(w): ce-b-M(n)
<i>Carex canescens</i>	CB	<i>Ledum palustre</i>	CB
<i>Carex chordorrhiza</i>	CB(d): c-b-a	<i>Liparis loeselii</i>	CB(d)
<i>Carex davalliana</i>	CE: ce-b	<i>Lycopodiella inundata</i>	CB: c-b-o
<i>Carex diandra</i>	CB	<i>Malaxis monophyllus</i>	CB(d)
<i>Carex dioica</i>	CB	<i>Menyanthes trifoliata</i>	CB
<i>Carex distans</i>	sa-CE(w)-M	<i>Orchis palustris</i>	CE-M(n)-IR(m)
<i>Carex echinata</i>	CB(d)	<i>Oxycoccus palustris</i>	CB(d)
<i>Carex flava</i>	CB: c-b-o	<i>Parnassia palustris</i>	CB(n)
<i>Carex heleonastes</i>	ES(n,w)	<i>Pedicularis palustris</i>	sa-ES
<i>Carex hostiana</i>	sa-CE: ce(w)-b	<i>Pedicularis sceptrum-carolinum</i>	ES
<i>Carex lasiocarpa</i>	CB	<i>Pedicularis sylvatica</i>	CE: sat
<i>Carex lepidocarpa</i>	AFA	<i>Pinguicula vulgaris</i>	CB(d)
<i>Carex limosa</i>	CB(n)	<i>Polygala amarella</i>	CE
<i>Carex nigra</i>	CB(d)	<i>Primula farinosa</i>	CE: a-ne
<i>Carex panicea</i>	sa-ES(w)-IR(m)	<i>Ranunculus flammula</i>	sa-ES(w)-M(n)
<i>Carex pauciflora</i>	A-A: a-a-a	<i>Rhynchospora alba</i>	CB: c-b-o
<i>Carex pulicaris</i>	sa-CE(w)	<i>Rhynchospora fusca</i>	AFA
<i>Carex rostrata</i>	CB	<i>Rubus chamaemorus</i>	CB: c-b-a
<i>Carex viridula</i>	CB(d)	<i>Salix myrtilloides</i>	CB
<i>Chamaedaphne calyculata</i>	CB	<i>Saxifraga hirculus</i>	CB: c-b-a
<i>Comarum palustre</i>	CB	<i>Scheuchzeria palustris</i>	CB(d)
<i>Dactylorhiza incarnata</i>	sa-ES-M(n)-IR(m)	<i>Schoenus ferrugineus</i>	CE: ce-b
<i>Dactylorhiza maculata</i>	sa-ES-M(n)	<i>Schoenus nigricans</i>	cosmop.
<i>Drosera anglica</i>	CB(d)	<i>Stellaria crassifolia</i>	CB(n)
<i>Drosera intermedia</i>	AFA	<i>Stellaria palustris</i>	ES
<i>Drosera rotundifolia</i>	CB: c-b-w	<i>Swertia perennis</i>	CB(d)
<i>Eleocharis mamillata</i>	ES(d)	<i>Tofieldia calyculata</i>	CE: a-ce
<i>Eleocharis quinqueflora</i>	CB(d)	<i>Triglochin palustre</i>	CB
<i>Empetrum nigrum</i>	CB(d)	<i>Vaccinium uliginosum</i>	CB
<i>Epipactis palustris</i>	sa-ES-M(n)-IR(m)	<i>Valeriana dioica</i>	sa-CE(w)
<i>Erica tetralix</i>	CE: at-w	<i>Veronica scutellata</i>	CB(d)
<i>Eriophorum angustifolium</i>	CB	<i>Viola epipsila</i>	CB: c-b-w
<i>Eriophorum gracile</i>	CB: c-b-w	<i>Viola palustris</i>	CB: c-b-o
<i>Eriophorum latifolium</i>	sa-ES(d)-M(n)		

Explanations: bold-faced species associated with the class *Oxycocco-Sphagnetea*, while the other species associated with the class *Scheuchzerio-Caricetea nigrae*; A-A: a-a-a – Amphi-Arctic-Alpic group, AFA – Amphi-Atlantic sub-element, CB – Circum-Boreal sub-element, CB: c-b-a – Circum-Boreal Arctic group, CB: c-b-o – Circum-Boreal Oceanic group, CB: c-b-w – Circum-Boreal group proper, CE – European-temperate sub-element, CE: a-ce – Alpic-Central-European distributional type, CE: a-ne – Alpic-North-European distributional type, CE: at-w – Atlantic proper distributional type, CE: ce-b – European-temperate Balkan distributional type, CE: ce-n – European-temperate-lowland group, CE: sat – Sub-Atlantic distributional type, ES – Euro-Siberian sub-element, M – Mediterranean element, IR – Irano-Turanian element, cosmop. – cosmopolitan element, (n) – northern, (m) – in mountain regions, (d) – disjunct range, (w) – western, sa – extension to the Atlantic region of Europe

Irano-Turanian (*Blysmus compressus*, *Orchis palustris*), and Euro-Siberian-Mediterranean-Irano-Turanian (*Dactylorhiza incarnata*, *Epipactis palustris*);

- Holarctic-Mediterranean, or more precisely: European-temperate-Mediterranean (*Carex distans*, *Juncus subnodulosus*) and Euro-Siberian-Mediterranean (*Dactylorhiza maculata*, *Eriophorum latifolium*, *Ranunculus flammula*);
- Holarctic-Irano-Turanian, or more precisely: Euro-Siberian-Irano-Turanian (*Carex panicea*);
- cosmopolitan (*Schoenus nigricans*).

Both in the class *Scheuchzerio-Caricetea nigrae* and in *Oxycocco-Sphagnetea*, most taxa are Circum-Boreal. The Arctic-Alpine sub-element (*Carex pauciflora*) is represented only in the class *Oxycocco-Sphagnetea*, while connective elements and Euro-Siberian and Amphi-Atlantic sub-elements are represented only in the class *Scheuchzerio-Caricetea nigrae*.

5.1.2. Mountain species recorded in lowlands

Among 118 mountain plant species found in Polish lowlands (Zajac M. 1996), only 3 are among the studied peatland species: *Carex pauciflora*, *Malaxis*

monophyllos, and *Tofieldia calyculata*. Their Pomeranian localities are at the limits of their general distribution. Ranges of *C. pauciflora* and *M. monophyllos* in northern Poland are related to the North European parts of their distribution ranges. Each of the species in Pomerania is associated with a different community type. *C. pauciflora* is linked with communities of raised bogs of the class *Oxycocco-Sphagnetea*; but *M. monophyllos* is recorded in fens and transitional bogs of the order *Scheuchzerietalia palustris*; while *T. calyculata* prefers springs and flushes, as well as calcareous fens of the order *Caricetalia davallianae*.

5.1.3. Directional elements

Poland is located at the border between 2 geobotanical provinces: western (affected by oceanic climate)

and eastern (influenced mostly by continental climate). This is the reason why numerous peatland plant species are found there. They immigrate mostly from the west, east, and north. Many of them are “transitional” species, which do not have in Poland any clear limit of distribution (Pawłowska 1977). However, some species reach there a limit of their ranges of distribution and thus represent various directional elements in the Polish flora.

This applies to 34 species (41%) of the total of 83 studied plant species of Pomeranian peatlands (Table 4). Most of them reach a southern limit (12 taxa), and thus are part of the northern element. They are Circum-Boreal except for *Hammarbya paludosa*, which is a European-temperate species. *Baeothryon cespitosum*, *Rubus chamaemorus*, and *Viola epipsila* have their limit in

Table 4. Pomeranian peatland plants that reach their range limits in Poland

Species	Geographic element	Range limit in Pomerania
Southern limit of distribution (12 species)		
<i>Baeothryon alpinum</i>	CB(d)	-
<i>Baeothryon cespitosum</i> *	CB(d)	+
<i>Calamagrostis stricta</i>	CB(n)	-
<i>Carex chordorrhiza</i>	CB(d): c-b-a	-
<i>Comarum palustre</i>	CB	-
<i>Hammarbya paludosa</i>	CE: ce-n	-
<i>Ledum palustre</i> *	CB	-
<i>Liparis loeselii</i>	CB(d)	-
<i>Rubus chamaemorus</i> *	CB(n)	+
<i>Saxifraga hirculus</i>	CB: c-b-a	-
<i>Stellaria crassifolia</i>	CB(n)	-
<i>Viola epipsila</i>	CB: c-b-w	+
South-western limit of distribution (1 species)		
<i>Chamaedaphne calyculata</i> *	CB	+
South-eastern limit of distribution (1 species)		
<i>Hydrocotyle vulgaris</i>	CE: sat	-
Western limit of distribution (4 species)		
<i>Carex brunnescens</i>	CB	+
<i>Malaxis monophyllos</i>	CB(d)	+
<i>Pedicularis sceptrum-carolinum</i>	ES	+
<i>Salix myrtilloides</i>	CB	+
Eastern limit of distribution (10 species)		
<i>Carex hostiana</i>	sa-CE: ce(w)-b	-
<i>Carex pulicaris</i>	sa-CE(w)	-
<i>Drosera intermedia</i>	AFA	+
<i>Erica tetralix</i> *	CE: at-w	+
<i>Juncus acutiflorus</i>	sa-CE: ce-b	+
<i>Juncus subnodulosus</i>	sa-CE(w): ce-b-M(n)	+
<i>Pedicularis sylvatica</i>	CE: sat	+
<i>Pinguicula vulgaris</i>	CB(d)	+
<i>Rhynchospora fusca</i>	AFA	+
<i>Schoenus nigricans</i>	cosmop.	+
Northern limit of distribution (3 species)		
<i>Carex davalliana</i>	CE: ce-b	+
<i>Swertia perennis</i>	CB(d)	-
<i>Tofieldia calyculata</i>	CE: a-ce	+
North-eastern limit of distribution (2 species)		
<i>Orchis palustris</i>	CE-M(n)-IR(m)	+
<i>Valeriana dioica</i>	sa-CE(w)	-
Northern and southern limit of distribution (1 species)		
<i>Carex heleonastes</i>	ES(n,w)	N

Explanations: + species reaching a range limit in Pomerania, - species not reaching a range limit in Pomerania, * species associated with the class *Oxycocco-Sphagnetea* (all the other species associated with the class *Scheuchzerio-Caricetea nigrae*)

Pomerania, but it does not reach the southern part of the region.

Ten species reach the eastern limit in Poland and thus constitute the western directional element. These are mostly the plants associated with the Atlantic Province (classified as Amphi-Atlantic, European-temperate with extension to the Atlantic region of Europe or with the Atlantic proper or Sub-Atlantic distributional types, and Circum-Boreal Oceanic species). Pomerania is crossed by the eastern limit of ranges of 7 species: *Drosera intermedia*, *Erica tetralix*, *Juncus acutiflorus*, *J. subnodulosus*, *Pedicularis sylvatica*, *Pinguicula vulgaris*, *Rhynchospora fusca*, and *Schoenus nigricans*. Except for *S. nigricans*, they reach the lower Vistula, while further east they are sporadic, found only in isolated localities.

Species of the eastern directional element less often penetrate the area of Pomerania. This element is represented by species reaching their western limit there: *Carex brunnescens*, *Malaxis monophyllos*, *Pedicularis sceptrum-carolinum*, and *Salix myrtilloides*. It must be noted that none of the Pomeranian records of *P. sceptrum-carolinum* was confirmed in the post-war period, while the other 3 species in Pomerania reach only a small part of their western limit, which extends much further, outside Poland, to the south-west.

The other directional elements are represented by only 1-3 species each. Most noteworthy among them is *Carex heleonastes*, reaching in Poland both the northern and southern limits of distribution (Table 4).

Pomeranian peatland plants associated with the class *Oxycocco-Sphagnetea* and reaching in Poland some limits of their distribution belong to the northern, north-eastern or western directional elements, while species associated with the class *Scheuchzerio-Caricetea nigrae* represent all directional elements except the north-eastern element.

5.1.4. Spectrum of life-forms

The dominant life-form among the studied peatland species are hemicryptophytes (Table 5). There are also many cryptophytes, including mostly geophytes, while therophytes are absent. Phanerophytes are represented mostly by nanophanerophytes – low shrubs.

Table 5. Spectrum of life-forms of Pomeranian peatland plants

Raunkiaer's life-forms		Pomerania [%]
F	Phanerophytes	2
Ch	Chamaephytes	11
H	Hemicryptophytes	54
C	Cryptophytes incl. geo-* hydro- and helophytes**	33 26* + 7**
T	Therophytes	-

It is interesting to compare the spectra of life-forms separately for the species of the 2 classes of peatland plants. Among species associated with the class *Oxycocco-Sphagnetea*, i.e. with raised bogs and wet heaths, chamaephytes are most numerous (57%, Fig. 5). There are also many hemicryptophytes (29%), while hydro- and helophytes as well as therophytes are absent. The dominance of chamaephytes and hemicryptophytes, is characteristic for cold climatic zones (Szafer 1964). The high percentage contributions of these life-forms in the studied group of plants is not surprising, considering that species associated with the class *Oxycocco-Sphagnetea* are found not only in the temperate but also in the Boreal (Sub-Arctic) part of the Holarctic region.

Species associated with the class *Scheuchzerio-Caricetea nigrae* are mostly hemicryptophytes (58%), but also geophytes are numerous (29%), while only few of them are hydro- or helophytes, chamaephytes and nanophanerophytes (Fig. 5). The dominance of hemicryptophytes

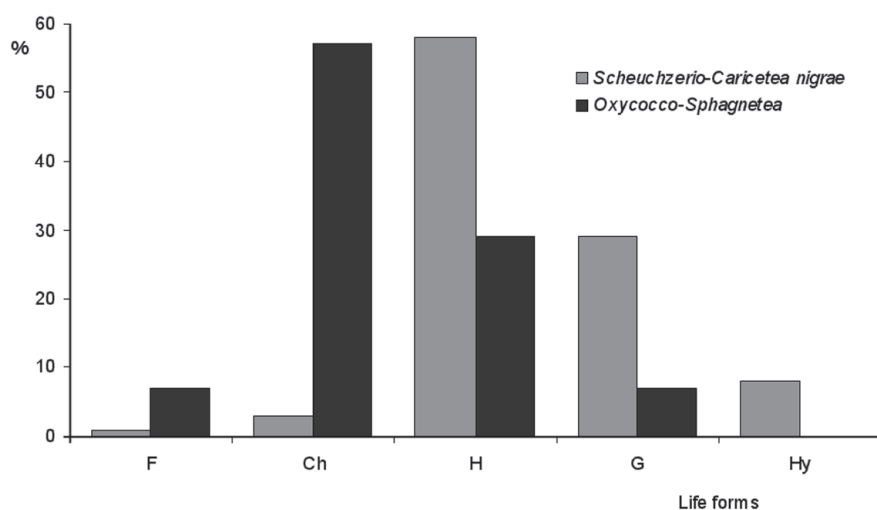


Fig. 5. Percentage contributions of life-forms in species associated with the classes *Scheuchzerio-Caricetea nigrae* and *Oxycocco-Sphagnetea* in Pomerania

Explanations: F – phanerophytes, Ch – chamaephytes, H – hemicryptophytes, G – geophytes, Hy – hydro- and helophytes

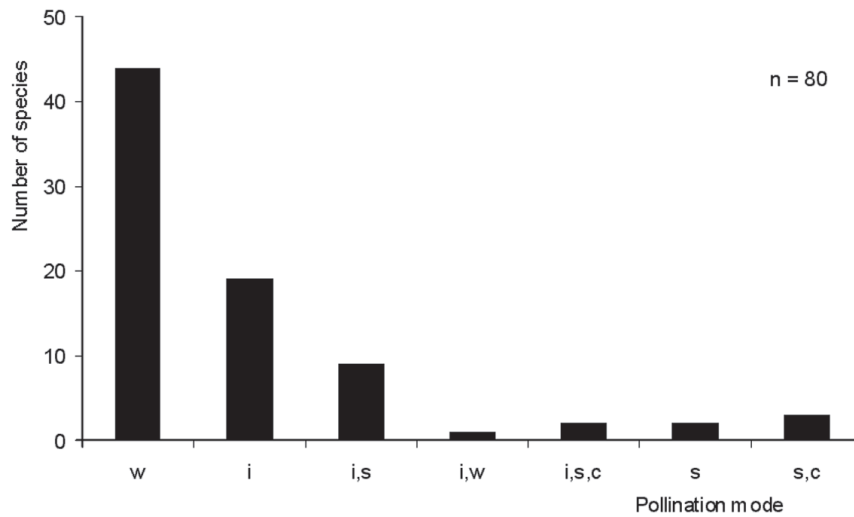


Fig. 6. Number of peatland plant species with various pollination modes
 Explanations: i – insects, c – cleistogamy, s – self-pollination, w – wind

in the life-form spectrum is characteristic for the flora of the cold-temperate zone (Szafer 1964).

5.1.6. Biological properties

Most of the studied species are pollinated by wind (44 species) or by insects (19 species, Fig. 6). They are present in all frequency categories, ranging from extremely rare to frequent. However, in all frequency categories, wind-pollinated species are most numerous.

The dispersal of diaspores (i.e. seeds or other dispersal units) of the studied species usually is not limited to only one mode (Annex). This increases the chance that the species will achieve reproductive success and enables it to colonize new sites. The most common mode of diaspores dispersal in this group is anemochory, associated with long-range transport (Fig. 7). An important role is also played by epizoochory and autochory. Anemochory prevails in all frequency cat-

egories, except extremely rare species, where autochory is more common (diaspores dispersed over small distances).

5.1.7. Life strategy

For 72 taxa of the 83 studied species of peatland plants, data are available about their life strategies (Frank & Klotz 1990; Cieszko & Kucharczyk 1999a, 1999b). Moreover, for *Rubus chamaemorus*, my own observations and published data provide sufficient information to determine the plant's life strategy.

Rubus chamaemorus is perennial but small, light-demanding. In suitable light conditions and moisture it spreads quickly, forming dense patches and producing flowers and fruits (Scholz 1968; Kruszelnicki & Fabiszewski 2001). By contrast, on shaded sites, it reproduces itself vegetatively. It is less competitive than most other plant species. It grows not only on natural sites but also

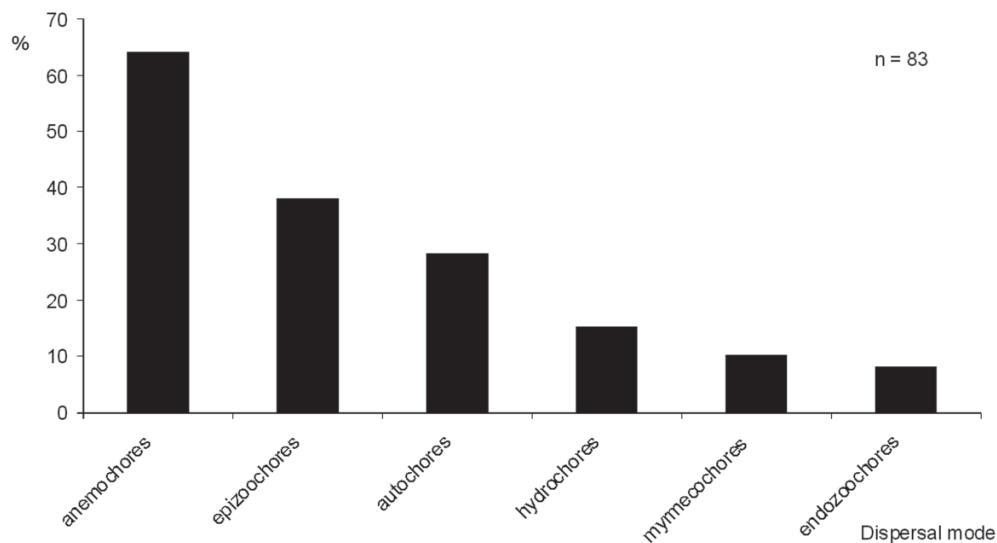


Fig. 7. Percentage contributions of various modes of diaspores dispersal among peatland plant species in Pomerania

on sites disturbed by human activity, e.g. at the edges of drainage ditches or close to them. It colonizes peat extraction sites, sometimes as one of the first species. All these features indicate that this species is highly resistant to stress and disturbance, showing life strategy S-R.

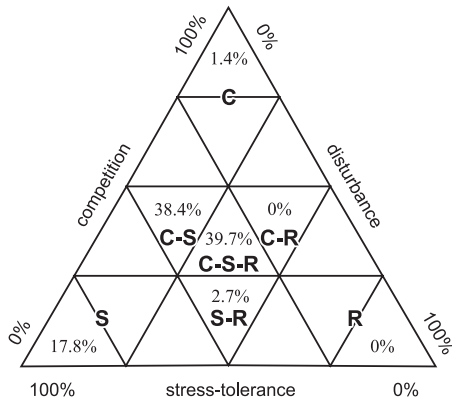


Fig. 8. Life strategies of species associated with the classes *Oxycocco-Sphagnetea* and *Scheuchzerio-Caricetea nigrae* in Pomerania (n = 73)
 Explanations: C – competitors, R – ruderals, S – stress tolerators, C-S, C-R, S-R, C-S-R – mixed strategies

Among the types of life strategies distinguished by Grime (1977, 1979), C-S-R and C-S are most numerous represented in the group of 73 species whose life strategy is known (Fig. 8). C-S-R species are adapted to limited competition and moderate stress and disturbance. C-S species are adapted to relatively undisturbed conditions and limited stress and competition. The peatland plant species include also some species with life strategy S, i.e. stress tolerators. Only one species – *Agrostis canina* – is classified as a competitor (C) and only two – *Lycopodiella inundata* and *Rubus cha-*

maemorus – prefer slightly disturbed, extreme habitats (S-R). Among the studied peatland plants, there are no plants representing the other strategies (R, C-R).

5.2. Regional patterns of distribution of peatland plant species

5.2.1. Frequency of individual species

Frequency analysis shows that species of both the phytosociological classes are found in each of the distinguished frequency categories.

The most numerous were peatland plants of category V (“moderately frequent”, Fig. 9), i.e. recorded at 200-401 ATPOL squares each. These include 2 species associated with the class *Oxycocco-Sphagnetea* (*Erica tetralix*, and *Empetrum nigrum*) and 21 associated with the class *Scheuchzerio-Caricetea nigrae* (e.g. *Calamagrostis stricta*, *Carex canescens*, *C. lasiocarpa*, *Stellaria palustris*, *Triglochin palustre*, and *Vaccinium uliginosum*). Most of them are found in a wide range of habitats, some of them also on disturbed sites. However, this group includes also some species that used to be more frequent but have disappeared from many sites. They are often associated with specific plant communities of one order, e.g. *Carex limosa* and *Scheuchzeria palustris* are components of the association of bog hollows, *Caricetum limosae* (order: *Scheuchzerietalia palustris*).

Frequency category III (“rare”) includes the smallest number of species, i.e. recorded in 50-101 ATPOL squares each. This group includes *Carex pulicaris*, *Eriophorum gracile*, *Hammarbya paludosa*, *Juncus subnodulosus*, *Liparis loeselii*, *Pedicularis sylvatica*, *Pinguicula vulgaris*, and *Stellaria crassifolia*. They reach the limits of their main ranges of distribution in

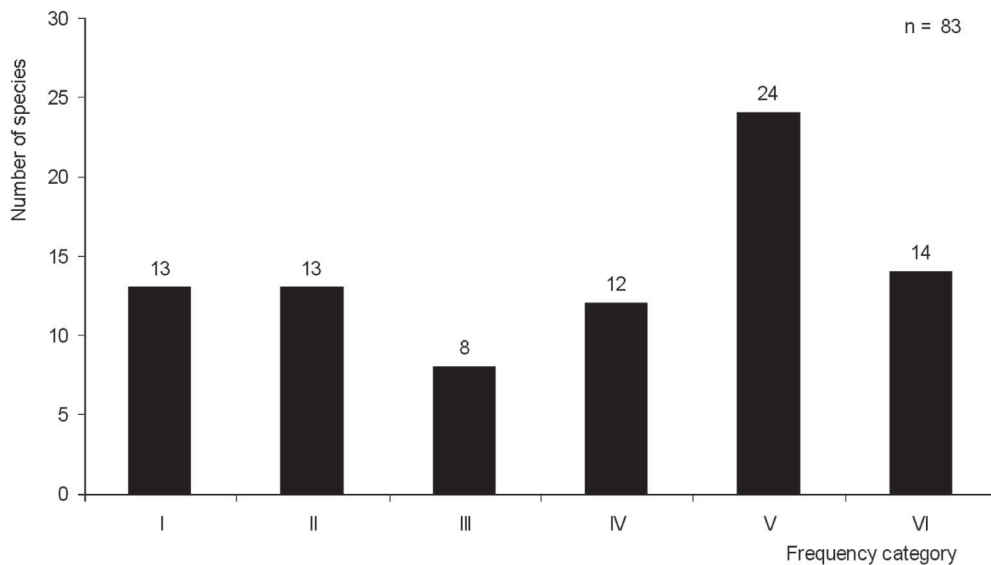


Fig. 9. Numbers of species in frequency categories
 Explanations: I – extremely rare (1-10 ATPOL squares each), II – very rare (11-50), III – rare (51-100), IV – infrequent (101-200), V – moderately frequent (201-400), VI – frequent (= 401)

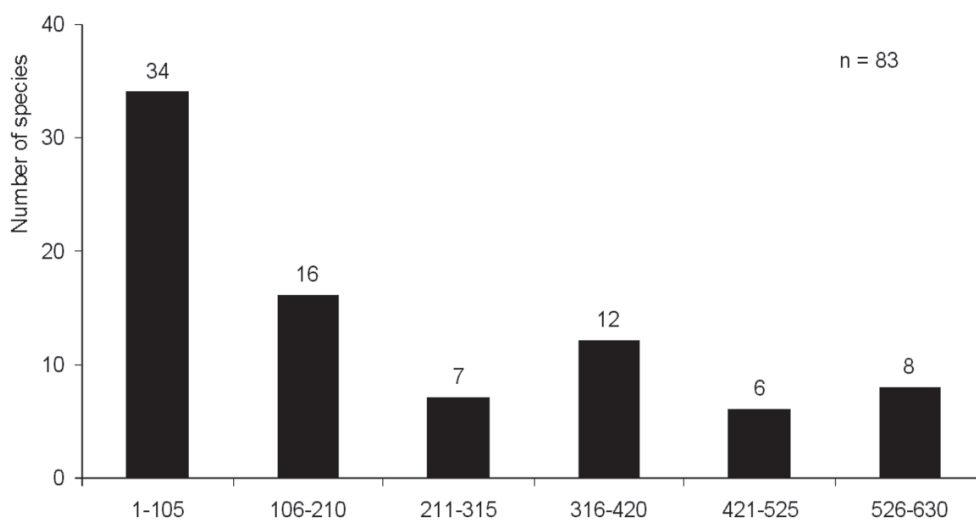


Fig. 10. Numbers of species in frequency classes based on an even division of the maximum number of records (630 ATPOL squares)

Poland. Some of them are associated with calcareous fens, which are infrequent in Pomerania.

The pattern of distribution is different if species are assigned to frequency classes based on an even division of the maximum number of records (630 ATPOL squares) into 6 equal intervals (Fig. 10). The dominant role is then played by the group of rare plants, which includes species of 3 earlier distinguished categories: “extremely rare”, “very rare”, and “rare”. This group jointly accounts for 40% of the studied species. Nearly all of them are rare also on the national scale, and 2/3 of them reach limits of their ranges in Poland. They are usually found only in specific plant communities. Many of them are associated with low sedge mires on calcareous deposits (alliance: *Caricion davallianae*), e.g. *Carex davalliana*, *Orchis palustris*, *Pinguicula vulgaris*, *Schoenus ferrugineus*, and *S. nigricans*. Some others are associated with dystrophic-mesotrophic communities of acid transitional bogs (alliance: *Caricion lasiocarpae*), e.g. *Carex chordorrhiza*, *C. heleonastes*, and *Stellaria crassifolia*. By contrast, species of the category “frequent”, in the new classification form 2 small groups. In general, these plants are found not only on natural sites, but often also on disturbed sites. They grow in many communities, which sometimes belong to various classes.

The rarest Pomeranian peatland plants include *Carex brunescens*, *Chamaedaphne calyculata*, *Primula farinosa* (2 ATPOL squares each), *Viola epipsila* (3), *Carex buxbaumii*, and *C. pauciflora* (5 each). The number of ATPOL squares in these species, corresponds to the number of sites where they were recorded. In contrast, the most frequent species are: *Comarum palustre* (630 ATPOL squares), *Carex nigra* (610), *Ranunculus flammula* (592), *Hydrocotyle vulgaris* (591), *Eriophorum angustifolium* (544), and *Ledum palustre* (539).

However, it must be noted that this analysis of frequency of peatland plants in Pomerania is based on both historical and current data. At present their frequency may differ to a large extent, because of disappearance of the species from some sites (this applies especially to rare species).

5.2.2. Types of regional ranges

Some of the studied species are distributed all over Pomerania. These include both relatively frequent species (e.g. *Carex nigra*, *Hydrocotyle vulgaris*, and *Menyanthes trifoliata*) and rarely recorded taxa (e.g. *Liparis loeselii* and *Hammarbya paludosa*). Their records are, however, usually concentrated in some parts of the region, while much rarer in other parts. Other taxa, e.g. *Carex pulicaris*, *Erica tetralix*, *Salix myrtilloides*, and *Schoenus nigricans*, are mostly or exclusively associated with only some parts of Pomerania. The varied species distribution is caused by differences in climatic and site conditions as well as historical factors.

The presented cartograms of distribution of peatland plants in Pomerania were compared to their ranges in Poland and to their general distribution. This made it possible to distinguish some regional distributional types (chorotypes). An initial classification of chorotypes, based on UPGMA (Fig. 11), was slightly corrected on the basis of a visual comparison. These changes concern, for example, subtype *Hammarbya paludosa*, in the all-Pomeranian type. It includes plants whose localities are mostly scattered throughout the region, but are concentrated in the south-eastern and eastern parts of the region. On the basis of the numerical analysis, this group includes also species like *Salix myrtilloides*, *Pedicularis sceptrum-carolinum*, and *P. sylvatica*. However, the first 2 species are not distributed all over Pomerania but exclusively in the south-eastern part of the region. In contrast, *P. sylvatica* is

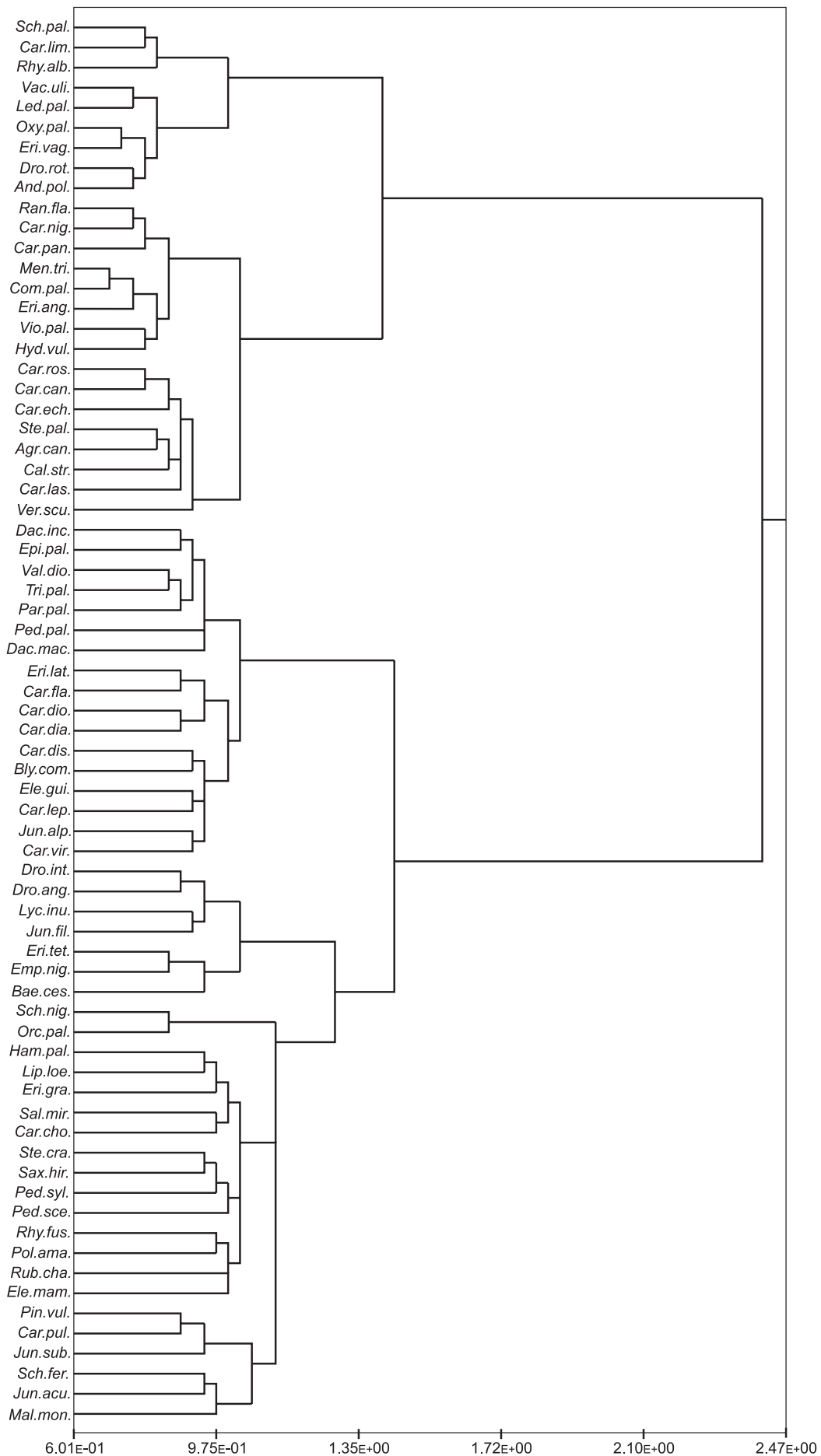


Fig. 11. Dendrogram showing the final classification of distributional types of 69 peatland plant species, based on Unweighted Pair Group Method with Arithmetic Mean (UPGMA)

found mostly in the mid-southern part, between the rivers Drawa and Wda, and additionally on the island of Wolin and in the Kashubian Coast. Consequently, *S. myrtilloides* and *P. sceptrum-carolinum* were assigned to a separate subtype *Salix myrtilloides*, within the eastern distributional type. This subtype includes also the rare *Tofieldia calyculata* and *Carex heleonastes*, which are similarly distributed but were not taken into account in the statistical analysis because of the small number of records. *P. sylvatica* was excluded from the classification because the applied criteria did not allow its assigning to any of the distinguished distributional types.

Similarly, *Polygala amarella* was excluded from the *Rhynchospora fusca* subtype, because outside the eastern part the plants are distributed differently in Pomerania. *P. amarella*, except for the east, is scattered in the southern part of the region, where the other 2 species of this subtype are absent. The structure of the Pomeranian range of *P. amarella* is very similar to that of *Carex chordorrhiza*, which was assigned to the all-Po-

meranian type, subtype *Hammarbya paludosa*. Thus it appeared justified to include both taxa in this same group.

The assignment of *Carex pulicaris* to the disjunct distributional type was also questionable. Plants of this type in Pomerania are found nearly exclusively at isolated localities or isolated groups of localities. *C. pulicaris* has a different distribution pattern but it is distributed mostly in the northern part of the region and does not reach far to the south, so it was finally assigned to the northern distributional type.

Table 6 shows the final classification of distributional types, after the above corrections of the UPGMA dendrogram. Five distributional types were distinguished: western, northern, eastern, all-Pomeranian, and disjunct. Within the eastern and all-Pomeranian types, which showed remarkable internal variation, several subtypes were distinguished. The eastern type includes the *Drosera anglica* subtype, *Salix myrtilloides* subtype, and *Rubus chamaemorus* subtype. The all-Pomeranian type includes the *Carex nigra* subtype, *Carex rostrata* subtype, *Dactylorhiza incarnata* subtype,

Table 6. Regional distributional types of peatland plant species in Pomerania

Type	Subtype	Species
Western type		<i>Orchis palustris</i> , <i>Schoenus nigricans</i>
Northern type		<i>Baeothryon cespitosum</i> , <i>Carex pulicaris</i> , <i>Empetrum nigrum</i> , <i>Erica tetralix</i>
Eastern type	<i>Drosera anglica</i> subtype	<i>Drosera anglica</i> , <i>D. intermedia</i> , <i>Juncus filiformis</i> , <i>Lycopodiella inundata</i>
	<i>Rubus chamaemorus</i> subtype	<i>Carex pauciflora</i> , <i>Rhynchospora fusca</i> , <i>Rubus chamaemorus</i> , <i>Viola epipsila</i>
	<i>Salix myrtilloides</i> subtype	<i>Carex heleonastes</i> , <i>Pedicularis sceptrum-carolinum</i> , <i>Salix myrtilloides</i> , <i>Tofieldia calyculata</i>
All-Pomeranian type	<i>Carex nigra</i> subtype	<i>Carex nigra</i> , <i>C. panicea</i> , <i>Comarum palustre</i> , <i>Eriophorum angustifolium</i> , <i>Hydrocotyle vulgaris</i> , <i>Menyanthes trifoliata</i> , <i>Ranunculus flammula</i> , <i>Viola palustris</i>
	<i>Carex rostrata</i> subtype	<i>Agrostis canina</i> , <i>Calamagrostis stricta</i> , <i>Carex canescens</i> , <i>C. echinata</i> , <i>C. lasiocarpa</i> , <i>C. rostrata</i> , <i>Stellaria palustris</i> , <i>Veronica scutellata</i>
	<i>Dactylorhiza incarnata</i> subtype	<i>Dactylorhiza incarnata</i> , <i>D. maculata</i> , <i>Epipactis palustris</i> , <i>Parnassia palustris</i> , <i>Pedicularis palustris</i> , <i>Triglochin palustre</i> , <i>Valeriana dioica</i>
	<i>Eriophorum latifolium</i> subtype	<i>Blysmus compressus</i> , <i>Carex diandra</i> , <i>C. dioica</i> , <i>C. distans</i> , <i>C. flava</i> , <i>C. lepidocarpa</i> , <i>C. viridula</i> , <i>Eleocharis quinqueflora</i> , <i>Eriophorum latifolium</i> , <i>Juncus alpino-articulatus</i>
	<i>Hammarbya paludosa</i> subtype	<i>Carex chordorrhiza</i> , <i>Eriophorum gracile</i> , <i>Hammarbya paludosa</i> , <i>Liparis loeselii</i> , <i>Polygala amarella</i> , <i>Saxifraga hirculus</i> , <i>Stellaria crassifolia</i>
	<i>Rhynchospora alba</i> subtype	<i>Andromeda polifolia</i> , <i>Carex limosa</i> , <i>Drosera rotundifolia</i> , <i>Eriophorum vaginatum</i> , <i>Ledum palustre</i> , <i>Oxycoccus palustris</i> , <i>Rhynchospora alba</i> , <i>Scheuchzeria palustris</i> , <i>Vaccinium uliginosum</i>
Disjunctive type		<i>Carex buxbaumii</i> , <i>C. hostiana</i> , <i>Herminium monorchis</i> , <i>Juncus acutiflorus</i> , <i>J. subnodulosus</i> , <i>Malaxis monophyllos</i> , <i>Pinguicula vulgaris</i> , <i>Schoenus ferrugineus</i>
Unclassified		<i>Baeothryon alpinum</i> , <i>Carex brunescens</i> , <i>C. davalliana</i> , <i>Chamaedaphne calyculata</i> , <i>Eleocharis mamillata</i> , <i>Pedicularis sylvatica</i> , <i>Primula farinosa</i> , <i>Swertia perennis</i>

Eriophorum latifolium subtype, *Hammarbya paludosa* subtype, and *Rhynchospora alba* subtype. Moreover, ranges of some species are intermediate between 2 or more groups.

Among the 83 studied species, 8 could not be assigned to any of the groups distinguished on the basis of the grouping criteria used. This applies to *Baeothryon alpinum* (*Trichophorum alpinum*), *Carex brunescens*, *C. davalliana*, *Chamaedaphne calyculata*, *Eleocharis mamillata*, *Pedicularis sylvatica*, *Primula farinosa*, and *Swertia perennis*. They represent the Circum-Boreal and European-temperate sub-elements. In Pomerania these species are found at scattered localities or – as in the case of *P. sylvatica* – their records are concentrated mostly in the mid-southern part of the region. In contrast, *E. mamillata* was generally sporadic, but more frequent in valleys of the rivers Brda and upper Wieprza.

Western type: *Orchis palustris* and *Schoenus nigricans*

This group is represented by only 2 species, which are rare both in Pomerania and generally in Poland. In Pomerania they are found mostly in the south-west (Fig. 12). *Orchis palustris* belongs to the connective European-temperate-Mediterranean-Irano-Turanian element

and in Poland it reaches the north-eastern limit of distribution. *Schoenus nigricans* is cosmopolitan, but its Polish records are concentrated at the eastern limit of its European range. The distribution of both species is similar in northern and central Poland. They are associated with calcareous fens of the alliance *Caricion davallianae*, and reach a phytocoenotic optimum in the same association: *Orchido-Schoenetum*. Additionally, *O. palustris* is recorded on moist and wet meadows of the class *Molinio-Arrhenatheretea*, and in tall sedge communities of the class *Phragmitetea*.

Northern type: *Carex pulicaris*, *Empetrum nigrum*, *Erica tetralix*, *Baeothryon cespitosum*

This distributional type includes the species associated mostly with northern Pomerania (Fig. 13). Their records may be also concentrated in the central and eastern part of the belt of Pomeranian Lakelands, but are absent or very rare in the south. *Carex pulicaris* and *Erica tetralix* represent the European-temperate sub-element. In Poland these species reach the eastern limits of their general distribution ranges. In contrast, *Empetrum nigrum* and *Baeothryon cespitosum* (*Trichophorum caespitosum*) belong to the Circum-Boreal sub-element, but the latter species reaches in Pomerania the southern

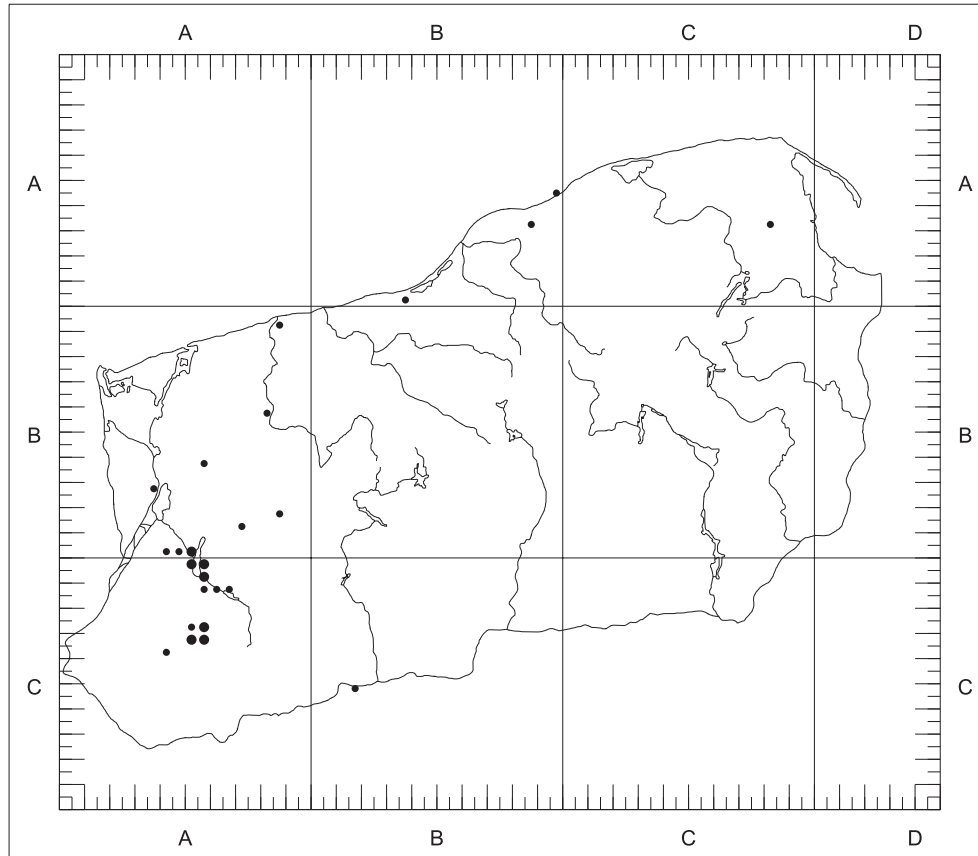


Fig. 12. Concentration of peatland plant species of the western distributional type in Pomerania. Explanations: dot size reflects the number of peatland plant species recorded in each ATPOL square (5 × 5 km square). The largest dot indicates 2 species per square

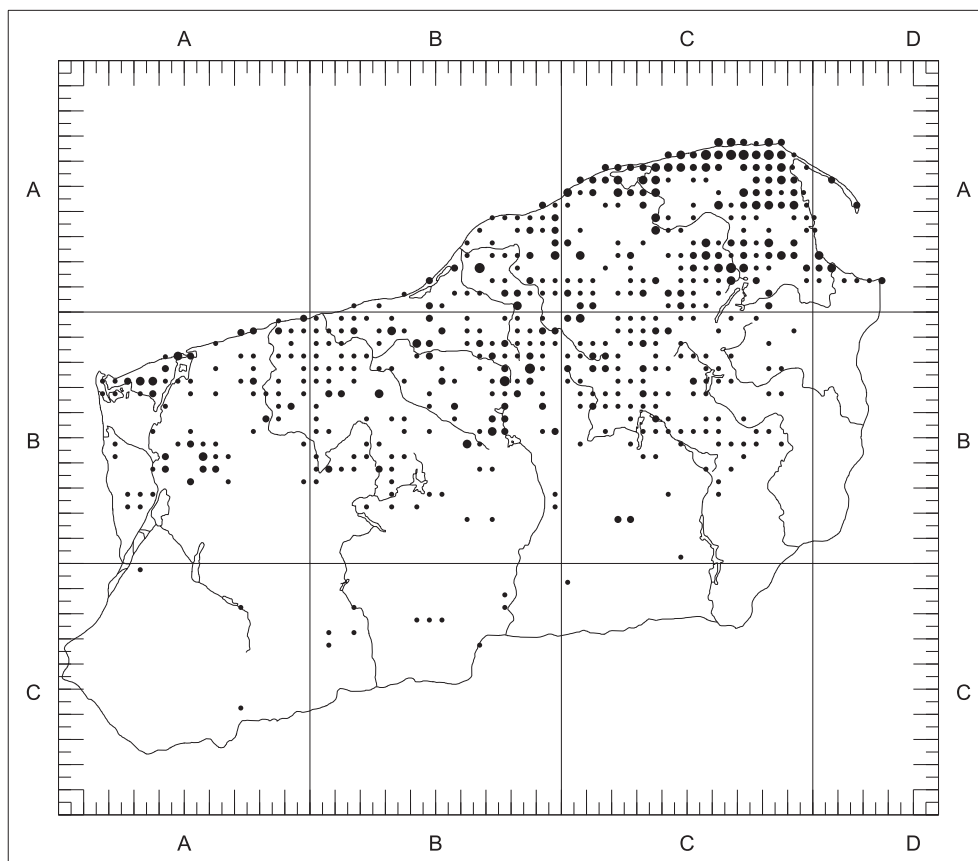


Fig. 13. Concentration of peatland plant species of the northern distributional type in Pomerania

Explanations: dot size reflects the number of peatland plant species recorded in each ATPOL square (5×5 km square). The largest dot indicates 4 species per square

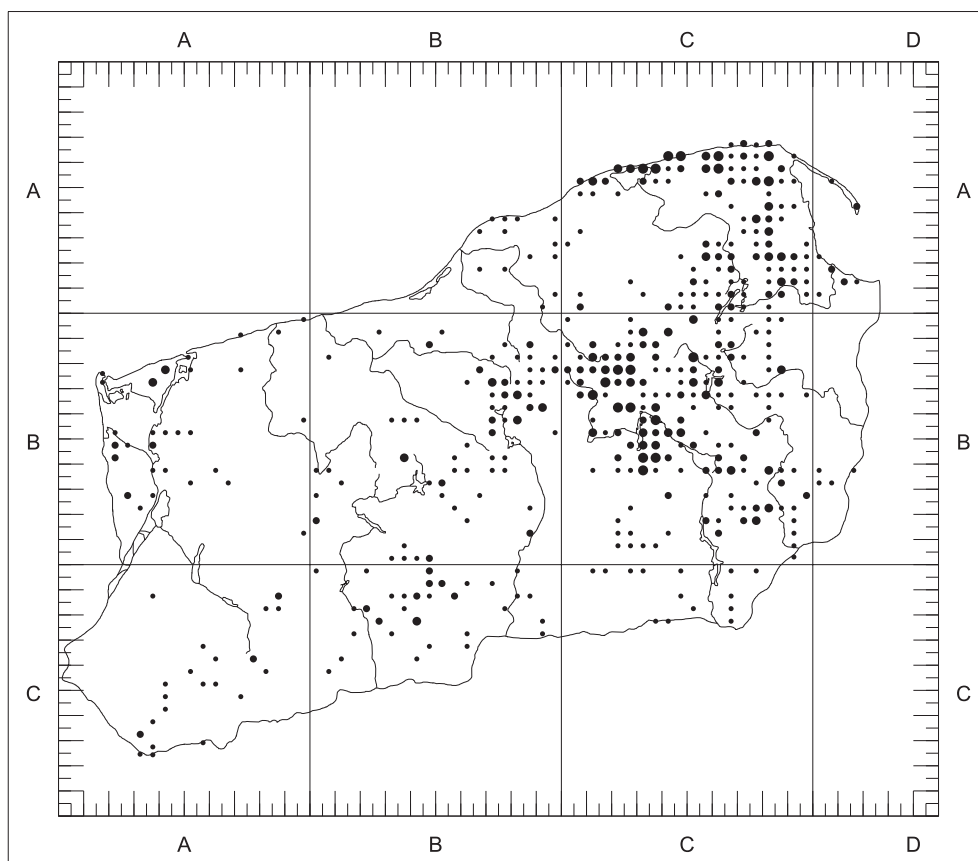


Fig. 14. Concentration of peatland plant species of the eastern distributional type, *Drosera anglica* subtype, in Pomerania

Explanations: dot size reflects the number of peatland plant species recorded in each ATPOL square (5×5 km square). The largest dot indicates 4 species per square

limit of its distribution. Both taxa have single isolated stands in the south of Poland.

Most of the fourth species of this group, namely *Baeothryon cespitosum*, *Erica tetralix*, and *Carex pulicaris*, grow in wet heaths of the order *Sphagno-Ericetalia*. Moreover, *C. pulicaris* is found in eutrophic low sedge mires. *Empetrum nigrum* and *E. tetralix* are recorded in coastal pine forests (*Empetro nigri-Pinetum*) and raised bogs of the order *Sphagnetalia magellanici*. *E. nigrum* is also associated with coastal crowberry heaths.

Eastern type

This type includes the species whose Pomeranian records are concentrated in the eastern and/or south-eastern parts of the region as well as the taxa found exclusively or mostly in the north-eastern part. This group is diverse, so 3 subtypes were distinguished, as follows.

Drosera anglica subtype: *Drosera anglica*, *D. intermedia*, *Juncus filiformis*, *Lycopodiella inundata*

These species are distributed mostly in the eastern and north-eastern part of Pomerania (Fig. 14), especially in the Charzykowy Plain (Równina Charzykowska), the Tuchola Forest, and in the eastern part of the Słowińskie Coast (Pobrzeże Słowińskie). Except for *Drosera inter-*

media, they are equally frequent in the Kashubian Lakeland, but all of them avoid the areas located west of the river Łeba: the Damnica Plateau (Wysoczyzna Damnicka) and the eastern part of the Polanów Plateau (Wysoczyzna Polanowska). In other parts of Pomerania they are rare and scattered. They belong to the Circum-Boreal sub-element, except for *D. intermedia*, which represents the Amphi-Atlantic sub-element and reaches in Poland the eastern limit of its distribution range. These taxa are generally associated with transitional bogs of the order *Scheuchzerietalia palustris*. Only *Juncus filiformis* is an exception and is found chiefly in acid low sedge mires of the order *Caricetalia nigrae*.

Rubus chamaemorus subtype: *Carex pauciflora*, *Rhynchospora fusca*, *Rubus chamaemorus*, *Viola epipsila*

This group is composed of 4 species that are rare in Pomerania and distributed mostly in the north-eastern part of the region (Fig. 15). Two of them, *Rubus chamaemorus* and *Viola epipsila*, reach in Pomerania the southern limit of distribution, and represent the Circum-Boreal sub-element. *Carex pauciflora* belongs to the Arctic-Alpine sub-element. Its localities in northern Poland are related to the North European part of its general distribution. *Rhynchospora fusca* is an Amphi-Atlantic species. Its distribution in Pomerania is intermediate

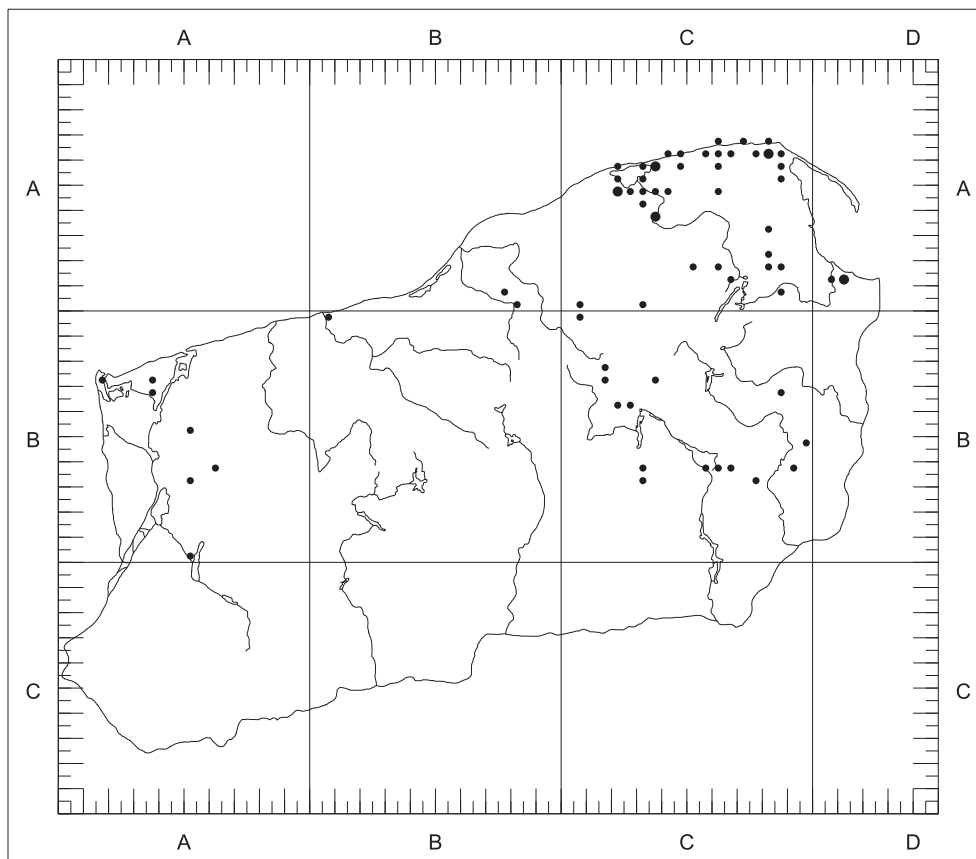


Fig. 15. Concentration of peatland plant species of the eastern distributional type, *Rubus chamaemorus* subtype, in Pomerania
 Explanations: dot size reflects the number of peatland plant species recorded in each ATPOL square (5 × 5 km square). The largest dot indicates 4 species per square

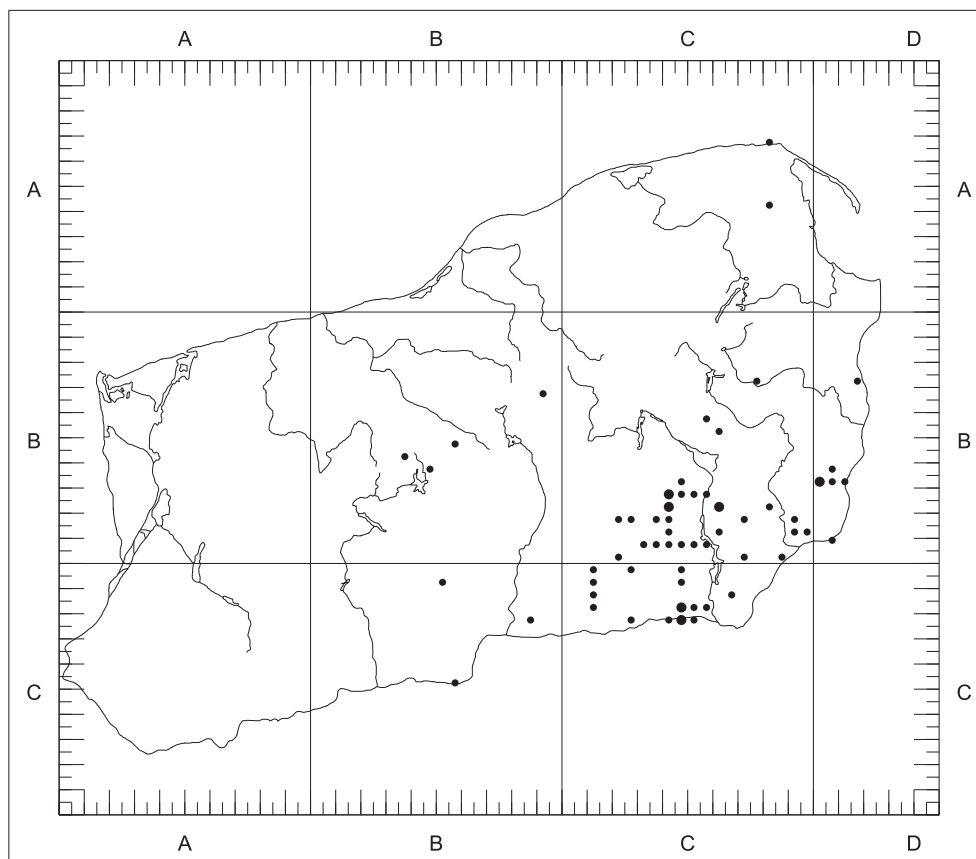


Fig. 16. Concentration of peatland plant species of the eastern distributional type, *Salix myrtilloides* subtype, in Pomerania
 Explanations: dot size reflects the number of peatland plant species recorded in each ATPOL square (5 × 5 km square). The largest dot indicates 4 species per square

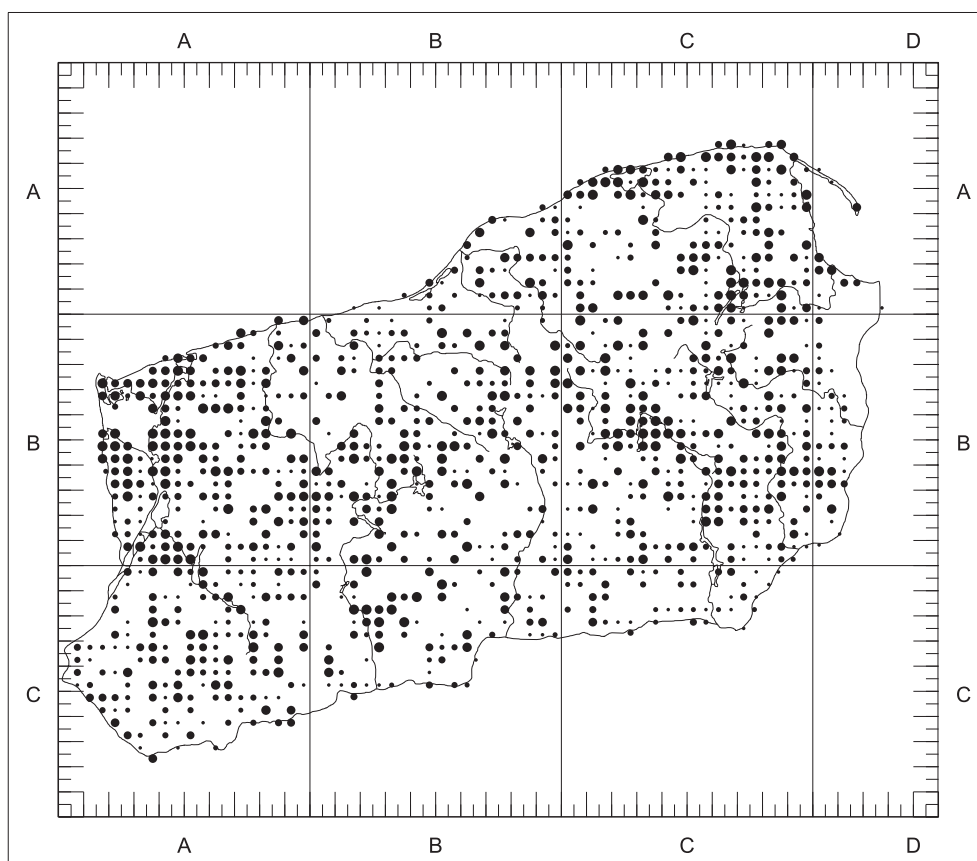


Fig. 17. Concentration of peatland plant species of the all-Pomeranian distributional type, *Carex nigra* subtype, in Pomerania
 Explanations: dot size reflects the number of peatland plant species recorded in each ATPOL square (5 × 5 km square). The largest dot indicates 8 species per square

between the *R. chamaemorus* subtype and the northern or disjunct type (this species is absent in central Pomerania). However, the taxon was included in this group because it is found mostly in north-eastern Pomerania. Moreover, such a classification is consistent with that generated by MULVA-5 software.

This group includes species associated with communities of raised bogs of the class *Oxycocco-Sphagnetea*: *Carex pauciflora* and *Rubus chamaemorus*. The latter is found also in wet coniferous forests and wet birch forests. By contrast, *Rhynchospora fusca* usually grows in the association *Rhynchosporium albae* of the alliance *Rhynchosporion albae*. The last species of this group, *Viola epipsila*, grows in alluvial forests (alliance: *Alno-Padion*), alder forests (class: *Alnetea glutinosae*), and low sedge mires (order *Caricetalia nigrae*).

Salix myrtilloides subtype: *Carex heleonastes*, *Pedicularis sceptrum-carolinum*, *Salix myrtilloides*, *Tofieldia calyculata*

This group includes species recorded mostly or exclusively in the south-eastern part of the region: in the Świecie Plateau (Wysoczyzna Świecka), the Brda valley, and Krajna Lakeland (Pojezierze Krajeńskie). In other parts of the region their records are scattered, isolated. The species are absent in the western part of Pomerania (Fig. 16). They belong to various geographic

sub-elements: Euro-Siberian (*Carex heleonastes*, *Pedicularis sceptrum-carolinum*), Circum-Boreal (*Salix myrtilloides*), and European-temperate (*Tofieldia calyculata*). Pomerania is crossed by the limits of their main ranges: northern limit of *T. calyculata* and *C. heleonastes*, while western limit of *P. sceptrum-carolinum* and partly also of *S. myrtilloides*.

These plants are associated mostly with acid transitional bogs of the order *Scheuchzerietalia palustris* or with eutrophic fens of the order *Caricetalia davallianae*, less often with mesotrophic low sedge mires of the order *Caricetalia nigrae* (*Tofieldia calyculata*).

All-Pomeranian type

This is the largest and the most diverse group, sharing a similar distribution pattern in the study area. It includes species found all over Pomerania or most of the region. This type includes 6 subtypes, as follows.

Carex nigra subtype: *Carex nigra*, *C. panicea*, *Comarum palustre*, *Eriophorum angustifolium*, *Hydrocotyle vulgaris*, *Ranunculus flammula*, *Menyanthes trifoliata*, *Viola palustris*

In Pomerania these species are most widespread among the studied peatland plants (Fig. 17). In the lower Vistula valley, *Hydrocotyle vulgaris* reaches a part of the eastern limit of its main range. Species of this group

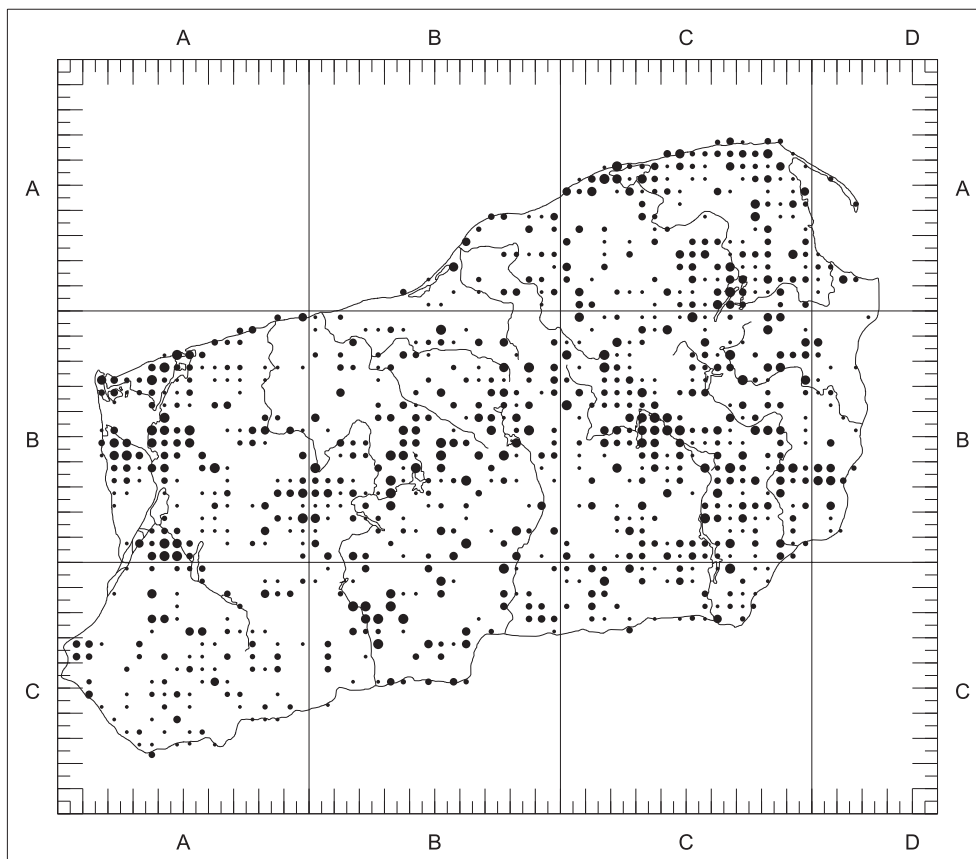


Fig. 18. Concentration of peatland plant species of the all-Pomeranian distributional type, *Carex rostrata* subtype, in Pomerania
 Explanations: dot size reflects the number of peatland plant species recorded in each ATPOL square (5 × 5 km square). The largest dot indicates 8 species per square

represent the Circum-Boreal sub-element or the Euro-pean-temperate sub-element, Sub-Atlantic distributional type (*H. vulgaris*), and connective elements: Euro-Siberian-Mediterranean (*Ranunculus flammula*) and Euro-Siberian-Irano-Turanian (*Carex panicea*). Plants of this group are found in a wide range of plant communities: usually in mires of the class *Scheuchzerio-Caricetea nigrae*, less often of the class *Oxycocco-Sphagnetea*. Sometimes they grow in reedbeds (class: *Phragmitetea*), moist meadows (order: *Molinietalia caeruleae*), sallow thickets (order: *Alnetalia glutinosae*), or wet alder or birch forests. Moreover, *H. vulgaris* is associated with some communities of the class *Litoretalia uniflorae*.

Carex rostrata subtype: *Agrostis canina*, *Calamagrostis stricta*, *Carex canescens*, *C. echinata*, *C. lasiocarpa*, *C. rostrata*, *Stellaria palustris*, *Veronica scutellata*

Species of this group are generally frequent in Pomerania but recorded mostly in the eastern part of the region, near the mouth of the river Odra and in the central part of the belt of Pomeranian Lakelands (Fig. 18). Most of them are Circum-Boreal, but *Agrostis canina* and *Stellaria palustris* represent the Euro-Siberian sub-element. Like species of the previous subtype, these plants have a wide phytocoenotic spectrum. They are found mostly in low sedge mires of the order *Caricetalia nigrae*, and in transitional bogs of the order *Scheuchzerietalia palustris*. Some of them are frequent also in wet and moist meadows (order: *Molinietalia*) and sallow thickets (order: *Alnetalia glutinosae*), while less often recorded in raised bogs and humid heaths (class: *Oxycocco-Sphagnetea*) or in tall sedge communities (alliance: *Magnocaricion*). An exception is *Carex rostrata*, which – although being an important component of communities of the order *Scheuchzerietalia palustris* – is associated primarily with tall sedge communities. In contrast, *Carex echinata* is found also in wet coniferous and wet birch forests.

Dactylorhiza incarnata subtype: *Dactylorhiza incarnata*, *D. maculata*, *Epipactis palustris*, *Parnassia palustris*, *Pedicularis palustris*, *Triglochin palustre*, *Valeriana dioica*

This subtype includes the species whose Pomeranian records are found chiefly near the mouth of the river Odra and in the east, whereas are scattered in other parts of the region (Fig. 19). This group is phytogeographically diverse. The species represent the Circum-Boreal (*Triglochin palustre*, *Parnassia palustris*), European-temperate (*Valeriana dioica*), Euro-Siberian (*Pedicularis palustris*) sub-elements, and connective elements: Euro-Siberian-Mediterranean (*Dactylorhiza maculata*), and Euro-Siberian-Mediterranean-Irano-Turanian (*Dactylorhiza incarnata*, *Epipactis palustris*).

Taxa of this group are associated mainly with communities of fens (acid low sedge mires, often on calcareous deposits) and transitional bogs of the class *Scheuchzerio-Caricetea nigrae*. Some species are also found in wet meadows, tall sedge communities, alluvial forests, and sallow thickets.

It must be noted that *Triglochin palustre* is included in this subtype but in fact its distribution is intermediate between the *Dactylorhiza incarnata* subtype and *Carex rostrata* subtype.

Eriophorum latifolium subtype: *Blysmus compressus*, *Carex diandra*, *C. dioica*, *C. distans*, *C. flava*, *C. lepidocarpa*, *C. viridula*, *Eleocharis quinqueflora*, *Eriophorum latifolium*, *Juncus alpino-articulatus*

Plants of this group are distributed all over Pomerania, but less frequent in the Central Coastal belt, reaching south to the West Pomeranian Lakeland (Fig. 20). Most of them belong to the Circum-Boreal sub-element, while others represent the Amphi-Atlantic sub-element (*Carex lepidocarpa*) and connective elements: European-temperate-Mediterranean-Irano-Turanian (*Blysmus compressus*), European-temperate-Mediterranean (*Carex distans*), and Euro-Siberian-Mediterranean (*Eriophorum latifolium*). Species of this subtype are associated with communities of the class *Scheuchzerio-Caricetea nigrae* (mostly of the order *Caricetalia davallianae*). They are found in fens and transitional bogs or spring-water mires. *B. compressus* and *C. distans* appear also in salt-marshes and frequently in floodplain grasslands (order: *Trifolio fragiferae-Agrostietalia stoloniferae*).

Hammarbya paludosa subtype: *Carex chordorrhiza*, *Eriophorum gracile*, *Hammarbya paludosa*, *Liparis loeselii*, *Polygala amarella*, *Saxifraga hirculus*, *Stellaria crassifolia*

These species are rare both in Pomerania and in other parts of Poland. An exception is *Polygala amarella*, which is more frequent in central and southern Poland. Their Pomeranian localities are mostly scattered, but more crowded in the south-east and east (Fig. 21), while those of *Liparis loeselii* also in the Płonia river valley and in the eastern part of the Myślubórz Lakeland. These species, in contrast to the *Eriophorum latifolium* subtype, are sporadic in the Bytów and Drawsko Lakelands. Moreover, they have never been recorded in the western part of the Myślubórz Lakeland. Except for *P. amarella* and *Eriophorum gracile*, all the species have the southern limits of their ranges in Poland. *Hammarbya paludosa* and *P. amarella* are European-temperate species, while others are Circum-Boreal.

Plants of this group are associated mostly with communities of flooded transitional bogs of the alliance *Caricion lasiocarpae* (*Stellaria crassifolia*, *Saxifraga*

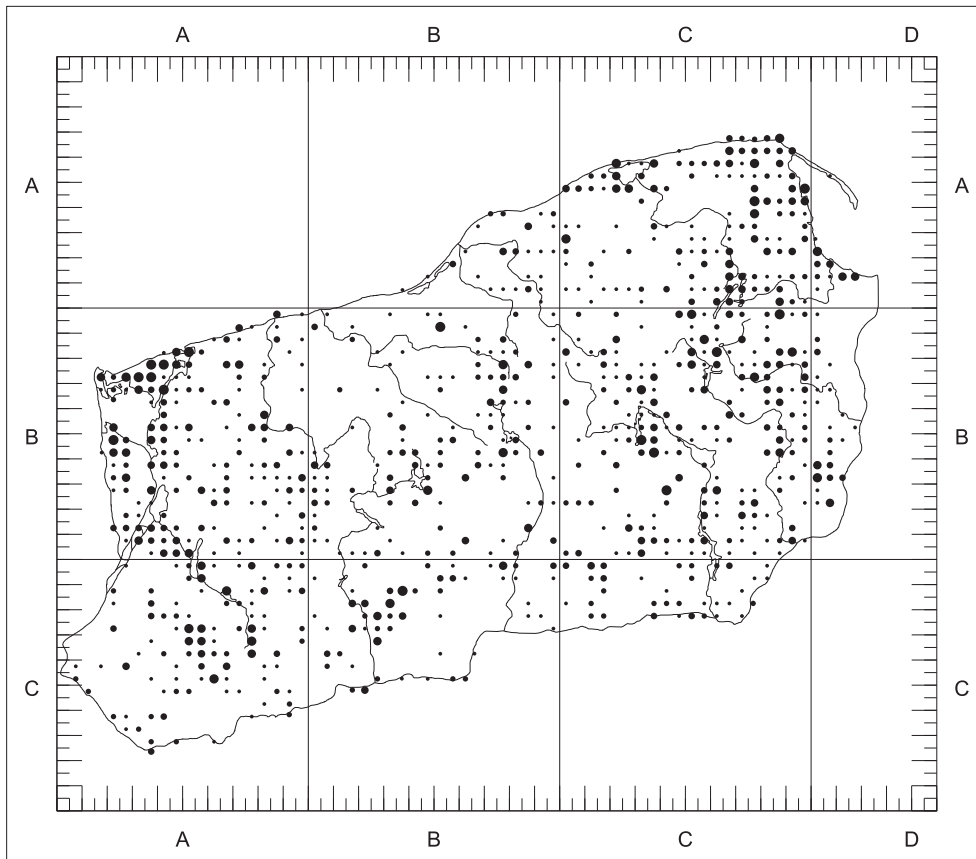


Fig. 19. Concentration of peatland plant species of the all-Pomeranian distributional type, *Dactylorhiza incarnata* subtype, in Pomerania
 Explanations: dot size reflects the number of peatland plant species recorded in each ATPOL square (5 × 5 km square). The largest dot indicates 7 species per square

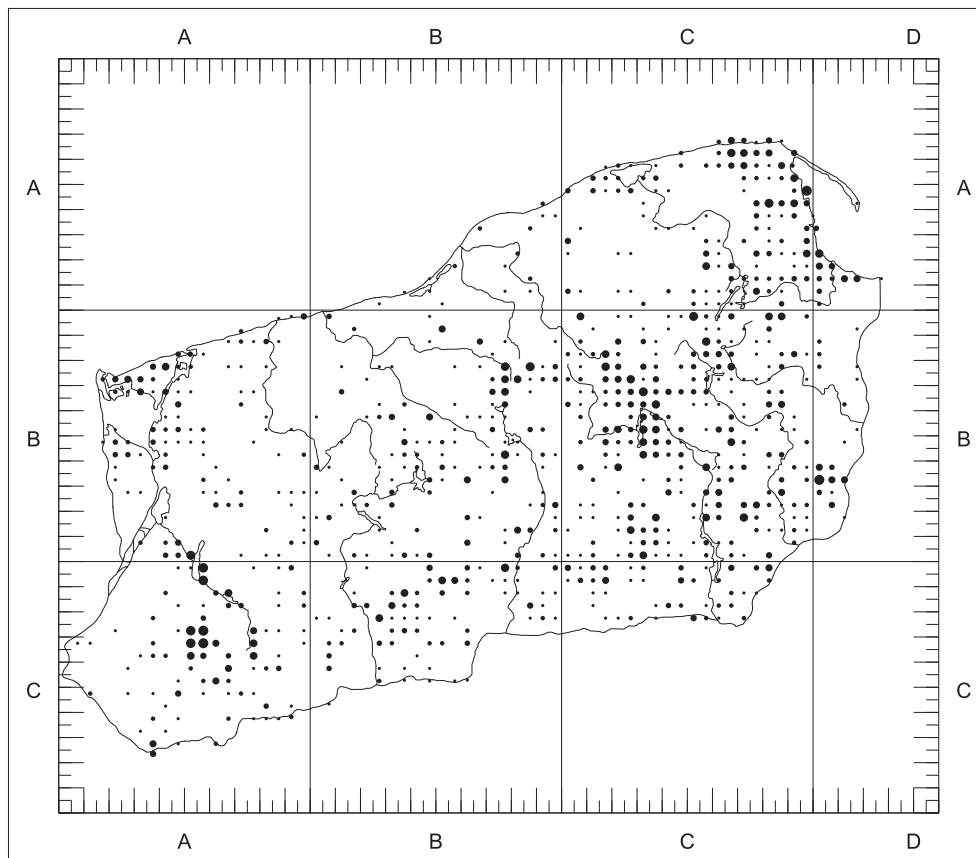


Fig. 20. Concentration of peatland plant species of the all-Pomeranian distributional type, *Eriophorum latifolium* subtype, in Pomerania
 Explanations: dot size reflects the number of peatland plant species recorded in each ATPOL square (5 × 5 km square). The largest dot indicates 10 species per square

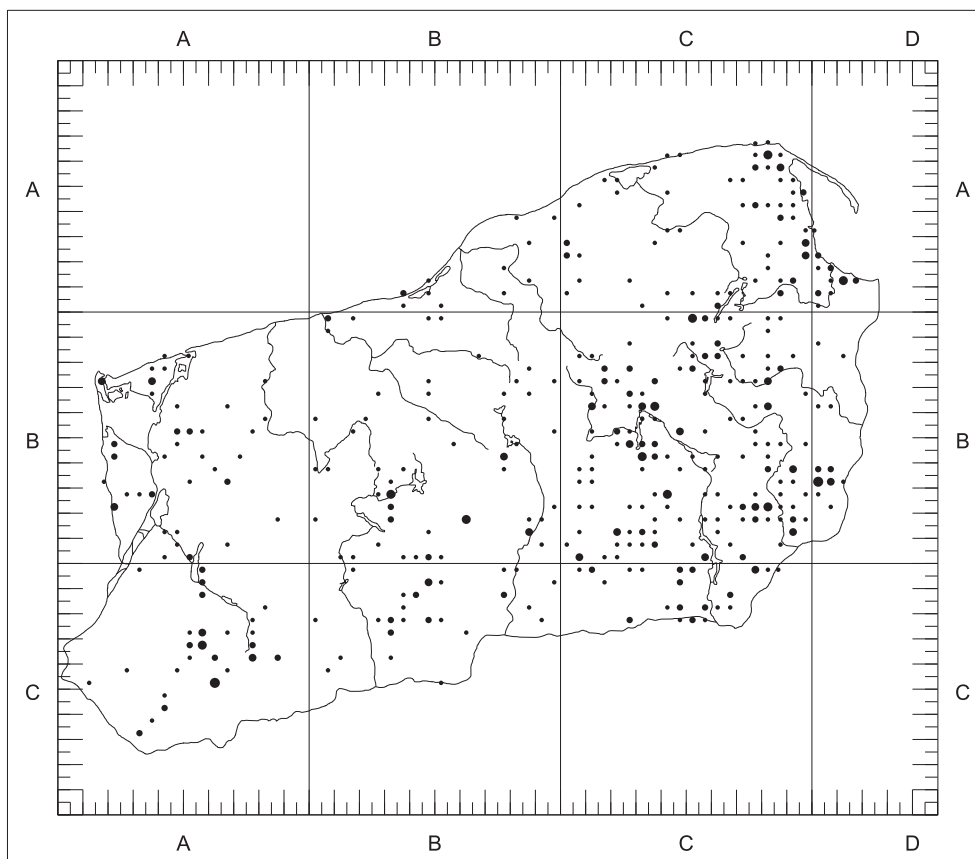


Fig. 21. Concentration of peatland plant species of the all-Pomeranian distributional type, *Hammarbya paludosa* subtype, in Pomerania
 Explanations: dot size reflects the number of peatland plant species recorded in each ATPOL square (5×5 km square). The largest dot indicates 7 species per square

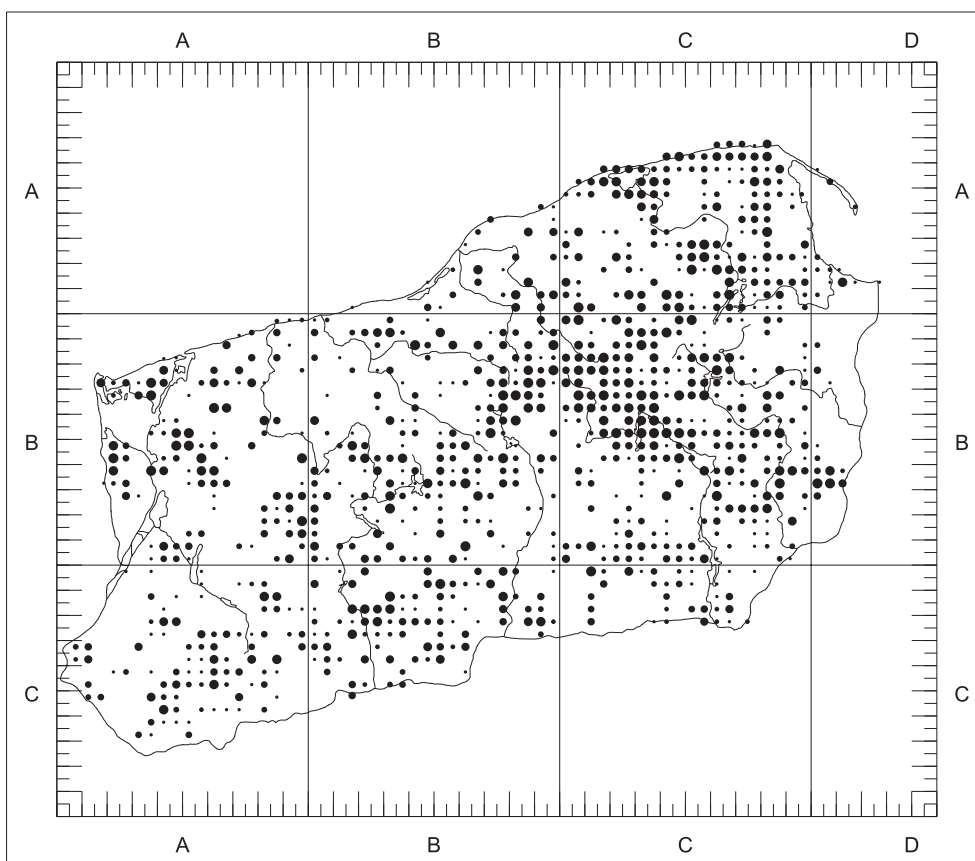


Fig. 22. Concentration of peatland plant species of the all-Pomeranian distributional type, *Rhynchospora alba* subtype, in Pomerania
 Explanations: dot size reflects the number of peatland plant species recorded in each ATPOL square (5×5 km square). The largest dot indicates 9 species per square

hirculus, *Eriophorum gracile*, *Carex chordorrhiza*), and with low sedge mires of the order *Caricetalia davallianae* (*Polygala amarella*, *Liparis loeselii*). *Hammabrya paludosa* is most frequent in transitional bogs of the alliance *Rhynchosporion albae*.

Rhynchospora alba subtype: *Andromeda polifolia*, *Carex limosa*, *Drosera rotundifolia*, *Eriophorum vaginatum*, *Ledum palustre*, *Oxycoccus palustris*, *Rhynchospora alba*, *Scheuchzeria palustris*, *Vaccinium uliginosum*

This subtype includes 9 taxa distributed all over Pomerania but most frequent in the Tuchola Forest, Charzykowy Plain, and Bytów Lakeland, and frequent in the Kashubian Lakeland and the eastern part of the Słowińskie Coast (Fig. 22). All the species are Circum-Boreal, associated with raised bogs of the class *Oxycocco-Sphagnetalia* (*Andromeda polifolia*, *Drosera rotundifolia*, *Eriophorum vaginatum*, *Ledum palustre*, *Oxycoccus palustris*, frequently also *Vaccinium uliginosum*), and transitional bogs of the order *Scheuchzerietalia palustris* (*Carex limosa*, *Rhynchospora alba*, *Scheuchzeria palustris*). Some of the species are found also in wet heaths (*A. polifolia*, *E. vaginatum*, *O. palustris*, *V. uliginosum*), and wet coniferous forest (*E. vaginatum*, *L. palustre*, *O. palustris*, *V. uliginosum*, rarely *A. polifolia*).

Disjunctive type: *Carex buxbaumii*, *C. hostiana*, *Herminium monorchis*, *Juncus acutiflorus*, *J. subnodulosus*, *Malaxis monophyllos*, *Pinguicula vulgaris*, *Schoenus ferrugineus*

This group is composed of rare species that are found in Pomerania nearly exclusively at isolated sites or isolated groups of sites (Annex, Figs. A10, A20, A47, A49, A52, A56, A64, A74). These species in Pomerania are outside their main range or at its limit. An exception is *Carex buxbaumii*, whose range includes Poland but its western European limit runs across Eastern Germany. The European-temperate sub-element in this group is represented by *Carex hostiana*, *Juncus acutiflorus*, and *Schoenus ferrugineus*. In contrast, *Herminium monorchis* is a Euro-Siberian-Asiatic species, while *Juncus subnodulosus* is European-temperate-Mediterranean. *C. buxbaumii*, *Microstylis monophyllos*, and *Pinguicula vulgaris* are Circum-Boreal, but their distribution in Pomerania is clearly disjunct.

All species of this group are found in communities of the class *Scheuchzerio-Caricetea nigrae* (mostly in low sedge mires of the order *Caricetalia davallianae*).

5.3. Modern dynamics of regional ranges of plant species of Pomeranian peatlands

Peatlands are some of the ecosystems that are most strongly and easily transformed by human activity. Environmental changes influence the dynamics of

peatland plant species. Many of them are characterized by a low tolerance to any changes in water conditions, so their local populations may disappear very quickly. To determine the dynamic trends of species, historical records are necessary, to allow a comparison of their distribution in the past with current floristic data. A lack of confirmation of local populations recorded in the past may result not only from their disappearance but, alternatively, from a lack of recent floristic research in some areas. For newly discovered localities, it is also difficult to determine how long they have existed there, since the given area may have not been studied by botanists earlier. For this reason, an attempt to determine the dynamic trends was made for only 24 species, for which the largest number of data about the history of their distribution are available, or their historical records have not been confirmed for nearly 60 years, in spite of later floristic exploration. Thus it must be remembered that the maps of species distribution presented here (with division into several periods), only roughly reflect their true long-term dynamic trends. All of the plants considered here are rare and are assigned to various threat categories on the scale of Poland (Zarzycki & Szela 2006), and of Pomerania (Żukowski & Jackowiak 1995; Markowski & Buliński 2004). Most of them are included in the Polish Red Data Book of Plants (Każmierczakowa & Zarzycki 2001). Limits of distribution of several species of this group cross Pomerania.

Species that are probably extinct in Pomerania

Four of the species that clearly decline in Pomerania are most probably extinct there: *Herminium monorchis*, *Pedicularis sceptrum-carolinum*, *Primula farinosa*, and *Tofieldia calyculata*. None of their records has been confirmed since 1950 (Annex, Figs. A47, A62, A66, A79). *H. monorchis* was earlier reported from 3 localities in the valley of the Brda and 2 localities on the island of Wolin. It was last recorded near Boryń on the island of Wolin in 1925 (Holzfuss 1925) or in Międzyzdroje (Czubiński & Urbański 1951, but it is unclear who and when recorded this species there). Currently this species does not exist in Międzyzdroje (oral communication, Szlachetko 2004), and it is unlikely to be found in Pomerania. *P. farinosa* was known from 2 localities but the one close to Zaspas near Gdańsk has been destroyed, while the other, close to Zieleniewo near Kołobrzeg, has not been confirmed in spite of intensive exploration (Każmierczakowa 2001). Similarly, unsuccessful attempts were made to find *P. sceptrum-carolinum* near Obrowo (Ceynowa-Giełdon 1993) and in the Noteć valley, where also *T. calyculata* was not confirmed (oral communication, Krasicka-Korczyńska 2009). Both the species in Pomerania reach limits of their ranges.

Species endangered in Pomerania

These species in the past were found in Pomerania in more localities but now are confirmed at only one or several sites. This group includes *Baeothryon alpinum*, *Malaxis monophyllos*, *Schoenus ferrugineus*, and *Swertia perennis*. Out of the earlier 10 localities of *B. alpinum*, only one is left now, in the nature reserve “Trzęsacz” (Annex, Fig. A5), while the others are not valid any more (Żukowski 2001). Similarly, *S. perennis*, which reaches in Poland its northern limit, has lost all its North-Pomeranian localities and only in the mire near Obrowo it was present at least till 1996 (oral communication, Ceynowa-Giełdon 2009) (Annex, Fig. A78). Also nearly all localities of *S. ferrugineus* are historical, except for the one located in the Zaborski Landscape Park, reported in the 1990s, so now it needs to be confirmed. This species has apparently died out near Lake Miedwie, where it was recorded in the 1970s. Its other records have not been confirmed for at least 40 years (Annex, Fig. A74). The last species of this group, *M. monophyllos*, whose western limit crosses Pomerania, used to be reported from 27 localities, but in the early 1990s it was recorded only in 3 localities in the valley of the Brda (Boiński 1992; Ceynowa-Giełdon 1993) (Annex, Fig. A56).

Species disappearing quickly from Pomerania

This is a well-defined group of species that quickly decline in Pomerania. These include *Carex chordorrhiza*, *Eriophorum gracile*, *Hammarbya paludosa*, *Liparis loeselii*, *Pinguicula vulgaris*, *Saxifraga hirculus*, and *Stellaria crassifolia*. Poland is crossed by the limits of their ranges of distribution. In the past, these plants were found in at least several dozen localities, but currently are known only from few sites, located mostly in lakelands. Most of the floristic records were made before 1950. Many localities have not been confirmed although field research has been done there, as evidenced by data on other species. *C. chordorrhiza* in Pomerania was found in about 50, generally scattered, localities (Annex, Fig. A12). Over the last nearly 40 years, it was recorded in 10 localities. In one of them it was recorded for the first time in the mid-1990s. By contrast, it has completely died out in 11 localities (Bloch-Orłowska 2007). Similarly, *E. gracile*, was recorded in nearly 80 localities, but in the last 40 years only 13 were confirmed or discovered, including one after 1990 (Annex, Fig. A43). *H. paludosa*, whose southern limit of distribution crosses Pomerania, was recorded in the past in over 80 scattered localities (Annex, Fig. A46). Many of them are probably historical, especially the coastal ones (Bróż *et al.* 2001), except the reserve “Mierzeja Sarbska”. Over the last 40 years, this species was found in 21 localities, but in only 7 after 1990.

L. loeselii was earlier reported from 100 localities in Pomerania (Annex, Fig. A54), but in many of them it probably has died out. It was recorded in 30 localities after the year 1970, and 12 after 1990, including 5 newly discovered ones. Some local populations have disappeared in Gdańsk Coast (oral communication, Szlachetko 2004) and near Lake Miedwie. Historical records have not been confirmed also near the river Noteć (oral communication, Krasicka-Korczyńska 2009). *P. vulgaris* was most frequent in the Kashubian Coast (Pobrzeże Kaszubskie), near the eastern limit of its distribution range. In this area there is also the largest number of historical records (Annex, Fig. A64). During the last 40 years, out of 60 its records, only 11 were confirmed, including 4 newly discovered ones. As many as 90 localities of *S. hirculus* were reported before 1950, including 16 exclusively in the 19th century (Annex, Fig. A72). They are located mainly in the eastern and south-eastern parts of the region. Since the mid-20th century, this species was detected only in 10 localities, including 5 after 1990 (4 of them, in the eastern part of the region, were confirmed historical records, and only the last one, in central Pomerania, was reported for the first time). *S. crassifolia* in Pomerania was found in about 70 localities (Annex, Fig. A76). In the 19th century and the early 20th century it was moderately frequent in the south-eastern part of the region, where for several dozen years most of its localities have not been confirmed, so some of them are probably historical. In all probability it is absent from the coastal zone, where it was recorded before 1950. Its presence has not been confirmed in the Noteć valley (oral communication, Krasicka-Korczyńska 2009). After the year 1970 it was recorded in 16 localities, but in only 6 after 1990, including 3 newly discovered ones.

Species disappearing from some parts of Pomerania

Several species tend to disappear from some parts of Pomerania, e.g. *Carex pulicaris*, *Lycopodiella inundata*, and *Rubus chamaemorus*. In comparison to the former distribution range of *C. pulicaris*, currently a gap is noticeable between its north-western localities and the others, located in the central and north-eastern parts of the region (Annex, Fig. A27). In the nature reserve “Wrzosowisko Sowno” near the town of Płoty, it was recorded as late as in 1977 (oral communication, Jasnowska 2009), but it has not been found there since 1998. By contrast, near Nadarzyce and Głodzino, it was last recorded in the early 20th century (Abromeit *et al.* 1898-1940; Müller 1911), and has not been confirmed since then. Some of its local populations have probably been destroyed as a result of urbanization, e.g. in Gdynia (Preuss 1910) and Sopot (Preuss 1928) near the Bay of Puck, as well as in Pilichowo and Glinki (Müller 1911),

which are now districts of Szczecin city. *L. inundata* in Pomerania was in the past moderately frequent in the east, while in other parts of the region it was scattered (Annex, Fig. A55). However, for over 50 years it was not recorded in the south-western part of the region. In spite of intensive explorations in the nature reserve "Jezioro Cęgi Małe" in the Charzykowy Plain (Sotek *et al.* 2006) and in other favourable sites near Szczecin, this species has not been found there recently. Also many eastern localities reported before 1950 have not been confirmed since then. Some of them are probably historical. *R. chamaemorus*, which reaches in Pomerania the southern limit of its distribution range, was known in this region from 26 localities (Annex, Fig. A70). The westernmost locality, Świdne Bagna on the Baltic island of Usedom (Polish: Uznam), was reported from 1869 (Marsson 1869) to 1958 (Kownas 1958), but in 1966 it was not found there (Piotrowska 1966). Its sites were also destroyed in the Gdańsk Coast: in Sienna Buda, near the village of Werblinia (Czubiński *et al.* 1977). It early disappeared from the Tuchola Forest, where it was recorded in the 19th century, but in the early 20th century it was classified as extinct in this area (Preuss 1907). Currently it sometimes appears on disturbed sites, e.g. on roadsides in Bielawskie Błoto (Kruszelnicki & Fabiszewski 2001).

Species relatively frequent in the
past, now less frequent but also
recorded at new localities

Some of the peatland plant species, although more frequent in the past, currently clearly decline but at the same time are recorded at new sites in Pomerania. This group includes *Carex limosa*, *Epipactis palustris*, and *Scheuchzeria palustris*. For over 50 years, *C. limosa* has not been confirmed in 82 localities, particularly in the eastern and south-western parts of the region, and probably it has died out in some of them (Annex, Fig. A23). However, after the year 1990, it was recorded for the first time at 76 new, generally scattered sites. For *E. palustris*, 57 of earlier records have not been confirmed since 1950, but 33 new ones were discovered after the year 1990 (Annex, Fig. A40). In the Kashubian Coast and Lakeland, in the early 1990s, only 17 records were confirmed out of the 42 reported earlier, whereas 5 were destroyed and the others were not found (mostly those from the 19th century and the early 20th century) (Kowalewska 1995). *S. palustris* was widespread in Pomerania (Annex, Fig. A73). In the 19th and the early 20th century, it was known mostly from the eastern and southern parts of the region, but later it was recorded again in only few localities. Since 1950, as many as 100 localities have not been confirmed. By contrast, after 1990, its 49 localities were recorded for the first time. Its current distribution shows that the spe-

cies is distributed chiefly in the Charzykowy Plain, and partly in the Tuchola Forest and the Bytów Lakeland.

Rare species that have disappeared
from some localities but are also
recorded at new localities

This group is represented in Pomerania by 2 of the 24 species whose dynamic trends were assessed. *Rhynchospora fusca* has here the eastern limit of its distribution range and is known from 36 localities (Annex, Fig. A69). Some of them are probably historical (Herbichowa 1988). However, among the 12 localities reported after 1990, as many as 8 are new: 7 found in the eastern and one in the western part of the region. Another example is *Salix myrtilloides*, which reaches in Pomerania the western limit of its distribution. In the past it was concentrated mostly in the lower Vistula valley (Annex, Fig. A71), but only 3 records have been confirmed (Kępczyński & Rutkowski 1988; oral communication, Rutkowski 2005). After 1970, in Pomerania 7 new localities of this species were discovered, including its 2 westernmost localities.

Species tending to spread

Erica tetralix is regarded as a species that tends to spread and colonize new sites (Pacowski 1967; Jasnowska & Jasnowski 1979; Herbichowa 1998a). Till the mid-20th century it was known from about 70 localities in Pomerania (Annex, Fig. A41), but 30 of them have not been confirmed since then, especially in the Kashubian Coast. However, after 1950, it was recorded for the first time from over 250 localities, and nearly all of them (over 90%) were discovered before 1990, at the time when the peatlands were subject to intensive floristic explorations. It often appears on secondary sites (e.g. Jasnowska & Jasnowski 1979; Herbichowa 1998a; Stasińska & Sotek 2010). Currently many localities need to be confirmed. So far, several localities near Kołobrzeg (Bosiacka 2003) and on the peatland Brzozowe Bagno near Czaplunek have not been confirmed.

5.4. Effect of selected climatic factors on floristic composition of peatlands in Pomerania

Most of climatic variables affect significantly ($P < 0.05$) the floristic composition of Pomerania (Table 7). These include: mean annual amplitudes at the lower ranges of $\leq 17.5^{\circ}\text{C}$ and $17.6-18.0^{\circ}\text{C}$, as well as the upper ranges of $19.1-19.5^{\circ}\text{C}$ and $20.1-20.5^{\circ}\text{C}$ ($P = 0.005$); mean July temperature at the lower range of $16.5-17.0^{\circ}\text{C}$ and the upper range of $18.0-18.5^{\circ}\text{C}$ ($P \leq 0.035$); mean daily maximum temperature in July at the upper ranges of $30.1-30.5^{\circ}\text{C}$, $30.6-31.0^{\circ}\text{C}$, and $31.1-31.5^{\circ}\text{C}$ ($P \leq 0.01$); mean daily minimum temperature in January at the lower ranges of -16.1 to -17.0°C , -17.1 to -18.0°C , and -18.1 to -19.0°C ($P \leq 0.045$); mean precipitation in

Table 7. Significance of climatic variables in explaining the floristic composition of Pomerania, based on Monte Carlo simulations with a zero model tested for 499 permutations

Variable	N	LambdaA	P	F
Jul17.0	470	0.05	0.005	15.7
gs215	541	0.03	0.005	7.28
amp17.5	119	0.02	0.005	5.27
gs210	293	0.02	0.005	7.27
amp18.0	82	0.01	0.005	2.53
amp19.5	446	0.01	0.005	1.77
amp20.5	43	0.01	0.005	2.80
mJul31.0	160	0.01	0.005	1.75
mJul31.5	273	0.01	0.005	4.30
mJan-19	326	0.01	0.005	2.09
pAS325	204	0.01	0.005	1.81
pAS350	506	0.01	0.005	3.87
pY550	249	0.01	0.005	2.72
pY575	387	0.01	0.005	1.75
pY600	185	0.01	0.005	1.80
gs220	212	0.01	0.005	3.96
Jan-1.0	210	0.01	0.005	2.71
mJan-18	269	0.00	0.005	2.06
pY700	181	0.00	0.005	2.02
Jan-2.0	319	0.01	0.010	1.63
mJul30.5	584	0.00	0.010	1.58
Jan-1.5	365	0.00	0.020	1.43
Jul18.5	266	0.01	0.035	1.45
mJan-17	303	0.00	0.045	1.44
amp20.0	79	0.00	0.110	1.33
ae500	163	0.00	0.110	1.23
ae550	570	0.01	0.225	1.13
amp18.5	72	0.00	0.270	1.08
Jan-0.5	31	0.00	0.315	1.12
gs230	12	0.01	0.330	1.05
Jul17.5	471	0.01	0.345	1.07
mJan-15	80	0.00	0.380	1.04
mJul29.5	149	0.00	0.550	0.95
gs225	201	0.00	0.555	0.94
pY650	199	0.00	0.605	0.93
ae600	432	0.01	0.645	0.92
amp19.0	401	0.01	0.690	0.91
pAS400	264	0.00	0.975	0.7
mJan-14.0	13	0.00	0.980	0.64
pAS375	194	0.00	0.990	0.64

Explanations: ae – mean areal evaporation, amp – mean annual amplitude of temperature, gs – growing season length, Jan – mean January temperature, Jul – mean July temperature, mJan – mean daily minimum temperature in January, mJul – mean daily maximum temperature in July, pAS – precipitation April-September, pY – annual precipitation; the numbers after the abbreviations denote the upper limits of ranges, except for growing season length, where they denote lower limits; in Monte Carlo simulations, the following classes were excluded because of their outlier position in the CCA diagram, ae 650 ($n = 96$), Jan -2.5 ($n = 336$), Jul 18.0 ($n = 266$), mJan -16.0 ($n = 303$), mJul 30 ($n = 95$), pAS 450 ($n = 93$), pY 750 ($n = 60$)

April-September at the lower ranges of ≤ 325 mm and 325-350 mm ($P = 0.005$); mean annual precipitation at the ranges of 525-550 mm, 550-575 mm, 575-600 mm, and 650-700 mm ($P = 0.005$); growing season length: 210-215, 215-220, and 220-225 days ($P = 0.005$); and mean January temperature at the medium ranges of -0.6 to -1.0°C, -1.1 to -1.5°C, and -1.6 to -2.0°C ($P \leq 0.02$).

Temperature variables

Temperature variables are significantly related to the occurrence of some Pomeranian peatland plants. The

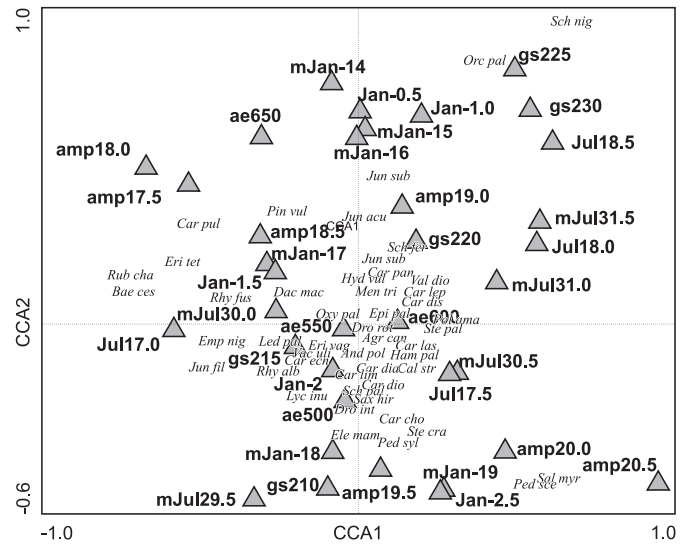


Fig. 23. Distribution of Pomeranian peatland plant species and temperature variables, areal evaporation, and growing season length along the first and second axis of canonical correspondence analysis (CCA)

Explanations: ae – mean areal evaporation, amp – mean annual amplitude of temperature, gs – growing season length, Jan – mean January temperature, Jul – mean July temperature, mJan – mean daily minimum temperature in January, mJul – mean daily maximum temperature in July; species abbreviations are composed of the first 3 letters of generic and specific names

main gradient of variation along the first CCA axis runs from low annual amplitudes, low July temperatures, and medium January temperatures, to high values of mean daily maximum temperature and mean temperature in July (Fig. 23). Many peatland plant species, especially those associated with the class *Oxycocco-Sphagnetea*, gravitate towards the left side of the diagram, i.e. the squares and areas associated with colder summers. The greatest preference for these areas is shown by *Baeothryon*

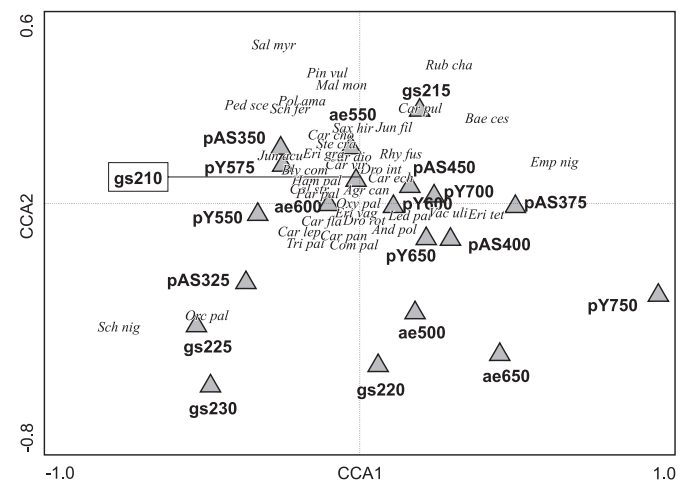


Fig. 24. Distribution of Pomeranian peatland plant species and precipitation variables, areal evaporation, and growing season length along the first and second axis of canonical correspondence analysis (CCA)

Explanations: ae – mean areal evaporation, gs – growing season length, pAS – precipitation April-September, pY – annual precipitation; species abbreviations are composed of the first 3 letters of generic and specific names

cespitosum, *Erica tetralix*, and *Rubus chamaemorus*. Areas with low annual amplitudes are preferred by *Carex pulicaris*.

Gradient of the second CCA axis runs from high mean values of daily minimum temperature in January ($\geq -14^{\circ}\text{C}$) and the highest (i.e. warmest) mean January temperature, associated with the highest mean temperature in July and the longest growing season, to the lowest values of mean daily maximum temperature in July, lowest values (i.e. coldest) of daily minimum temperature and mean January temperature, with the highest mean annual amplitude of temperature and the shortest growing season. This coldest range of temperature variables is optimal for *Pedicularis sceptrum-carolinum* and *Salix myrtilloides*. In the range defined by warm winters and hot summers, conditions are favourable for *Orchis palustris* and *Schoenus nigricans* (Fig. 23).

Precipitation variables

Precipitation variables are strongly and significantly related to the occurrence of peatland plant species in the study area. The main gradient of species distribution runs from low precipitation (both annual and in April-September) and long growing seasons, to the highest annual precipitation (Fig. 24). *Orchis palustris* and *Schoenus nigricans* are associated with low precipitation.

Season length

The second CCA axis is designated by a gradient associated with growing season length. In the areas where its length is minimum (=210 days), some species are more frequent than elsewhere, e.g. *Carex echinata*, *C. viridula*, and *Drosera intermedia*. A short growing season, lasting 210-215 days, is preferred by *Rubus chamaemorus*, *Carex pulicaris* and, to a lesser extent, by *Baeothryon cespitosum*. By contrast, *Orchis palustris* and *Schoenus nigricans* are found mostly in areas with the longest growing season (Fig. 24).

6. Discussion

6.1. History of migrations of peatland plant species in Pomerania in the late glacial period and the Holocene

Current palaeobotanical research brings us closer to answering questions about the time of arrival and routes of plant migration onto the areas exposed after the last glacial period. Particularly important sources of knowledge are isopol maps of individual species of trees, shrubs, and some herbaceous plants (Huntley & Birks 1983; Ralska-Jasiewiczowa 1983, 1999; Ralska-Jasiewiczowa *et al.* 2004), showing synthetic results of pollen analysis. Frequently, macroscopic plant remains are analysed in parallel, which allows identification of the plant material to species level. In the reconstruction

of the postglacial vegetation history not only results of palynological research are used, but also indirect data, e.g. palaeoclimatic, geomorphological, and information on the current distribution ranges of species, their ecological spectrum, and biological properties (e.g. Fałtynowicz 1991; Zając M. 1996; Popiela 2004).

However, it must be noted that direct extrapolation of current data far into the past, especially of those concerned with ecological preferences of species, may be misleading. Over the long time that has passed since the late glacial period, individual species could change their ecological spectra. Moreover, some of the species could be also components of non-analog communities, whose species composition differed from that of currently known communities (Williams & Jackson 2007). Nevertheless, research has revealed a high similarity of postglacial vegetation to present-day tundra, cold steppe, and taiga. Examples include the postglacial vegetation in Eastern-Central Europe compared with current plant formations of southern Siberia (Kuneš *et al.* 2008), and the postglacial vegetation of wetlands of Poland compared with the vegetation of peatlands of present-day tundra (Kloss & Żurek 2004).

The questions of routes and time of plant migration in the postglacial period into Pomerania were first discussed in the early 20th century by Wangerin (1920, 1923) and Leick (1926), followed by Szafer (1930, 1935), and Czubiński (1950). A lot of information on this subject has been provided by modern palaeobotanical studies e.g. those conducted by Tobolski (1987), Latałowa (2003b), Ralska-Jasiewiczowa *et al.* (2004), and Milecka (2005). They allowed verification of some earlier hypotheses. An attempt to reconstruct the postglacial history of lichen flora of Pomerania was made by Fałtynowicz (1991), while of herbaceous forest species, by Popiela (2004).

In this study, the above questions are considered in relation to peatland plants. The considerations are based on the available direct and indirect data. Apart from palaeobotanical, palaeoclimatic, and palaeoecological data, also the general range of the studied species and their distribution in Poland and Pomerania were taken into account, as well as their biological properties, ecological preferences, and phytocoenotic spectrum. Moreover, attention was paid to analogous relationships between the current plant formations, where the studied species are found, and the vegetation of the late glacial period (the end of the Pleistocene) and the Holocene. I also made use of results of biogeographic studies and relationships between fungal markers (microfungi) and some of the species considered here. When assessing the most probable directions of species migrations, important hints were often provided by their range limits, especially those crossing Poland. Because of the small available amount of direct palaeobotanical data, the

considerations below are hypothetical for most of the species.

Pleistocene: late glacial period

During the last glacial period, the whole Pomerania was covered by the ice sheet. Thus, no refugia were left there. Considering this, it seems that the *tabula rasa* hypothesis can be accepted for this region. This means that after complete elimination of the earlier biota, this area was recolonized from scratch by plants and animals when the ice sheet retreated.

Initially, plant succession depended exclusively on climatic and site conditions, as there was no competition. This favoured the plants of cooler climates, which did not need to base their life strategies on high competitiveness (see section 5.1.7). Most probably, plant migration from remote refugia was easy at that time (Ralska-Jasiewiczowa 1999). This led to the colonization of Pomerania by plants characteristic of tundra. The newcomers at that period formed the so-called dryas flora (Iversen 1973). The presence of *Empetrum nigrum* in this region since the late glacial period (Alleröd and Younger Dryas) is confirmed by palaeobotanical data (e.g. Latałowa 1982, 1999; Marsz & Tobolski 1993) and fungal markers (Chlebicki 2002). According to Popiela (2004), this species probably immigrated to this region from the south. At the sites that were not waterlogged, patches of moist tundra were spreading. In such conditions, *Rubus chamaemorus* appeared near the present area of the Szczecin Lagoon (Zalew Szczeciński) and Kramarzyny in Pomerania (Latałowa & Święta 2003; Marek 1991). It is found mostly in areas with cool summer and short growing season (see section 5.4, Figs. 23 and 24). The presence of *Saxifraga hirculus* in the late glacial period is evidenced by its pollen in peat deposits dating back from this period in the peatland Siwe Bagno in Chojnice County (after Tobolski 1975/1976).

At that time, also many other species, currently found in tundra and associated with peatlands, could arrive in Pomerania. This applies to *Andromeda polifolia*, *Baeothryon alpinum*, *Carex brunescens*, *C. chordorrhiza*, *C. heleonastes*, *Eriophorum vaginatum*, *Ledum palustre*, *Pedicularis sceptrum-carolinum*, *Salix myrtylloides*, *Stellaria crassifolia*, *Vaccinium uliginosum*, and *Viola epipsila*. Most of them, except *A. polifolia*, *E. vaginatum*, and *V. uliginosum*, were classified by Czubiński (1950) as glacial relicts. Their general distribution reach far north. This suggests that they are very resistant to low temperatures. Currently only *A. polifolia*, *E. vaginatum*, *L. palustre*, and *V. uliginosum* are relatively frequent in Pomerania, while the others are rare, and some of them decline there (see section 5.3). In the late glacial period, they could be more widespread (because of little or no competition with other species) and could participate in communities of moist

tundra. Many of the plants prefer areas with a shorter growing season and generally lower air temperature (see section 5.4, Fig. 23). Because of this, the cool climate of the postglacial period created favourable conditions for their migration. Most of the above-mentioned plant species are dispersed by wind, which facilitates the colonization of new areas. Pomerania was colonized probably mostly from the east and south-east by, e.g. *P. sceptrum-carolinum*, *S. myrtylloides*, and *V. epipsila*. Similarly, *C. heleonastes* could derive from European refugia in the south or the east. Such directions of migrations are suggested by the distribution patterns of these species in Pomerania and all over Poland, as well as by their general ranges. Some of the species reach their western or southern limit of distribution in Poland, often in Pomerania (see section 5.1.3) or near its borders.

Both palynological data and information on macroscopic plant remains document the existence of bog communities in Pomerania in the late Pleistocene. They were composed mostly of *Carex* spp., *Menyanthes trifoliata*, *Comarum palustre*, and *Ranunculus flammula* (Latałowa 1982, 1999; Marek 1991; Marsz & Tobolski 1993; Latałowa *et al.* 2003; Milecka 2005). They developed in the telmatic (i.e. periodically flooded) zone of water bodies. The sedges present there at that time included *Carex canescens*, *C. lasiocarpa*, *C. limosa*, *C. nigra*, and *C. rostrata* (Latałowa 1982, 1999; Marek 1991, 1994; Marsz & Tobolski 1993). All of them are eurytopic. It seems possible that the above plants could migrate from various directions into the study area, and spread widely since the Younger Dryas. They have extensive ranges and currently are frequent or moderately frequent in Pomerania (Annex). In the late Pleistocene or early Holocene, *Viola palustris* was also already present in this region. Its pollen grains were found in deposits dating back from the Younger Dryas in the mire near Lake Żarnowieckie on the river Piaśnica (Latałowa 1982).

In the late glacial period, the young soil cover was alkaline and relatively rich in calcium carbonate. Moss or sedge peat was frequently accumulated then. This may indicate that communities of low sedge mires (mostly of order *Caricetalia davallianae*) developed there. Considering this, *Parnassia palustris* had favourable conditions for expansion. Its presence is detected in materials dating back from the late glacial period near Lake Wielkie Gacno (Hjelmroos-Ericsson 1981). *Swertia perennis* probably accompanied it in the migration into Pomerania. Both the species were recorded in pollen diagrams in soil samples from the Oldest Dryas collected from Lake Gościąż, located SE of Włocławek, near the borders of Pomerania (Ralska-Jasiewiczowa *et al.* 1998).

Schoenus-like pollen grains, dating back from the late Pleistocene, were found in sediments of Lake

Ostrowite, in the Tuchola Forest (Milecka 2005). Presumably, it was *Schoenus ferrugineus*, classified by Czubiński (1950) as a glacial relict, component of the so-called dealpine meadows at the Baltic coast (Meusel 1943). Its scattered distribution may suggest that it was present in the study area for a very long time. It immigrated to Pomerania from the south, i.e. from its localities in the Wielkopolska region, or from the west, i.e. from its German localities (map in Benkert *et al.* 1998). In Younger Dryas deposits of Lake Żarnowieckie *Carex* nuts of the *flava* group were found (Latałowa 1982). Sedges of this group are often associated with calcium-rich soils. Their current ranges suggest that both *Carex flava* and *C. viridula* could be found there. They are Circum-Boreal taxa, and their ranges reach the northern edges of Scandinavia (Hultén 1964). They migrated to Pomerania probably from the south or south-east. Perhaps at the same time, *Carex buxbaumii*, *C. dioica*, and *Eriophorum latifolium* also arrived in this region. They find favourable conditions in eutrophic low sedge mires of the order *Caricetalia davallianae*. Their ranges reach in Scandinavia as far as 70°N. Moreover, the range of *E. latifolium* is very similar to the ranges of *C. flava* and *C. viridula*. This may suggest a similar rate of migration. On the basis of their distribution in other parts of Poland and in Pomerania, it can be assumed that *C. buxbaumii* and *E. latifolium* invaded the study area from the south-east, while *C. dioica* from the north-east. Probably at that time *Primula farinosa* could arrive there from the mountains of Central Europe. This species is also listed by Czubiński (1950) among glacial relicts. Currently it is absent from all its former lowland localities in Poland. Also *Pinguicula vulgaris* could then find there favourable conditions for migration (availability of suitable habitats and low competition). Wangerin (1923) was convinced that it arrived early in Pomerania, and considered it as a glacial relict in this region.

In the Younger Dryas some mountain species appeared in the Tuchola Forest, e.g. *Pleurospermum austriacum* and *Lycopodium selago* (Tobolski 1975/1976). Perhaps at that time the plants migrating into Pomerania included also another mountain species found in the lowlands – *Tofieldia calyculata*. In contrast to the 2 above-mentioned species, it is associated with peatlands. In pollen diagrams from Lake Gościąg in the Vistula river valley, the genus *Tofieldia* was recorded from the Oldest Dryas till the end of Bölling (Ralska-Jasiewiczowa *et al.* 1998). This could be *T. calyculata*, the only member of this genus in the present flora of Poland. This seems to document its migration route from the south-east, along the Vistula Valley, towards the Brda valley, where all its Pomeranian localities are concentrated. Considering the relatively small distance from Lake Gościąg to Pomerania, as well as its effective seed dispersal (e.g. by wind) and the lack

of barriers, it can be presumed that *T. calyculata* appeared early. Czubiński (1950) considered it as a glacial relict found in fens rich in calcium. He listed it among plants migrating to the lowlands from the mountains of West and Central Europe. According to Zajac M. (1996), *T. calyculata* was present in lowlands at least since the Pre-Boreal period. She noted also that some of its local populations could be even older.

Holocene:

(a) Pre-Boreal period

In the early Holocene, due to ice melt, numerous lakes and shallow water bodies were formed in the areas exposed by the retreating ice sheet. Peat deposits gradually accumulated in them. In many places, local site conditions favoured the development of communities dominated by mosses or low sedges. Probably at that time, if not earlier, the flora of Pomerania could be enriched with species like *Agrostis canina*, *Baeothryon cespitosum*, *Calamagrostis stricta*, *Carex diandra*, *C. pauciflora*, *Juncus alpino-articulatus*, *J. filiformis*, and *Scheuchzeria palustris*. Their general ranges are extensive and reach far north. On the basis of the distribution of most of these species, it is difficult to hypothesize about directions of their migrations. However, it seems probable that they could arrive in this region from various directions simultaneously. The presence of *C. diandra* at that time is documented by macroscopic plant remains originating from peat deposits near Lake Żarnowieckie (Latałowa 1982). Pollen grains of *S. palustris* were recorded already in late Pre-Boreal deposits in the Tuchola Forest (Filbrand-Czaja 2009). A mountain species “descending” to lowlands, *C. pauciflora*, according to Zajac M. (1996) could be present in Polish lowlands at least since the Pre-Boreal period (as older localities are possible). It immigrated to Pomerania from the mountains or from the north-east, as indicated by its distribution in Poland (Zajac A. & Zajac M. 2001) and in Germany (Benkert *et al.* 1998). In Poland it is found in the south (mountains) and in the north (Suwałki Region, Warmia, Kashubian Lakeland, and Słowińskie Coast), while in eastern Germany it is reported only from mountains in the south.

(b) Boreal period

Probably in the early Boreal or late Pre-Boreal period (or even earlier), *Eriophorum angustifolium*, *E. gracile*, *Drosera rotundifolia*, *Oxycoccus palustris* (*Vaccinium oxycoccus*) and some other species could arrive in Pomerania. These species are Circum-Boreal, associated with raised bogs and low sedge mires. It is difficult to determine the possible direction of their migration into the study area. They could invade it simultaneously from several directions. Palaeobotanical data confirming

the presence of *E. angustifolium* and *O. palustris* near Żarnowiec, date back from the early Boreal period (Latałowa 1982). Probably at that time *Herminium monorchis* was already present in Pomerania. It could immigrate from the east or south-east. Its early arrival is suggested not only by its Euro-Siberian-Asiatic range but also by some gaps in it, e.g. in Poland and in Germany. It has disappeared nearly completely from Poland, except for one confirmed local population in Masuria (Zajac A. & Zajac M. 2001). Similarly, in eastern Germany only one lowland locality was preserved and several in the mountains (Benkert *et al.* 1998). At an earlier phase of the Boreal period, dense forests were not formed yet. The telmatic (i.e. periodically flooded) zone of water bodies was covered by tall emergent vegetation (e.g. reedbeds and tall sedges). At their edges, small patches of peatlands developed. This is reflected in the presence of *Sphagnum* spores found in sediments from that period. Thus the availability of suitable sites and the lack of barriers, in the form of dense forests, as well as climatic conditions, could be favourable for migrations of plants that are now classified as Euro-Siberian (*Pedicularis palustris*, *Stellaria palustris*) or Circum-Boreal (*Carex echinata*, *Drosera anglica*, *Triglochin palustre*, and *Veronica scutellata*), or represent connective elements: Euro-Siberian-Mediterranean-Irano-Turanian (*Dactylorhiza incarnata*) and Euro-Siberian-Irano-Turanian (*Carex panicea*). Their ranges reach far south. It cannot be excluded that some of the species appeared in Pomerania earlier than in the Boreal period. Most of them, probably, migrated into this region from various directions, e.g. from the south-east and the north-west, as indicated by the concentration of their localities in those regions.

The group of riparian forests plants migrating from the east could include *Dactylorhiza maculata*. Currently it is associated with riparian forests, fens, transitional bogs, and wet meadows. The mountain species *Malaxis monophyllos* also could migrate from the east, as indicated by its present distribution (western limit at the Polish-German border, many localities in north-eastern Poland, a clear disjunction in Central Polish Lowlands). Zajac M. (1996) suggests that this species “descended” to the lowlands in the Boreal period. At that time it could appear in Pomerania, as a component of communities of fens and transitional bogs. It could also grow in moist deciduous forests (class *Quercus-Fagetea*).

In the early Boreal period, when temperature and humidity gradually increased, perhaps also some other peatland plant species appeared, e.g. *Blysmus compressus*, *Eleocharis mamillata*, *E. quinqueflora*, *Epipactis palustris*, *Hammarbya paludosa*, *Polygala amarella*, and *Rhynchospora alba*. These plants do not reach far north. In Scandinavia, as a rule, they are not found in the areas where growing season is shorter than

140 days (Hultén 1964, 1971). They could immigrate to Pomerania from the south-east. This applies particularly to *E. mamillata* and *P. amarella*, as their localities are concentrated in this part of the region, while their western limits of distribution are in eastern Germany, close to the Polish border. *E. palustris* and *H. paludosa* migrated most probably from the east. At the same time, also *Liparis loeselii* could arrive in Pomerania from the east or south-west, as the environmental and climatic conditions were favourable then. It is found on soils rich in nutrients, containing calcium carbonate. According to Summerhayes (1985), it thrives in regions with abundant rainfall and it tolerates extreme temperatures (low in winter, high in summer).

The first Atlantic species, e.g. *Carex lepidocarpa*, *Drosera intermedia*, and *Rhynchospora fusca*, could appear in the late Boreal period, when temperature and humidity in the study area were even higher. They migrated from the west. *C. lepidocarpa* entered Pomerania probably from Mecklenburg. The current distribution of the other 2 species indicates that their route led through Lusatia and Brandenburg to Pomerania and to the south of Poland. The early arrival of *R. fusca*, at the time when humidity started to increase, was suggested already by Czubiński (1950), on the basis of its Eastern European records, reaching far inland. This hypothesis is confirmed also by the spectrum of its ecological preferences. As a stenotopic species, it is sensitive to competition. Both in Poland and in West Europe it is characterized by a very narrow phytocoenotic spectrum (Dierssen 1982; Herbichowa 1988), which limits the possibilities of its migration.

(c) Atlantic period

During the Holocene climatic optimum, the area could be invaded by species that reach in Poland or close to it their eastern or south-eastern limits of distribution, and whose main ranges of distribution cover most of the West and Central Europe. The group of taxa reaching in Poland or close to it the eastern limit includes, e.g. *Carex distans*, *C. hostiana*, *C. pulicaris*, *Erica tetralix*, *Juncus acutiflorus*, *J. subnodulosus*, *Lycopodiella inundata*, and *Pedicularis sylvatica*, whereas, *Hydrocotyle vulgaris* has its south-eastern limits here. These plants immigrated to Pomerania mostly from the west or south-west. Climatic conditions at that time were favourable for their migrations. An example is *J. subnodulosus*, which is sensitive to frost and high temperature variation (Tobolski 1997a). A clear relationship with the mild and humid maritime climate is noticed in *E. tetralix*. In SE Norway it prefers warm, moist areas (Økland 1989). In Pomerania it is found mostly at the sites with a high mean annual precipitation, exceeding 600 mm, and high precipitation in April-September (section 5.4, Fig. 24). It is sensitive to water

deficits in summer, but in winter it is highly resistant to frost (< -20°C) (Bannister 1966; Bannister & Polwart 2001). Its isolated localities reach as far as the Arctic Circle, near the western coasts of Scandinavia. According to Herbichowa (1998a), this species has only recently become a member of the flora of Pomeranian peatlands. A relationship with the mild climate is noticed also in *C. pulicaris*, which in Pomerania exists mostly in the areas characterized by low annual amplitudes of temperature (section 5.4, Fig. 23). The presence of *L. inundatum* in the study area in the Atlantic period is evidenced by palynological data from the Darżlubie Forest (Latałowa 1982). Many fruits and pollen grains of *H. vulgaris* were found in Sub-Boreal sediments from the peatlands in the Darżlubie Forest and near Lake Żarnowieckie (Latałowa 1982). This, however, does not exclude the possibility of its arrival in Pomerania even earlier, in the Atlantic period.

The flora of Pomeranian peatlands during the climatic optimum could be enriched also with *Carex davalliana* and *Valeriana dioica*. The former species apparently immigrated from the south, as indicated by its distribution in Poland and Germany. In Pomerania it is very rare, reaching here its northern limit. It is associated with spring-water mires. By contrast, *V. dioica*, which reaches in Poland the north-eastern limit of its main range, could immigrate to Pomerania from various directions simultaneously. It is characterized by a wide phytocoenotic spectrum.

The Atlantic period is probably also linked with the immigration of *Orchis palustris* and *Schoenus nigricans*, as indicated by their general ranges and distribution in Poland and in Pomerania. Currently they are found mostly in a part of the region, characterized by warm winters, hot summers, and the longest growing season (section 5.4, Fig. 3). They are associated with low sedge mires of the alliance *Caricion davallianae*. Their phytocoenotic optimum is in the same association: *Orchido-Schoenetum*. In Europe, their northernmost localities are found only at the southern edges of Scandinavia. They could immigrate to Pomerania from the west, from the adjacent German Lowland.

Among the peatland plant species analysed in this study, no attempt was made to determine the time of migration of *Chamaedaphne calyculata*. According to Chlebicki (2002), in Polish sites of this species, the presence of Sub-Arctic (Boreal) fungal markers confirms that it is a glacial relict in Poland. However, it arrived relatively recently in the Drawa National Park (nature reserve "Sicienko"), i.e. at its westernmost locality in Europe (Latałowa 2001).

The estimated times of arrival of peatland plant species in Pomerania are summarized in Table 8.

A characteristic feature of the analysed group of peatland plant species associated with the class *Oxycocco-*

Table 8. Estimated time of immigration of peatland plant species into Pomerania

Pleistocene: late glacial period	
<i>Andromeda polifolia</i>	<i>Ledum palustre</i>
<i>Baeothryon alpinum</i>	<i>Menyanthes trifoliata</i> ¹
↑ <i>Carex buxbaumii</i>	<i>Parnassia palustris</i> ¹
<i>Carex brunescens</i>	<i>Pedicularis sceptrum-carolinum</i>
<i>Carex canescens</i> ¹	<i>Pinguicula vulgaris</i>
<i>Carex chordorrhiza</i>	<i>Primula farinosa</i>
↑ <i>Carex dioica</i>	<i>Ranunculus flammula</i> ¹
<i>Carex flava</i>	↑ <i>Rubus chamaemorus</i> ¹
↑ <i>Carex heleonastes</i>	↑ <i>Salix myrtylloides</i>
<i>Carex lasiocarpa</i> ¹	<i>Saxifraga hirculus</i> ¹
<i>Carex limosa</i> ¹	<i>Schoenus ferrugineus</i>
<i>Carex viridula</i>	<i>Stellaria crassifolia</i>
<i>Carex nigra</i> ¹	<i>Swertia perennis</i>
<i>Carex rostrata</i> ¹	↑ <i>Tofieldia calyculata</i>
<i>Comarum palustre</i> ¹	<i>Vaccinium uliginosum</i>
<i>Empetrum nigrum</i> ¹	<i>Viola epipsila</i>
↑ <i>Eriophorum latifolium</i>	<i>Viola palustris</i> ¹
<i>Eriophorum vaginatum</i>	
	Holocene: (a) Pre-Boreal period
<i>Agrostis canina</i>	↓ <i>Carex pauciflora</i>
<i>Baeothryon cespitosum</i>	<i>Juncus alpino-articulatus</i>
<i>Calamagrostis stricta</i>	<i>Juncus filiformis</i>
<i>Carex diandra</i> ¹	<i>Scheuchzeria palustris</i> ¹
	Holocene: (b) Boreal period
<i>Blysmus compressus</i>	↓ <i>Eriophorum gracile</i>
<i>Carex echinata</i>	<i>Hammarbya paludosa</i>
* <i>Carex lepidocarpa</i>	<i>Herminium monorchis</i>
<i>Carex panicea</i>	<i>Liparis loeselii</i>
<i>Dactylorhiza incarnata</i>	<i>Malaxis monophyllos</i>
<i>Dactylorhiza maculata</i>	↓ <i>Oxycoccus palustris</i> ¹
<i>Drosera anglica</i>	<i>Pedicularis palustris</i>
* <i>Drosera intermedia</i>	<i>Polygala amarella</i>
↓ <i>Drosera rotundifolia</i>	<i>Rhynchospora alba</i>
<i>Eleocharis mamillata</i>	* <i>Rhynchospora fusca</i>
<i>Eleocharis quinqueflora</i>	<i>Stellaria palustris</i>
<i>Epipactis palustris</i>	<i>Triglochin palustre</i>
↓ <i>Eriophorum angustifolium</i> ¹	<i>Veronica scutellata</i>
	Holocene: (c) Atlantic period
<i>Carex davalliana</i>	<i>Juncus subnodulosus</i>
<i>Carex distans</i>	<i>Lycopodiella inundata</i> ¹
<i>Carex hostiana</i>	<i>Orchis palustris</i>
<i>Carex pulicaris</i>	<i>Pedicularis sylvatica</i>
<i>Erica tetralix</i>	<i>Schoenus nigricans</i>
↑ <i>Hydrocotyle vulgaris</i>	<i>Valeriana dioica</i>
<i>Juncus acutiflorus</i>	

Explanations: bold-faced species associated with the class *Oxycocco-Sphagnetea*, while all the others associated with the class *Scheuchzerio-Caricetea nigrae*, ↓ – could immigrate earlier, ↑ – could immigrate later, * – probably immigrated in the late Boreal period, ¹ – based on palaeobotanical data

Sphagnetea, is the prevalence of chamaephytes and hemicryptophytes in the spectrum of life-forms (see section 5.1.4). This is associated with their distribution not only in the temperate zone but also in the Sub-Arctic (Boreal) zone. Considering that they are adapted to the harsh climatic conditions, and simultaneously are less competitive than other plant species, probably most of them could immigrate to Pomerania in the late glacial period or in the early Holocene (Table 8). Transportation from remote refugia was possible thanks to their effective seed dispersal, e.g. by wind (anemochory) and by animals (epizoochory). At that time, in the study area, particularly in patches of moist tundra, they found

favourable growth conditions, enabling their reproduction. These plants usually represent life strategy CS, and thus are adapted to moderate stress which limits competition (Annex). Similarly, many species associated with the class *Scheuchzeria-Caricetea nigrae* probably also immigrated to Pomerania in the late glacial period and early Holocene (Table 8). They were often associated with the telmatic zone of the water bodies created at that time, as well as with waterlogged sites and with young postglacial soils, rich in calcium carbonate. Most of the species are widely distributed, e.g. Circum-Boreal or Euro-Siberian, reaching far north. This suggests that they can tolerate a short growing season as well as cold and waterlogged or wet soils. Their diaspores can be transported over large distances, because they are mostly dispersed by wind and/or birds (Annex). These plants are adapted to conditions of moderate stress, which limits competition (strategy CS), or additionally also with a moderate level of disturbance (strategy CSR) (Annex). Thus they could find favourable conditions for migration and development in Pomerania in the late glacial period and the early Holocene, not only because of favourable sites but also because of little or no competition.

Peatland plants, like aquatic plants, are the first symptoms of improved climatic conditions, as they often migrate quickly and react faster than trees to higher temperatures (Iversen 1954). Considering this, it seems likely that species of the above classes, distinguished by high thermal requirements and associated with this specific habitat type, could immigrate to Pomerania already in the late Boreal period or at the beginning of the climatic optimum.

The improved climatic conditions in the late Boreal period and in the Atlantic period caused changes in hydrological conditions. This contributed to the elimination of many sites of bog plant species. Such a phenomenon was recorded also in some pollen diagrams, as conspicuous declines of these species or even their temporary absence (e.g. Latałowa 1982; Schubert 2003). In the next 2 periods – Sub-Boreal and Sub-Atlantic – as a result of gradual cooling and increasing humidity, the processes of peat accumulation and formation of ombrotrophic raised bogs were intensified (Latałowa & Tobolski 1989; Latałowa 2003b). Thus it seems possible that some of bog plant species could disappear partly or completely from Pomerania in unfavourable conditions, but later on, when suitable sites became available, they migrated into this region once again. A probable example is *Rubus chamaemorus*, which in Pomerania was already present in the late glacial period. It could immigrate to north-west Poland in that period from the Jutland peninsula, which was only partly covered by the ice sheet during the last glaciation (Jacobsen 1984). At present in Jutland it is recorded in

areas of the late glacial raised sea-floor (Vestergaard & Kjeld 1989). It also cannot be excluded that it migrated from eastern refugia, e.g. from the glacial refugia in the lowland of East Europe and the Ural Mountains (Ehrich *et al.* 2008). However, it seems unlikely that it migrated from southern Europe. The low level of genetic variation of the population of *R. chamaemorus* in Europe, and the lack of rare markers, questions the presence of southern glacial populations. Considering this, it has been hypothesized that its southern records in Poland (Koczur 2004) and in Germany (Taylor 1971) may be scattered localities of long-distance colonizers, rather than glacial relicts (Ehrich *et al.* 2008).

In north-eastern Pomerania, *Rubus chamaemorus* seems to be a new arrival, as indicated, e.g. by its local populations in Kluki, near Lisia Góra (at the SW edge of Lake Łebsko), in Słowińskie Błoto, Janiewickie Bagno, and Bielawskie Błoto. Tobolski (1981, 1987, 1997b), on the basis of research on vegetation history of the Gardno-Łeba Lowland, believes that this species could colonize the peatlands in Kluki and near Lisia Góra not earlier than in the early Sub-Boreal period, and in the Sub-Atlantic period, when the association *Vaccinio uliginosi-Betuletum pubescentis* appeared there. By contrast, Słowińskie Błoto and Janiewickie Bagno relatively recently, i.e. about 2000 years ago, became ombrotrophic, which then favoured its colonization by *R. chamaemorus* (Herbichowa 1997, 1998a, 1999). Its local populations in Bielawskie Błoto are also young, as the peatland started to be formed as late as at the end of the climatic optimum (Czubiński *et al.* 1954). Currently, this species in peatlands appears more and more frequently on sites disturbed by humans, e.g. near drainage ditches or near sites of peat extraction, and it is initially expansive there (Czubiński *et al.* 1954; Scholz 1968; Herbichowa 1998a). This species is recorded in Pomerania mostly in the north-east (Annex, Fig. A70). This suggests that during the period of unfavourable climatic conditions and in the absence of suitable sites, it could at least partly, if not completely, disappear from this region and reappear in the late Atlantic or early Sub-Boreal period. Probably it immigrated then from the north-east.

The chorotypes of peatland plant species, distinguished in this study, are groups of species that have similar distribution patterns in Pomerania, but also often have similar ecological preferences, and some of them belong to the same type of general distribution range. Considering this, some of the grouped species could have a similar history of migrations in Pomerania. When analysing individual chorotypes, it can be concluded that this assumption applies only to some groups, but usually not to all species within a group. However, there are some chorotypes grouping species that could arrive in Pomerania in the same period. An example is

the eastern type, *Salix myrtilloides* subtype (see section 5.2.2, Table 6). The species belonging to this group probably immigrated to the study area already in the late glacial period. They probably migrated by various routes, as indicated by their general ranges and distribution in Poland. Despite this, it seems that at least 3 of them (*Pedicularis sceptrum-carolinum*, *Salix myrtilloides*, and *Tofieldia calyculata*) immigrated to Pomerania from the south-east, as suggested, e.g. by concentration of their records. Moreover, *P. sceptrum-carolinum* and *T. calyculata* have similar habitat preferences and similar patterns of distribution (their sites are found mostly in the valley of the Brda). This may suggest a similar time of their migration and spread. Another example is the all-Pomeranian type, *Rhynchospora alba* subtype. Plants of this subtype (see section 5.2.2, Table 6) probably were present in the study area for a long time. Most of them could arrive already in the late glacial period, and are associated mostly with patches of moist tundra (e.g. *Eriophorum vaginatum*, *Ledum palustre*, and *Vaccinium uliginosum*). Presumably, *Drosera rotundifolia*, *Oxycoccus palustris*, and *Rhynchospora alba* were the latest immigrants of this group, which reached Pomerania in the late Pre-Boreal period or the early Boreal period. These species are associated with peatlands. Similarly, species representing the all-Pomeranian type, *Carex rostrata* subtype (see section 5.2.2, Table 6), could also appear early in Pomerania. Some of them were present already in the late glacial period (*Carex canescens*, *C. lasiocarpa*, and *C. rostrata*), probably as components of tall sedge communities. The latest immigrants of this group, which could arrive in the Boreal period, were: *Carex echinata*, *Stellaria palustris*, and *Veronica scutellata*. These plants are associated mostly with acid low sedge mires. By contrast, late newcomers probably include both species of the western chorotype: *Orchis palustris* and *Schoenus nigricans*. Because of their ecological preferences, they probably arrived in the Atlantic period. On the basis of their general distribution it seems that they could immigrate to Poland by various routes. However, they probably migrated from the same area – the German Lowland. They arrived in Poland probably roughly in the same period. This is suggested by their similar distribution patterns not only in Pomerania but all over Poland, and by their phytocoenotic optimum in the same community type.

Certainly also currently the peatland plant species are migrating, as indicated by some of their recent records. An example is *Ledum palustre*, which was found in the soil reserve “Bielice Gackie” on a dune slope – a habitat typical for the Boreal zone (Tobolski 1997b). Some of the studied species now tend to expand their distributional ranges. These include, e.g., *Erica tetralix* (see section 5.3, Annex, Fig. A41), found also

on sites disturbed by human activity (Pacowski 1967; Jasnowska & Jasnowski 1979; Herbichowa 1998a; Stasińska & Sotek 2010).

The current progress in palaeobotany, palaeoecology, and palaeoclimatology, provides more and more new data. This allows a much more reliable reconstruction of vegetation history in the late glacial period and the Holocene. Besides, research on the genetic variation of populations and distribution patterns of haplotypes may help to estimate the time and directions of species migrations in the past. Thus it can be expected that in the near future at least some of the above hypothetical considerations will be verified.

6.2. Decline of peatland plant species in Pomerania

The gradual disappearance of many peatland plant species in Poland has been observed for a long time but its rate has increased in the last few decades (e.g. Czubiński *et al.* 1954; Polakowski 1962; Jasnowski *et al.* 1968; Jasnowski 1972; Herbichowa 1976, 1979; Budyś 2008; Sotek in print). This results from the natural and anthropogenic transformations of peatland vegetation, caused by changes in their sites, mostly due to direct and indirect human interference. The major causes of deep transformation of peatland ecosystems include, e.g. drainage, peat cutting, farming, fire, afforestation, and human settlement (e.g. Jasnowski *et al.* 1968; Herbichowa 1976; Kloss & Wilpiszewska 1999; Herbich & Herbichowa 2002; Prajs *et al.* 2006; Budyś 2008; Pawlikowski 2008; Sotek & Stasińska 2010). The ecosystems are also threatened by eutrophication, e.g. because of surface run-off from adjacent fields, subject to inorganic fertilization, or as a result of direct fertilization of semi-natural plant communities on peatlands used as grasslands (e.g. Jasnowska & Jasnowski 1977a; Herbichowa & Jąkalska 1985; Kurzac & Kucharski 1991; Kucharski & Grzyl 1993; Sotek *et al.* 2004). The lowering of the water level in peatlands is significantly affected also by changes in hydrological conditions in surrounding areas.

The scope of human transformation of peatland ecosystems in the 20th century aroused anxiety that if all the plans of drainage of peat wetlands are implemented, then more than half of the species associated with such habitats may die out or become threatened (Michalik 1977). The scale of the problem is evidenced by the high rate of disappearance of Boreal taxa (13 extinct species – mostly peatland plants), and slightly slower of Atlantic plants (9 species) in a complex of mire habitats in the Kashubian Coast (Budyś 2006). Stenotopic species are at a greater risk of extinction because they are characterized by low ecological tolerance and frequently also by inefficient sexual reproduction (Jasnowski 1975; Kornaś 1981; Michalik 1988). Peatland species with a narrow phytocoenotic spectrum, e.g.

Herminium monorchis, *Pedicularis sceptrum-carolinum*, *Primula farinosa*, *Schoenus ferrugineus*, *Swertia perennis*, and *Tofieldia calyculata*, are probably extinct or endangered in Pomerania (see section 5.3, Annex, Fig. A47, A62, A66, A74, A78, A79). Special attention should be paid to *P. sceptrum-carolinum* and *T. calyculata*, as in Pomerania they reach limits of their ranges. Thus, as a result of their retreat from this region, their ranges are shrinking. These species exemplify that at the limits of their ranges, taxa often show recessive trends, as reported earlier, e.g. by Kornaś (1976) and Wolejko (1983). Among the peatland plants that reach in Poland the limits of their general distribution ranges, such trends in Pomerania can be noticed also in, e.g. *Carex chordorrhiza*, *C. pulicaris*, *Pinguicula vulgaris*, and *Stellaria crassifolia*. The number of their localities gradually decreases throughout the region or in some of its parts (see Annex, Fig. A12, A27, A43, A64, A76).

The decline of peatland plant species in some parts of Pomerania may lead to local disjunctions or enlargement of the earlier gaps in their distribution. An example is *Eriophorum gracile*, whose disappearance from the south-eastern and eastern parts of the region resulted in a local gap in its distribution (see Annex, Fig. A43). Similarly, the decline of *Hammarbya paludosa* in north-western Poland enlarged the pre-existent distributional gap in northern Germany. Additionally, its disappearance from many Pomeranian localities may lead to its disjunct distribution in this region (see Annex, Fig. A46). The retreat of *Swertia perennis* from northern Pomerania (see Annex, Fig. A78) and from most of its localities in north-eastern and central Poland, enlarged the earlier gaps in its disjunct distribution. Another noteworthy example is the distribution of *Stellaria crassifolia*, whose north-Pomeranian localities (see Annex, Fig. A76), like nearly all eastern German localities, were not confirmed after 1950. This may indicate that a distributional gap is being formed there. In the future, this may lead to a shrinking of the range of this species.

The taxa declining in some parts of Pomerania include also *Lycopodiella inundata* and *Rubus chamaemorus*, which have disappeared from some sites, but at the same time also their apophytism is observed. This means that they sometimes appear on sites disturbed by human activity, at early stages of succession. For example, *L. inundata* has been reported from abandoned sandpits, sites of peat extraction, as well as shores of lakes and ponds (Cieszko & Kucharczyk 1999a, 1999b; Czarnecka 2000). Similarly, *R. chamaemorus* was recorded near sites of peat extraction (Czubiński *et al.* 1954), on roadsides (Kruszelnicki & Fabiszewski 2001), and near drainage ditches (e.g. in the nature reserve “Czarne Bagno” in the Łeba river valley, own observations). At such sites, both the species are expansive at the begin-

ning, but their success is usually short-lived, as they are less competitive than other plant species.

If the ecological balance is disturbed, small populations are most threatened (Szlachetko 1987; Tyszkowski 1995). An example is *Epipactis palustris*, which formed mostly small local populations in the Kashubian Coast and Lakeland, and many of the localities were not confirmed later (Kowalewska 1995). This species, quite frequent in the past, has disappeared from many sites, but has recently been recorded at some new sites (see section 5.3). It grows on natural sites but also on sites disturbed by human activity (Czylok 1997; Wyrzykiewicz-Raszewska 2001). Apophytism is not rare in orchids (Dickson 1990; Adamowski & Conti 1991; Godefroid 1995; Czarnecka 2000; Adamowski 2006), but still they are some of the most threatened groups of plants both in Poland and all over Europe (e.g. Michalik 1975; Żukowski 1976; Jasnowska & Jasnowski 1977b; Martin 1980; Procházka & Velisek 1983; Summerhayes 1985; Żukowski & Jackowiak 1995; Kaźmierczakowa & Zarzycki 2001; Zarzycki & Szelağ 2006). This is associated with their specific biology, a narrow range of suitable habitats, and a decreasing number of available sites. Among the 5 orchid species, whose dynamic trends in Pomerania are presented, the most threatened in this region are: *Herminium monorchis* – probably extinct; *Malaxis monophyllos* – endangered; and *Hammarbya paludosa* – declining quickly (see section 5.3).

The group of species that used to be relatively frequent in the study area, but now are declining in some areas, like *Epipactis palustris*, includes also *Carex limosa* and *Scheuchzeria palustris* (see Annex, Fig. A23, A73). Both the species, being the major components of the association *Caricetum limosae*, are found in bog hollows and transitional bogs. Although recorded recently at some new sites, they decline as a result of site destruction, mostly due to human activity. The scale of this process is reflected in a comparison of data on their distribution at present and in the past, based on subfossil data from upper layers of peat deposits. As reported by Jasnowski (1972), the number of localities of *S. palustris* is about 5-fold lower, and over 8-fold lower in the case of *C. limosa*.

Each species is adapted to a range of environmental conditions, and thus to some habitat types, outside which it is outcompeted by other species (Whittaker 1975). It has its own life strategy, which allows it to survive and give offspring (Grime 1977, 1979, 1988; Urbanska 1981, 1984, 1985; Falińska 1997). According to Grime, the strategy is determined by the type of selection pressure: competition (C), stress (S), and disturbance (R), which simultaneously affect plants, but often with varying intensity.

Most of peatland plant species are characterized by low tolerance to environmental changes. They are par-

ticularly sensitive to disturbances in water conditions, which results from their life strategies. Most of them represent life strategies C-S and C-S-R, i.e. are adapted to competition limited by stress, or to competition limited by both moderate stress and disturbance. Consequently, they are not highly competitive (see section 5.1.7, Fig. 8). Another important group are species that tolerate a high level of stress – strategy S (Annex). The studied plants do not include any species highly resistant to disturbance of their sites (strategy R). Tolerance of only limited competition and the lack of adaptation to strong disturbance may result in disappearance of these plants from many localities, due to transformation of their sites.

Important features of life strategies, enabling plant species to survive, include those concerning reproduction. Most of the studied peatland plant species are pollinated by wind or insects (see section 5.1.6). Their diaspores are dispersed mostly by wind (anemochory) and on animals (epizoochory) (see section 5.1.6, Fig. 7), which enable them to cover long distances. However, seed germination may be difficult because of the thick layer of *Sphagnum* peat. This is often reflected in the low effectiveness of sexual reproduction, so that vegetative reproduction often predominates. The plants reproduced vegetatively are much more likely to survive in difficult site conditions than those reproduced by seeds. This is associated with a more advanced stage of development of the young individual at the time of gaining independence (e.g. Falińska 1982, 1985; Smirnova 1987; Szmeja 1987). The studied species typically have a long life cycle, as none of them are therophytes, i.e. annuals (see section 5.1.4). Such life strategies do not ensure the survival of peatland plant species in strongly disturbed environmental conditions and under strong competition.

Current changes in the peatland flora include disappearance of many rare species but also synanthropization of the vegetation (e.g. Jasnowski 1972, 1975, 1977; Budyś 2008). Substitute communities formed in disturbed peatlands include some new taxa favoured by the changed environmental conditions. This initially causes an enrichment of species composition of peatlands. However, this does not compensate for the loss of rare species associated with these ecosystems. In contrast, due to competition, this leads to their disappearance, and consequently to impoverishment of the typical peatland flora.

7. Conclusions

The phytogeographic analysis of 83 peatland plant species associated with the classes *Oxycocco-Sphagnetetea* and *Scheuchzerio-Caricetea nigrae* showed that most of the studied Pomeranian peatland plant species (in both classes) are widely distributed, Circum-Boreal.

The Arctic-Alpine sub-element is represented only in the class *Oxycocco-Sphagnetetea*, while connective elements and Euro-Siberian and Amphi-Atlantic sub-elements are represented only in the class *Scheuchzerio-Caricetea nigrae*. Out of the studied group of species, 34 represent directional elements of the Polish flora, and 20 of them reach limits of their ranges in Pomerania. Northern and western directional elements are most numerous among them.

In the biological spectrum of the studied flora, hemi-cryptophytes are the dominant life-form, but cryptophytes are also numerous, while therophytes are absent. Most of the species are wind-pollinated and insect-pollinated, while their diaspores are dispersed mainly by wind, although an important role is also played by epizoochory and autochory. Vegetative reproduction is often preferred. The studied species usually represent life strategy C-S-R (adapted to competition limited by stress and disturbance) or C-S (adapted to competition limited by stress).

Most of the considered climatic variables related to temperature, precipitation, and growing season length, show a significant ($P < 0.05$) effect on the distribution of peatland plant species in Pomerania.

Within Pomerania, 5 regional distributional types (chorotypes) were distinguished among peatland plant species. Two types showed considerable internal variation, so some subtypes were distinguished within them. Most of the groups are composed of species representing various geographic elements. For example, in the northern type, some species have their centre of distribution in the Atlantic part of Europe, while others, in the Boreal continental part. This is because the study area is affected by both the oceanic and continental climate. However, in some groups of species, the regional distribution pattern is related to the type of general distribution and geographic element. An example is the *Rhynchospora alba* subtype (all-Pomeranian type), which includes exclusively Circum-Boreal species. Sometimes also a clear relationship with specific environmental conditions can be noticed. This applies, for instance, to groups composed mostly of species found on calcareous sites (western type as well as all-Pomeranian type, *Eriophorum latifolium* subtype).

On the basis of dynamic maps of distribution, several groups of species, showing various dynamic trends in Pomerania, were distinguished:

- probably extinct species, e.g. *Herminium monorchis* and *Tofieldia calyculata*;
- endangered species, e.g. *Baeothryon alpinum* and *Swertia perennis*;
- species disappearing quickly, e.g. *Carex chordorrhiza* and *Stellaria crassifolia*;
- species disappearing from some parts of Pomerania, e.g. *Carex pulicaris* and *Rubus chamaemorus*;

- species relatively frequent in the past, now less frequent but also recorded at new localities, e.g. *Carex limosa* and *Scheuchzeria palustris*;
- rare species disappearing from some localities but also recorded at new localities, e.g. *Rhynchospora fusca* and *Salix myrtilloides*;
- species tending to spread: *Erica tetralix*.

Most of the species associated with the class *Oxycocco-Sphagnetea* probably immigrated to Pomerania in the late glacial period or in the early Holocene, as they found favourable conditions for growth in patches of moist tundra. Similarly, many species associated with the class *Scheuchzerio-Caricetea nigrae* could at the same time immigrate to the study area. They were often associated with the telmatic zone of water bodies created at that time, as well as with wetlands or with young postglacial soils rich in calcium carbonate. Late arrivals, in both classes, were the species with high thermal requirements. They could reach Pomerania in the late Boreal period or the early Atlantic period.

Species of the same regional distributional type may have a similar history of colonization of Pomerania in the postglacial period. However, this usually does not apply to all species within a group. Some species with similar general distribution ranges and similar habitat preferences were likely to immigrate to Pomerania in roughly the same period.

The floristic variation of Pomeranian peatlands is significantly dependent on climatic conditions. Many peatland plant species more or less strongly prefer the areas with cooler summers. The decline of peatland plant species in many parts of Pomerania is often due to strong disturbances of their sites and their poor competitiveness in relation to other groups of plant species.

As a result of the disappearance of some peatland plant species from various parts of Pomerania, local gaps are formed in their distribution ranges, or the earlier gaps are expanded. In the species that reach in Pomerania some limits of their distribution, local extinction may

lead to shrinking of their range limits. Assessment of dynamic trends of some species of peatland plants forms a basis for their assignment to IUCN threat categories.

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Annex

Characteristics and distribution of peatland plant species

Each of the studied species is briefly described below. Each species description includes the binomial name, its most commonly used synonyms, geographic element, distribution in Poland and in Pomerania, frequency in Pomerania (on a scale of I to IV, where I – extremely rare, while VI – frequent), cartogram number, regional distributional type, phytocoenotic spectrum, and biological properties (pollination mode, dispersal of diaspores, life strategy). Sometimes data on distribution of the given species in eastern Germany is also given (Benkert *et al.* 1998).

To illustrate better the distribution of individual plant species, geographic names most commonly used here are shown on a map of Poland (Fig. A1), and of Pomerania (Fig. A2).

Symbols used in cartograms

Dynamic cartograms

(with division into several periods):

recorded before 1901	○
in 1901-1950	◐
in 1951-1970	◑
in 1971-1990	◒
after 1990	●
no longer found at the locality	+

Other cartograms

(without division into several periods):

unverified locality	●
doubtful locality	?



Fig. A1. Map of Poland, with major geographic names used in this paper (map by J. Prajs, on the basis of numerous resources)

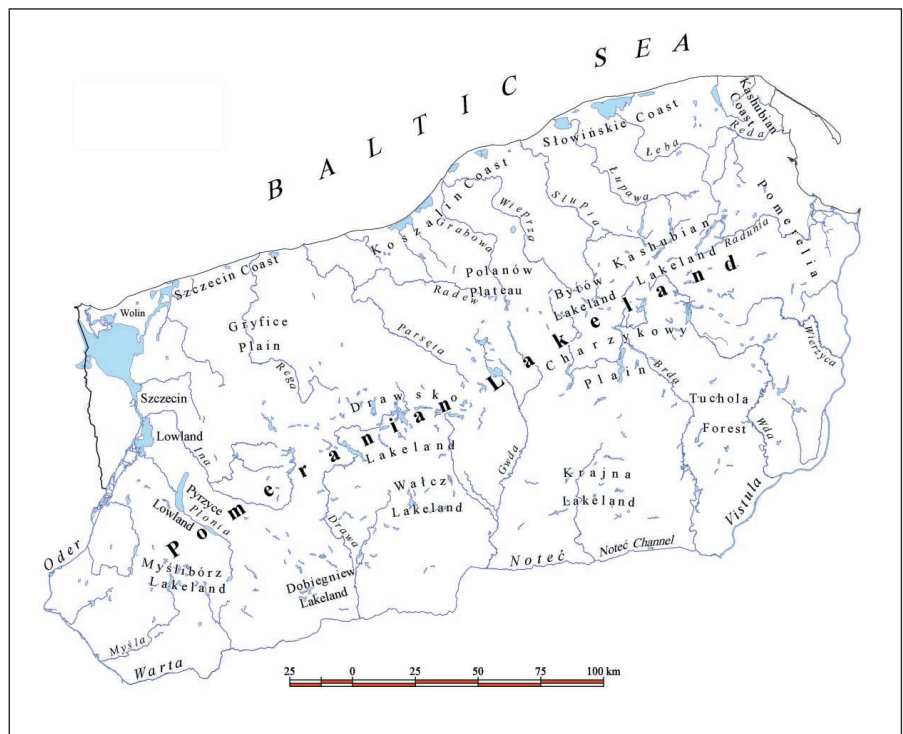


Fig. A2. Map of Pomerania, with major geographic names used in this paper (map by J. Prajs, on the basis of numerous resources)

Agrostis canina L. s. str.

Euro-Siberian sub-element, extending to the Atlantic region of Europe. Distributed all over Poland, common in Polesie, the Lublin Upland, Roztocze, and Małopolska Upland. In Pomerania¹ moderately frequent (frequency category V), particularly in the eastern and north-western parts (Fig. A3). All-Pomeranian distributional type, *Carex rostrata* subtype. Associated with plant communities of the class *Scheuchzerio-Caricetea nigrae*. Found also in wet and moist meadows and sallow thickets, rarely in tall sedge communities, raised bogs, and humid heaths. Hemicryptophyte. Pollination: wind. Dispersal: anemochory. Life strategy: C.

¹ It must be remembered that only the Polish part of Pomerania is considered in this article

Andromeda polifolia L.

Circum-Boreal sub-element. In Poland frequent in lowlands, except for the Central Polish Lowlands (Niziny Śródkowopolskie), where it is very rare or absent. In the mountains infrequent, found in scattered localities. In Pomerania frequent (VI), widespread, most frequent in the Tuchola Forest (Bory Tucholskie), Charzykowy Plain (Równina Charzykowska), as well as the Bytów and Kashubian Lakelands (Fig. A4). All-Pomeranian distributional type, *Rhynchospora alba* subtype. Associated with plant communities of wet heaths and raised bogs of the class *Oxycocco-Sphagnetetea*, particularly with moss-dominated patches of the order *Sphagnetalia magellanici*. Found also in patches of dystrophic communities of the alliance *Rhynchosporion albae*, or rarely in wet coniferous forests. Chamaephyte. Pollination: wind. Dispersal: anemochory. Life strategy: CS.

Baeothryon alpinum (L.) T. V. Egorova

Circum-Boreal sub-element (disjunctive range). In Poland rare, found in scattered localities, reaching its southern limit of distribution. Most frequent in the north-eastern part of the country. Recorded also in Pomerania, the Lubusz Lakeland (Pojezierze Lubuskie), Opole Plain (Równina Opolska), Silesian Upland, Sudetes (Sudety), and Tatra Mountains. In northern Poland it has a disjunct distribution, as it is absent in the area between the rivers Parsęta and Gwda and Lake Śniardwy. In Pomerania very rare (II), recorded in single localities in the Parsęta river valley, in the Szczecin Lowland, Wałcz Lakeland (Pojezierze Wałeckie), and at the confluence of the river Brda (Fig. A5). The species does not belong to any of the distinguished distributional types. Found in springs and flushes as well as transitional bogs. Associated with plant communities of the class *Scheuchzerio-Caricetea nigrae*. Geophyte, hemicryptophyte. Pollination: wind. Dispersal: anemochory. Life strategy: CS.

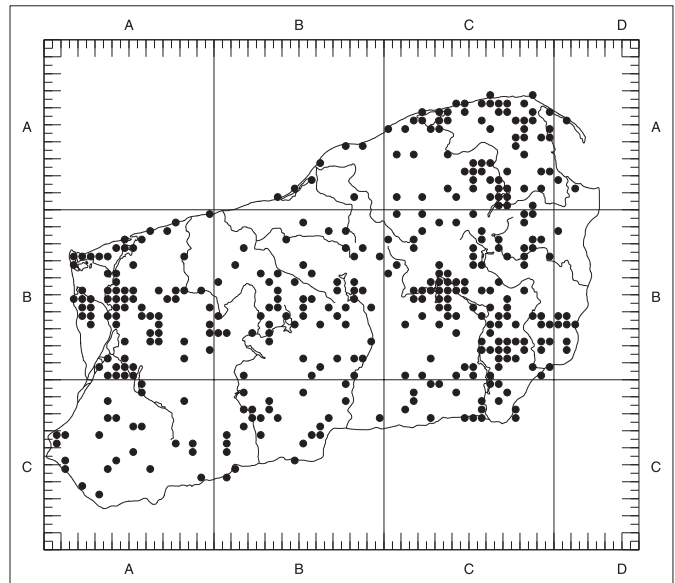


Fig. A3. *Agrostis canina* L. s. str.

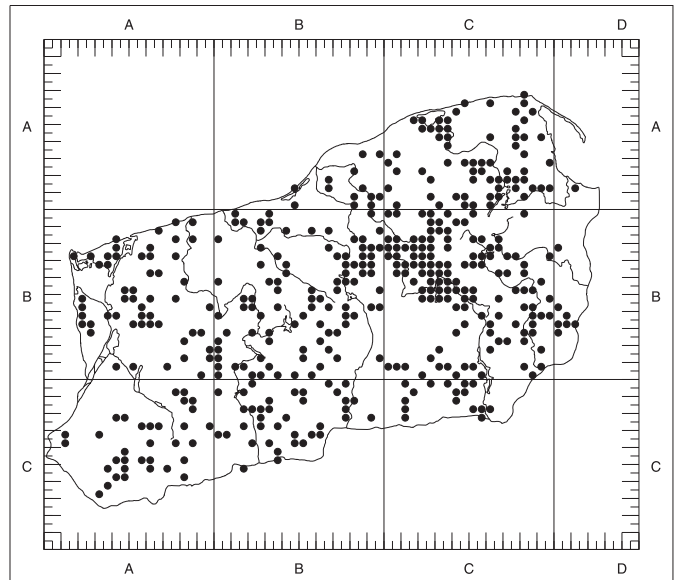


Fig. A4. *Andromeda polifolia* L.

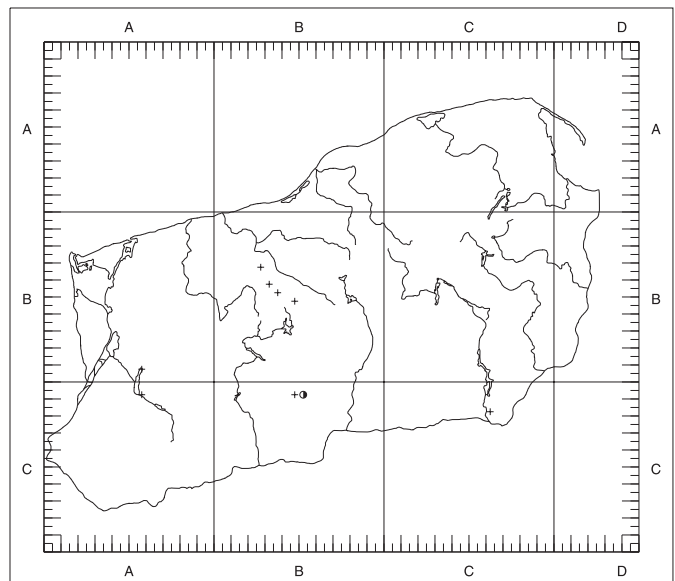
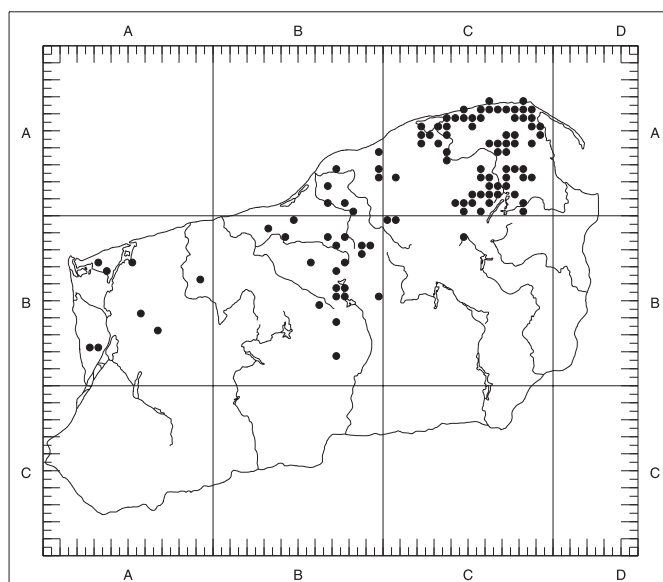


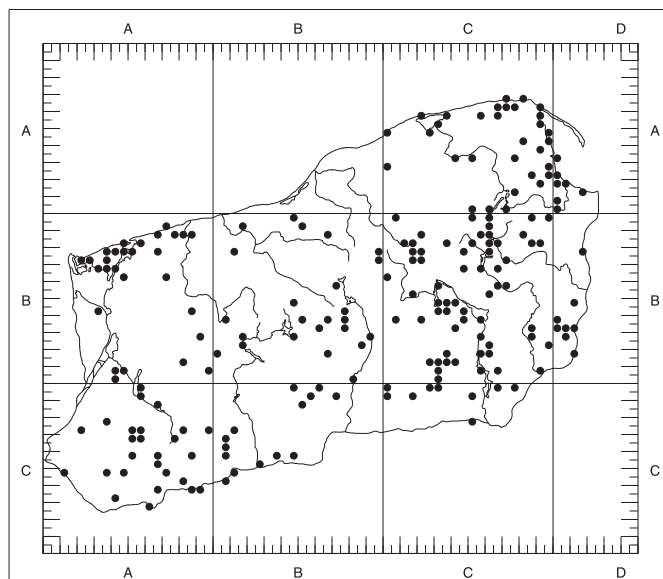
Fig. A5. *Baeothryon alpinum* (L.) T. V. Egorova

Baeothryon cespitosum (L.) A. Dietr.

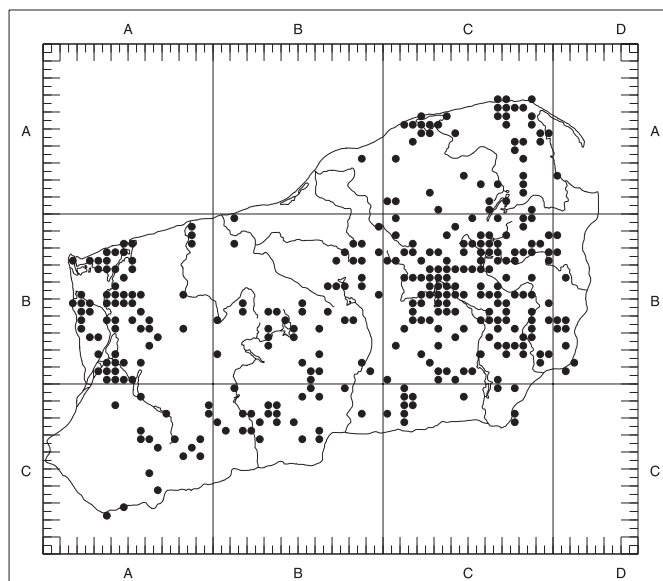
Circum-Boreal sub-element (disjunctive range). North Poland is crossed by the southern limit of distribution of this species. Recorded mostly in Pomerania and Masurian Lakeland. Found also in single localities in the Sudetes and Silesian Upland. In Pomerania infrequent (IV), noted in the northern part, most frequent on the Kashubian Coast (Pobrzeże Kaszubskie), increasingly scattered westwards (Fig. A6). Northern distributional type in Pomerania. Associated with raised bogs, present in patches of communities of the alliance *Ericion tetralicis*, i.e. in Northern Atlantic wet heaths. In the mountains found in *Eriophoro-Trichophoretum caespitosi* and *Empetro-Trichophoretum austriaci*. Hemicryptophyte. Pollination: wind. Dispersal: anemochory. Life strategy: CS.

Fig. A6. *Baeothryon cespitosum* (L.) A. Dietr.*Blysmus compressus* (L.) Panz. ex Link

Connective element, linking European-temperate, Mediterranean (northern), and Irano-Turanian (mountains) elements. Distributed all over Poland. Most frequent in the Carpathians, Polesie, Roztocze, and the Lubusz Lakeland, Wielkopolska Lakeland, and Chełmno-Dobrzyń Lakeland (Chełmińsko-Dobrzyńskie Lakeland). In Pomerania moderately frequent (V), except for the Szczecin Lowland and the central part of the Polish Baltic coast (Fig. A7). All-Pomeranian distributional type, *Eriophorum latifolium* subtype. Frequent component of flood plain communities of the order *Trifolio fragiferae-Agrostietalia stoloniferae*, and spring-water mires of the order *Carietalia davallianae*. Recorded also in salt-marshes. Geophyte. Pollination: wind. Dispersal: epizoochory, anemochory. Life strategy: CSR.

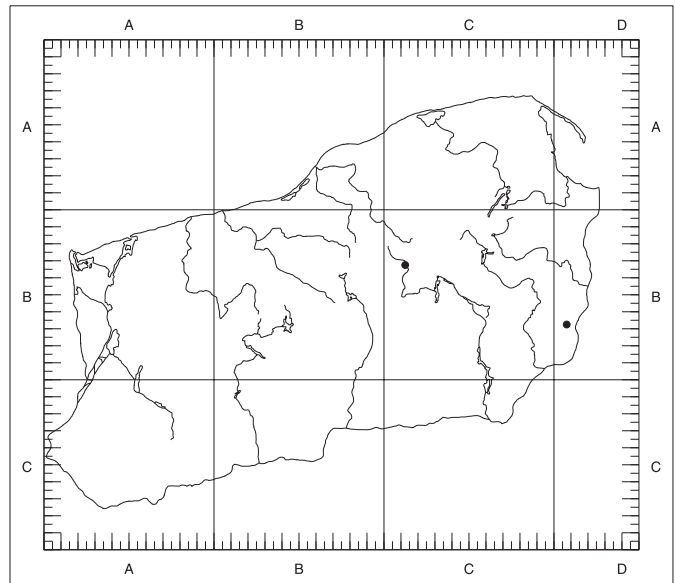
Fig. A7. *Blysmus compressus* (L.) Panz. ex Link*Calamagrostis stricta* (Timm) Koeler

Circum-Boreal sub-element (northern). In southern Poland the species has its southern limit of distribution. Frequent in the northern part of the country, in South Baltic Lakelands as well as in Polesie and Roztocze. Scattered in other parts of Poland, except for the North Masovian Lowland (Nizina Północnomazowiecka) and Carpathians, where it has not been recorded yet. In Pomerania moderately frequent (V), particularly in the east and north-west. Very rare near the south-western limits of the region and on the Koszalin Coast (Pobrzeże Koszalińskie) (Fig. A8). All-Pomeranian distributional type, *Carex rostrata* subtype. Found mostly in low sedge mires of the order *Carietalia nigrae*, and in transitional bogs of the order *Scheuchzerietalia palustris*, less often in tall sedge communities of the alliance *Magnocaricion*. Hemicryptophyte. Pollination: wind. Dispersal: anemochory, epizoochory. Life strategy: CS.

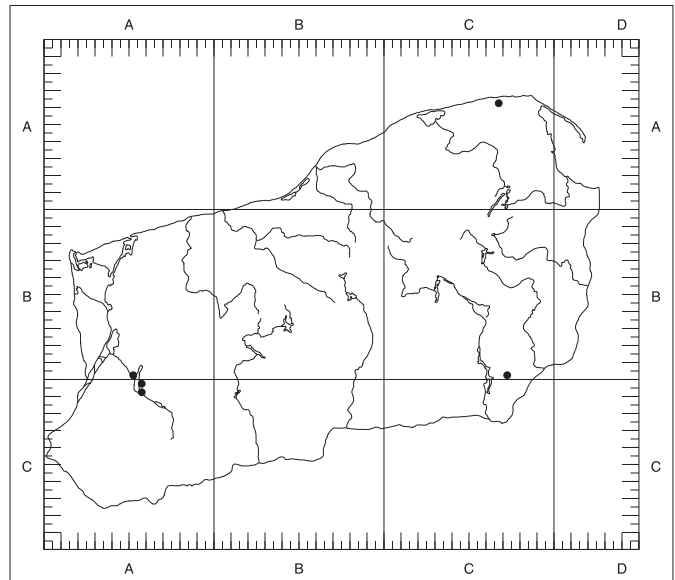
Fig. A8. *Calamagrostis stricta* (Timm) Koeler

Carex brunnescens (Pers.) Poir.

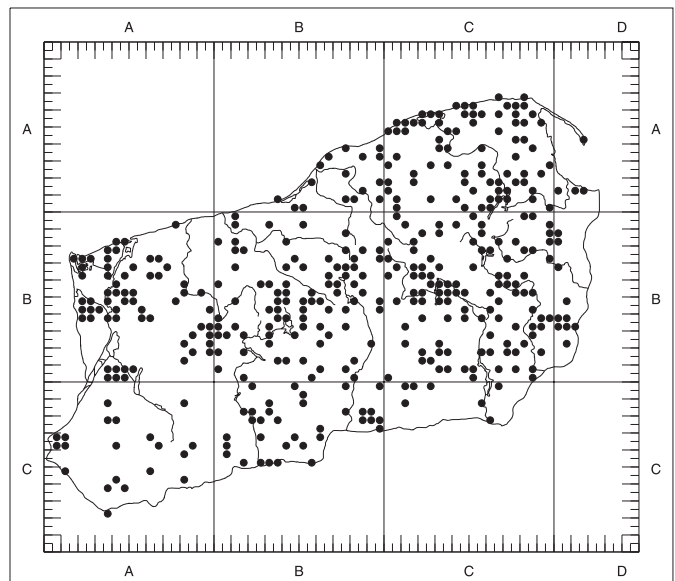
Circum-Boreal sub-element. In Poland the species reaches the western limit of its European range of distribution. Recorded in only few localities in Podlasie, the Suwałki Region, and in Pomerania. In Pomerania extremely rare (I), it was found in the valley of the upper Brda (near the village of Stara Brda) and in the Vistula river valley, near the village of Nowe (Fig. A9). The species does not belong to any of the distinguished distributional types. Found in patches of low sedge mires of the order *Caricetalia nigrae*. Hemicryptophyte. Pollination: wind. Dispersal: epizoochory.

Fig. A9. *Carex brunnescens* (Pers.) Poir.*Carex buxbaumii* Wahlenb.

Circum-Boreal sub-element (disjunctive range). Scattered in Poland. Most frequent in the eastern part of the country: in Polesie and the Suwałki Lakeland (Pojezierze Suwalskie). Moreover, recorded in Podlasie, Pomerania, Masovian and South Wielkopolska Lowlands, and the Kraków-Częstochowa Upland. In Pomerania extremely rare (I), single localities are scattered in the Szczecin Lowland, on the Kashubian Coast, and south-east of the Tuchola Forest (Fig. A10). Disjunctive distributional type. Found in patches of communities of the alliance *Magnocaricion* and *Caricion davalianae* (Dierssen 1982; Jutrzenka-Trzebiatowski & Szarejko 2001). Sometimes present, although not numerous, in patches of the order *Molinietalia*. It forms its own, rare plant association: *Caricetum buxbaumii*. Geophyte. Pollination: wind. Dispersal: epizoochory, anemochory, autochory. Life strategy: CS.

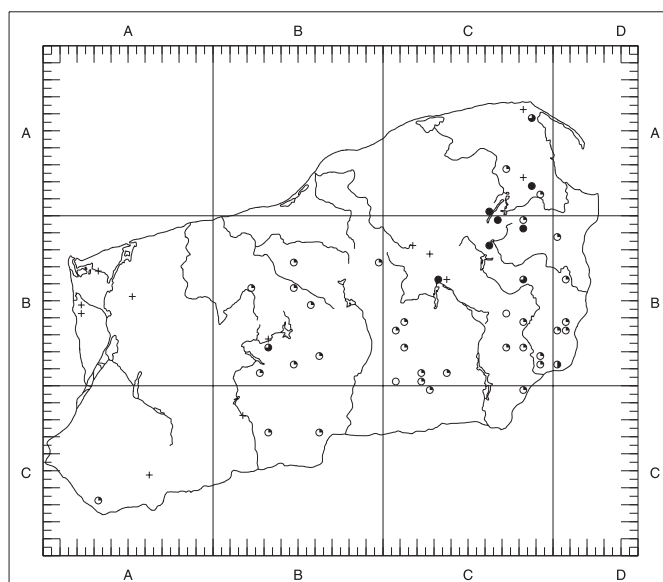
Fig. A10. *Carex buxbaumii* Wahlenb.*Carex canescens* L.

Circum-Boreal sub-element. Distributed all over Poland, less frequent in the belt of Central Polish Lowlands, in the west and south-west. In Pomerania frequent (VI), except for the south-west (Fig. A11). All-Pomeranian distributional type, *Carex rostrata* subtype. Associated with plant communities of the class *Scheuchzerio-Caricetea nigrae*, mostly with acid low sedge mires. Found also in tall sedge communities, sallow thickets, and raised bogs. Hemicryptophyte. Pollination: wind. Dispersal: hydrochory, epizoochory, anemochory, autochory. Life strategy: CSR.

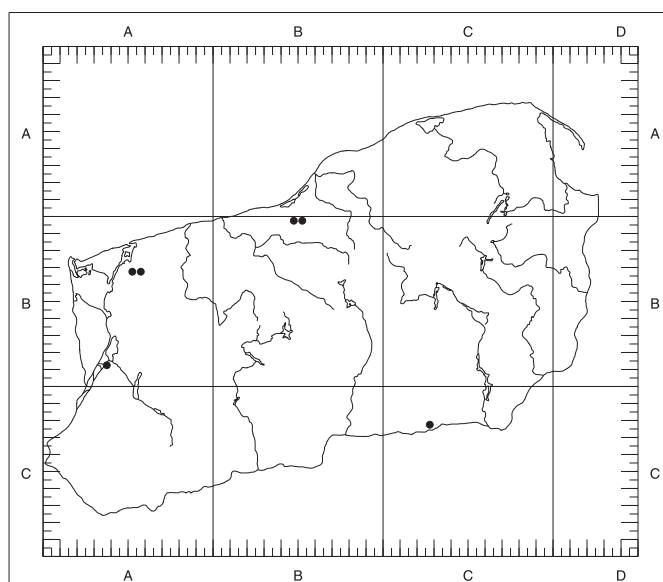
Fig. A11. *Carex canescens* L.

Carex chordorrhiza L.f.

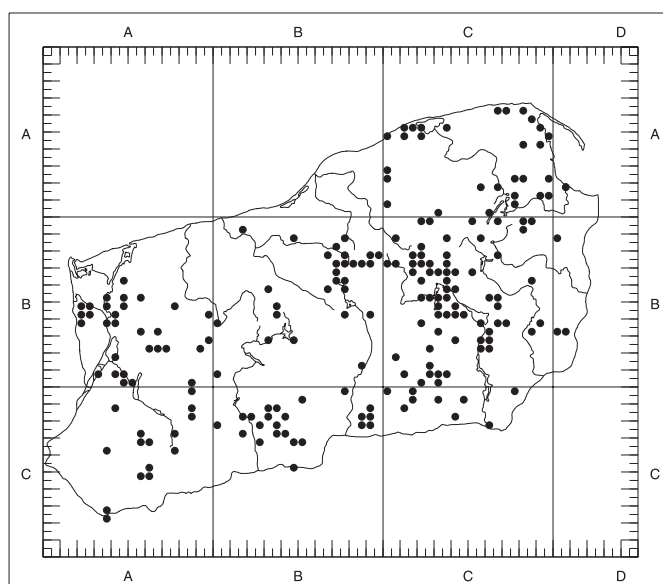
Circum-Boreal sub-element (disjunctive range), Circum-Boreal Arctic group. In Poland it reaches the southern limit of its main distribution range. Most frequent in the Masurian Lakeland, Polesie, and Roztocze. Scattered in Pomerania and in the south-eastern part of the country, with single isolated stands in central Poland. Very rare in Pomerania (II), All-Pomeranian distributional type, *Hammarbya paludosa* subtype. Found in the eastern and southern parts of this region, but rarely west of the rivers Drawa and Rega (Fig. A12). Most often found in patches of moss-sedge communities of the alliance *Caricion lasiocarpae*. Within its main distribution range also present in communities of the alliance *Rhynchosporion albae*, and of the class *Oxycocco-Sphagnetea*. Geophyte, hydrophyte, helophyte. Pollination: wind. Dispersal: epizoochory.

Fig. A12. *Carex chordorrhiza* L.f.*Carex davalliana* Sm.

European-temperate sub-element, European-temperate-lowland group, European-temperate Balkan distributional type. In Poland the species reaches the northern limit of its range. Frequent in the Sudetes and Tatras, and in the belt of Polish Uplands. In the lowlands and at the south-eastern margins of Poland recorded only in single localities. In eastern Germany the species shows a similar pattern of distribution as in Poland. In Pomerania extremely rare (I), it has been reported from 6 localities in the Szczecin Lowland, on the Koszalin Coast, and on the river Noteć (Fig. A13). The species does not belong to any of the distinguished distributional types. Associated with eutrophic fens in the mountains and spring-water mires. Hemicryptophyte. Pollination: wind. Dispersal: epizoochory, anemochory, autochory. Life strategy: CSR.

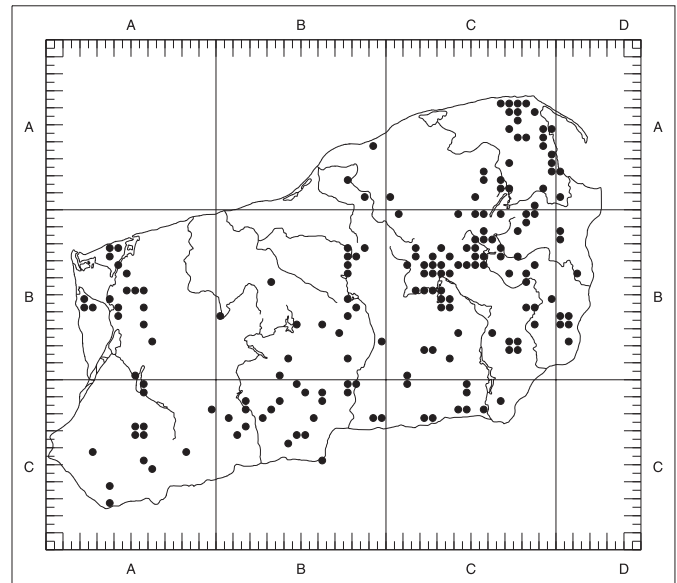
Fig. A13. *Carex davalliana* Sm.*Carex diandra* Schrank

Circum-Boreal sub-element. Distributed all over Poland; frequent in the north, increasingly scattered southwards. In Pomerania moderately frequent (V), present except in the western and southern part of the South Baltic Coasts (Pobrzeża Południowobałtyckie) (Fig. A14). All-Pomeranian distributional type, *Eriophorum latifolium* subtype. Associated with fens and transitional bogs of the class *Scheuchzerio-Caricetea nigrae*, particularly with communities of the order *Scheuchzerietalia palustris* (phyto-coenotic optimum in the association *Caricetum diandrae*). Found also in wet meadows of the order *Molinietalia caeruleae* and in tall sedge communities of the alliance *Magnocaricion*. Geophyte, hemicryptophyte. Pollination: wind. Dispersal: epizoochory, anemochory, autochory. Life strategy: CSR.

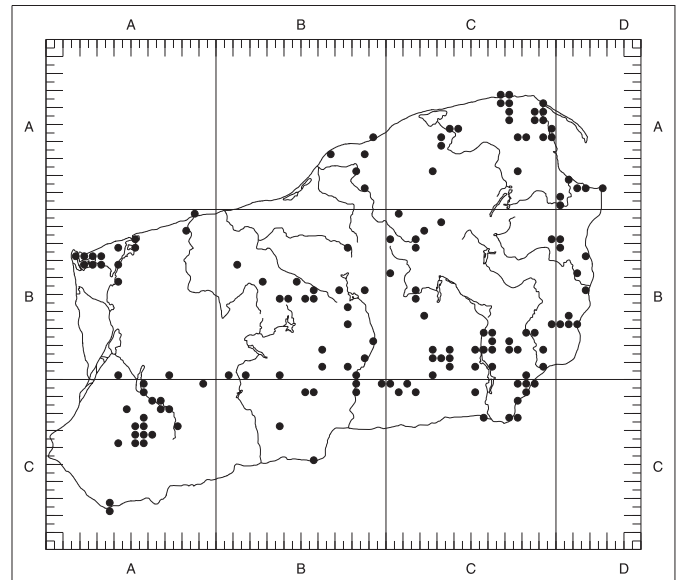
Fig. A14. *Carex diandra* Schrank

Carex dioica L.

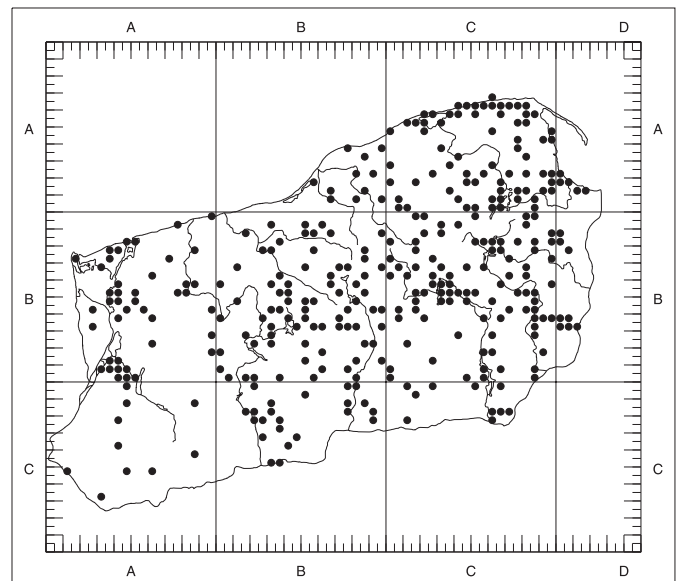
Circum-Boreal sub-element. Distributed all over Poland, except for the south-eastern margins. In central Poland scattered. In Pomerania infrequent (IV), very rare in the central part of the South Baltic Coasts (Fig. A15). All-Pomeranian distributional type, *Eriophorum latifolium* subtype. Found in fens and transitional bogs of the class *Scheuchzerio-Caricetea nigrae*, primarily in communities of the order *Caricetalia davallianae* (phytocoenotic optimum in the association *Valeriano-Caricetum flavae*). Recorded also in wet meadows of the order *Molinietalia caeruleae*. Geophyte. Pollination: wind. Dispersal: epizoochory, anemochory, autochory, hydrochory. Life strategy: CS.

Fig. A15. *Carex dioica* L.*Carex distans* L.

Connective element, linking European-temperate (western) and Mediterranean elements, extending to the Atlantic region of Europe. Most frequent in south-eastern Poland, on Sudetian Foothills (Przedgórze Sudeckie), in the Silesian Lowland, and Wielkopolska Lakeland. In other parts of Poland generally scattered. Found all over Pomerania but infrequent (IV), recorded mostly on the island of Wolin, in the Myślubórz Lakeland (Pojezierze Myśluborskie), on the Kashubian Coast, and in the south-eastern part of the region (Fig. A16). All-Pomeranian distributional type, *Eriophorum latifolium* subtype. Recorded in halophilous communities of the class *Asteretea tripolium*, meadow communities of the class *Molinio-Arrhenatheretea* (particularly in floodplain grass communities of the order *Trifolio fragiferae-Agrostietalia stoloniferae*), and in fens of the order *Caricetalia davallianae*. Hemicryptophyte. Pollination: wind. Dispersal: epizoochory, anemochory, autochory. Life strategy: CS.

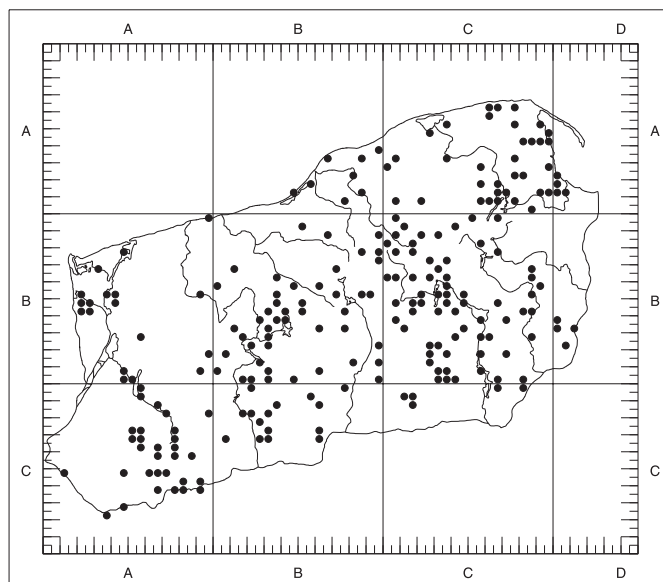
Fig. A16. *Carex distans* L.*Carex echinata* Murray

Circum-Boreal sub-element (disjunctive range). In Poland frequent, except for the Masurian Lakeland, Masovian Lowlands, Wielkopolska Lakeland, and north-western part of Poland. Increasingly scattered in central lowlands and in eastern Germany. In Pomerania moderately frequent (V), recorded less often only at the south-western margins of the region (Fig. A17). All-Pomeranian distributional type, *Carex rostrata* subtype. Associated mostly with acid low sedge mires. Moreover, found in patches of transitional bogs, wet meadows, tall sedge communities, but also in wet coniferous forest, and wet birch forest. Hemicryptophyte. Pollination: wind. Dispersal: epizoochory, anemochory, autochory. Life strategy: CSR.

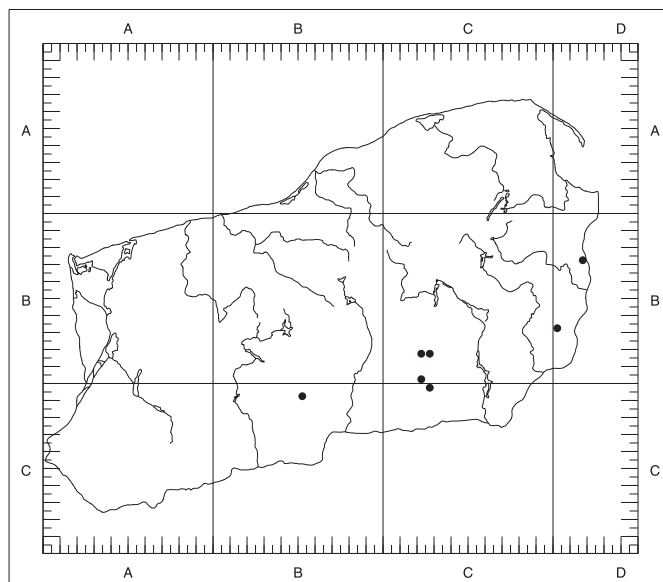
Fig. A17. *Carex echinata* Murray

Carex flava L.

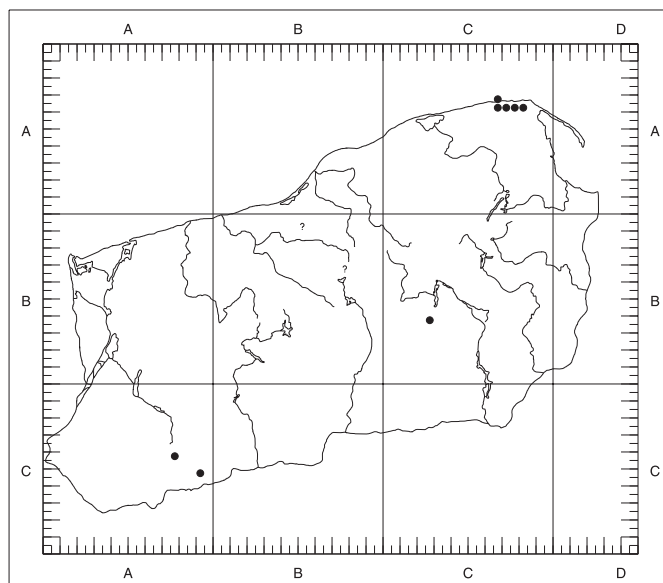
Circum-Boreal sub-element, Circum-Boreal-Oceanic group. Widely distributed in Poland, particularly in its south-eastern part. Less frequent in the belt of Central Polish Lowlands and in eastern Germany. In Pomerania moderately frequent (V) except for the Gryfice Plain (Równina Gryficka), Szczecin Lowland, and the south-western margins of the region (Fig. A18). All-Pomeranian distributional type, *Eriophorum latifolium* subtype. Usually found in low sedge mires of the order *Caricetalia davallianae*. Recorded also in acid low sedge mires, on wet meadows and in tall sedge communities. Hemicryptophyte. Pollination: wind. Dispersal: hydrochory, epizoochory, anemochory, autochory. Life strategy: CSR.

Fig. A18. *Carex flava* L.*Carex heleonastes* Ehrh. in L.f.

Euro-Siberian sub-element (northern, western). In Poland the species reaches northern and southern limits of its distribution range, which is disjunct, as the species also appears in the mountains of South Europe. Rare in the Masurian Lakeland, Masovian Lowlands, and Polesie, with few isolated populations in Pomerania and the Lubusz Lakeland. In Pomerania extremely rare (I), recorded exclusively in the south-eastern part of the region (Fig. A19). Eastern distributional type in Pomerania, *Salix myrtilloides* subtype. Associated with dystrophic-mesotrophic communities of transitional bogs of the alliance *Caricion lasiocarpae* (phytocoenotic optimum in the association *Caricetum heleonastes*). Hemicryptophyte. Pollination: wind. Dispersal: epizoochory.

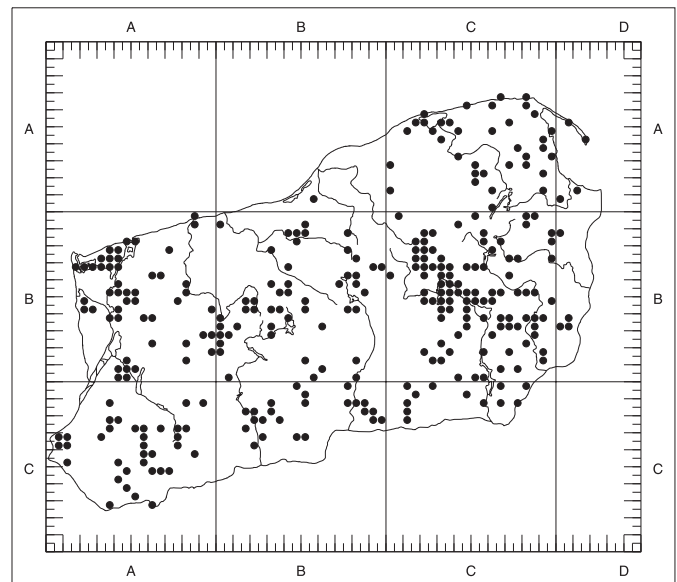
Fig. A19. *Carex heleonastes* Ehrh. in L.f.*Carex hostiana* DC.

European-temperate sub-element, European-temperate-lowland group, European-temperate Balkan (western) distributional type, extending to the Atlantic region of Europe. In Poland, the species reaches the eastern limit of its distribution range. Recorded mostly in the west and southwest, as well as in the Silesian-Kraków Upland and Małopolska Upland. Sporadically reported from the Masurian Lakeland, and Pomerania, while its records in the Carpathians are doubtful. In Pomerania extremely rare (I), known from single localities in the Dobięgniew Lakeland, Myślubórz Lakeland, Krajna Lakeland (Pojezierze Krajeńskie), Bytów Lakeland, as well as from the Koszalin Coast and Kashubian Coast (Fig. A20). Disjunctive distributional type. Found mostly in low sedge mires but also in moist meadows of the alliance *Molinion caeruleae*. Hemicryptophyte. Pollination: wind. Dispersal: epizoochory, anemochory, autochory. Life strategy: CS.

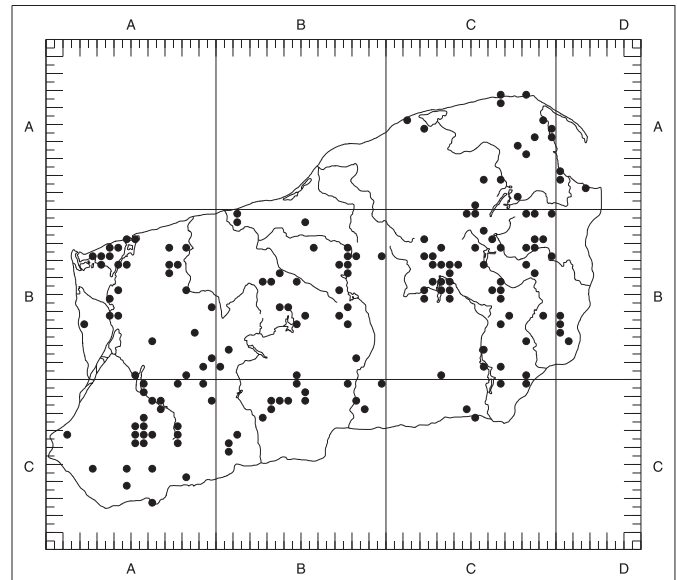
Fig. A20. *Carex hostiana* DC.

Carex lasiocarpa Ehrh.

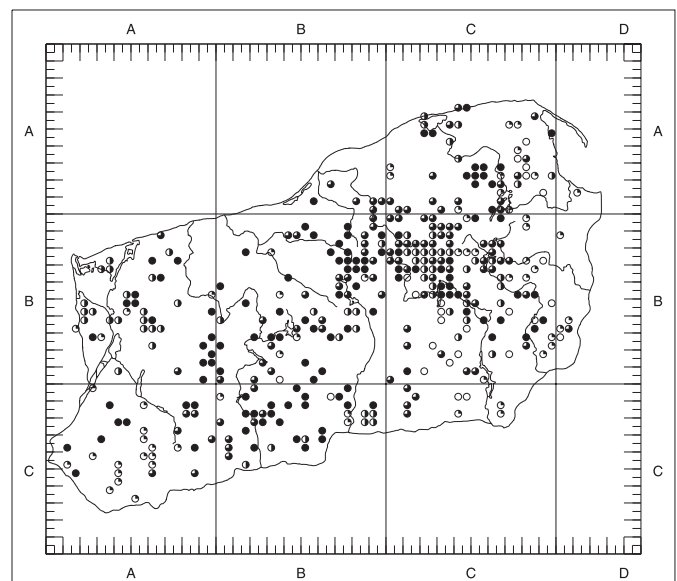
Circum-Boreal sub-element. Rare in the Sudetes and Carpathians, not reported from submontane areas. In other parts of Poland frequent, but less common in the belt of Central Polish Lowlands. In Pomerania moderately frequent (V), but relatively rare on the Koszalin Coast (Fig. A21). All-Pomeranian distributional type, *Carex rostrata* subtype. Associated with plant communities of the order *Scheuchzerietalia palustris* (phytocoenotic optimum in the association *Caricetum lasiocarpae*). Often found also in tall sedge communities, wet heaths, wet meadows, and sallow thickets. Hemicryptophyte, hydrophyte, helophyte. Pollination: wind. Dispersal: hydrochory, epizoochory, anemochory, autochory. Life strategy: CS.

Fig. A21. *Carex lasiocarpa* Ehrh.*Carex lepidocarpa* Tausch

Amphi-Atlantic sub-element. Found all over Poland, except for the North Masovian Lowland. Frequent particularly in the central Western Carpathians, Bieszczady Mountains, and Roztocze. In Pomerania infrequent (IV) but widely distributed, except for the Koszalin Coast (Fig. A22). All-Pomeranian distributional type, *Eriophorum latifolium* subtype. Usually reported from fens of the alliance *Caricion davallianae*. Found also in wet meadows, transitional bogs, and tall sedge communities. Hemicryptophyte. Pollination: wind. Dispersal: epizoochory, anemochory, autochory. Life strategy: CS.

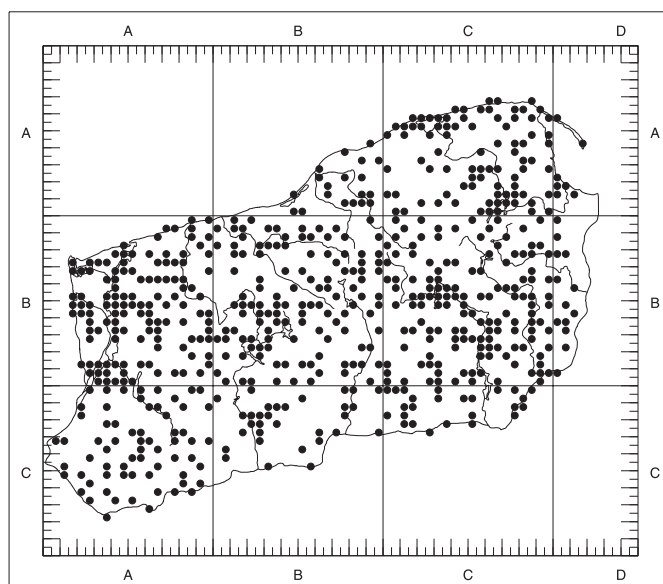
Fig. A22. *Carex lepidocarpa* Tausch*Carex limosa* L.

Circum-Boreal sub-element (northern). In Poland recorded mostly in Pomerania, the Masurian Lakeland, Polesie, and in Roztocze. In contrast, very rare in the southern, central and south-eastern parts of the country. In Pomerania moderately frequent (V), reported mostly from the Tuchola Forest, Charzykowy Plain, and the Bytów and Kashubian Lakelands, while scattered in other parts of the region (Fig. A23). All-Pomeranian distributional type, *Rhynchospora alba* subtype. Found in transitional bogs but also in raised bogs (of Atlantic and Baltic types), in patches of the association *Caricetum limosae*. It participates in the first stages of plant succession in dystrophic and dystrophic-eutrophic lakes. Associated with plant communities of the order *Scheuchzerietalia palustris*. Hemicryptophyte, geophyte. Pollination: wind. Dispersal: epizoochory, anemochory, autochory. Life strategy: S.

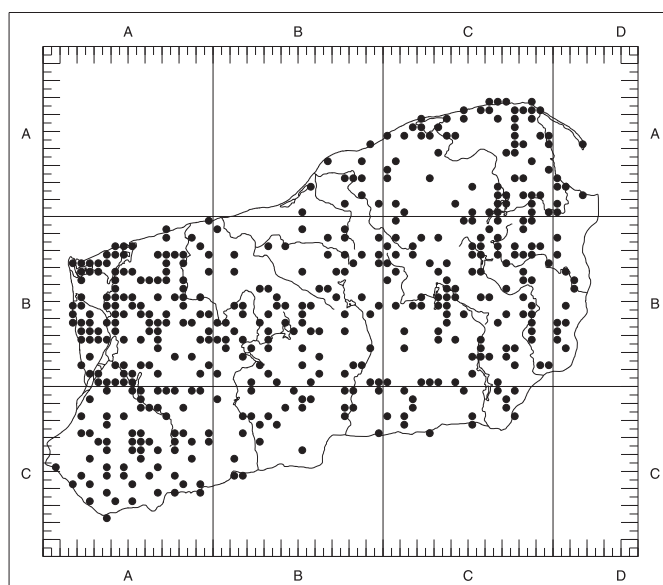
Fig. A23. *Carex limosa* L.

Carex nigra Reichard

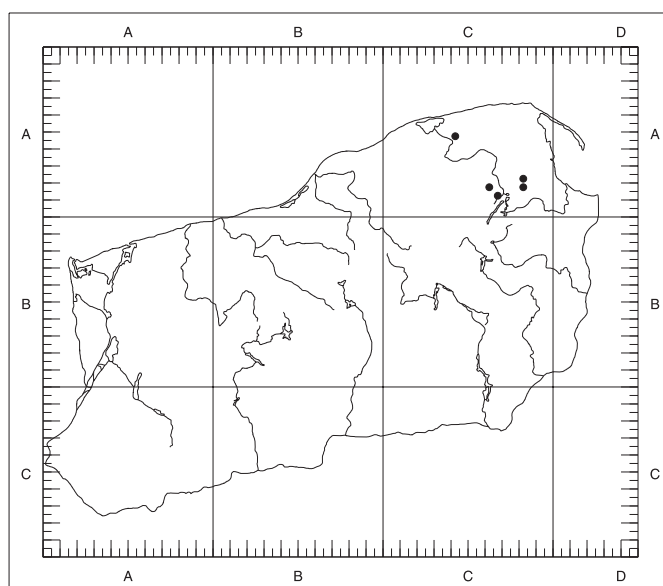
Circum-Boreal sub-element (disjunctive range). In Poland frequent, or common in some areas. Frequent (VI) in Pomerania (Fig. A24). All-Pomeranian distributional type, *Carex nigra* subtype. Found in patches of communities of the class *Scheuchzerio-Caricetea nigrae*. Frequent component of moist meadows of the alliances *Calthion palustris* and *Molinion caeruleae*. Less often reported from tall sedge communities, and sallow thickets. Associated with acid low sedge mires and with snow-patch communities on lime in the Tatras. Geophyte. Pollination: wind. Dispersal: epizoochory, anemochory, autochory. Life strategy: S.

Fig. A24. *Carex nigra* Reichard*Carex panicea* L.

Connective element, linking Euro-Siberian (western) and Irano-Turanian (mountains) elements, extending to the Atlantic region of Europe. Frequent in Poland; common in the south-eastern part of the country, except for the Sandomierz Basin (Kotlina Sandomierska) and the San river valley. In Pomerania frequent (VI), especially in the western part of the region (Fig. A25). All-Pomeranian distributional type, *Carex nigra* subtype. Found in communities of the classes *Molinio-Arrhenatheretea*, *Phragmitetea*, and *Scheuchzerio-Caricetea nigrae*. Commonly recorded in moist meadows, acid low sedge mires, tall sedge communities, as well as eutrophic fens in the mountains and spring-water mires. Geophyte, hemicryptophyte. Pollination: wind. Dispersal: epizoochory, anemochory, autochory, hydrochory. Life strategy: CSR.

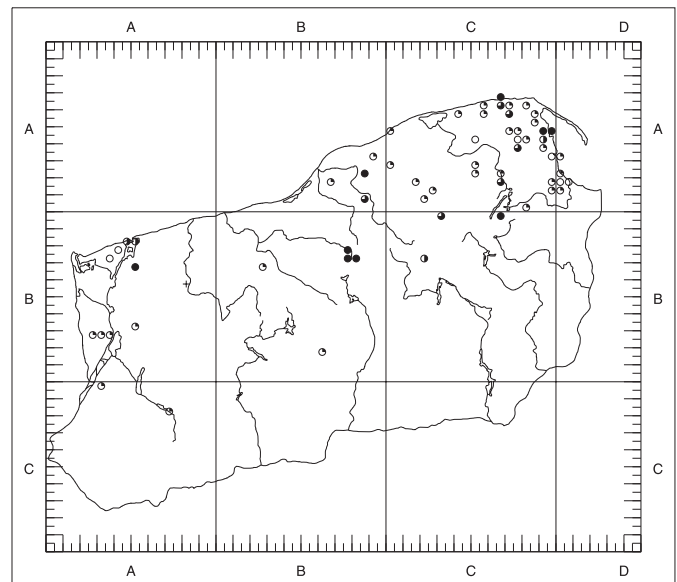
Fig. A25. *Carex panicea* L.*Carex pauciflora* Lightf.

Arctic-Alpic sub-element, Amphi-Arctic-Alpic group. Species typical of mountains, but found also in the lowlands. In Poland recorded mostly in the south: in the Bieszczady Mts, Gorce Mts, Tatras, Beskid Żywiecki Mts, and in the Sudetes. From the Sudetes it has spread also to the neighbouring areas of the Silesian-Lusatian Lowland (Nizina Śląsko-Łużycka). Its range is disjunct, as the species appears also in Pomerania, Warmia, and the Suwałki Region. Its range in northern Poland is related to the North European part of its main range of distribution. In Pomerania extremely rare (I), recorded exclusively in the Kashubian Lakeland and on the Słowińskie Coast (Pobrzeże Słowińskie) (Fig. A26). Eastern distributional type in Pomerania, *Rubus chamaemorus* subtype. Associated with various communities of raised bogs. In the mountains, found in mesotrophic sedge mires of the alliance *Caricion fuscae*, and in patches the raised bog community *Eriophoro-Trichophoretum caespitosi*. Geophyte. Pollination: wind. Dispersal: epizoochory, anemochory, autochory. Life strategy: S.

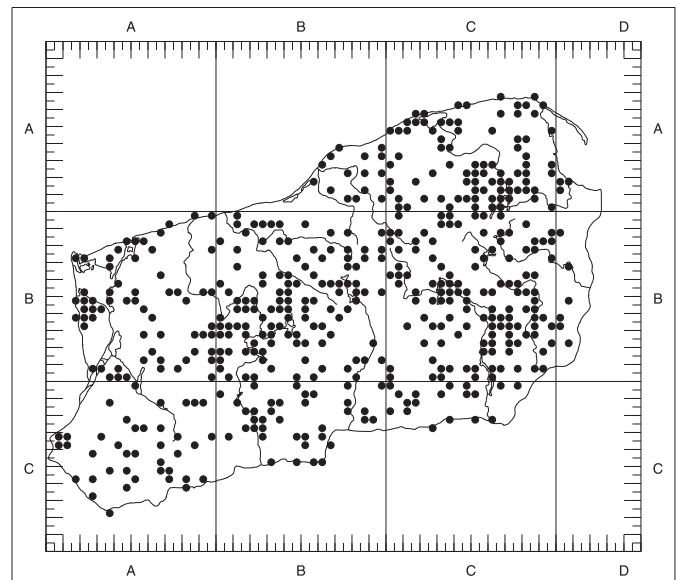
Fig. A26. *Carex pauciflora* Lightf.

Carex pulicaris L.

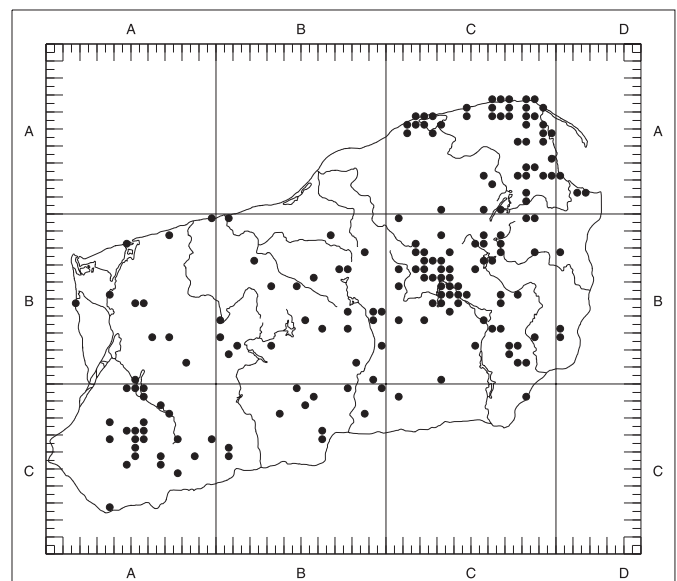
European-temperate (western) sub-element, extending to the Atlantic region of Europe. In Poland this species reaches the eastern limit of its general distribution. Recorded in Pomerania, the Silesian and Silesian-Lusatian Lowlands, Małopolska Upland, Sudetes, and Western Carpathians. Northern distributional type in Pomerania. Rare (III). In the past, the species was mostly recorded in the north-eastern part of the region. At present, its records are scattered and less numerous in the whole northern area (Fig. A27). Associated with plant communities of the order *Caricetalia davallianae*. Also found in wet heaths, purple moor-grass meadows with varied soil moisture content, as well as in montane *Nardus* grasslands of the alliance Nardion, and in sallow thickets. Hemicryptophyte. Pollination: wind. Dispersal: epizoochory. Life strategy: CSR.

Fig. A27. *Carex pulicaris* L.*Carex rostrata* Stokes

Circum-Boreal sub-element. Widespread in Poland, but less often reported from the Central Polish Lowlands and the south-eastern part of the country. In Pomerania frequent (VI) throughout the region (Fig. A28). All-Pomeranian distributional type, *Carex rostrata* subtype. Associated mostly with tall sedge communities, and with transitional bogs (order: *Scheuchzerietalia palustris*, rarely order: *Caricetalia nigrae*). Found also in raised bogs, wet and moist meadows, and sallow thickets (order: *Alnetalia glutinosae*). Hemicryptophyte, hydrophyte, helophyte. Pollination: wind. Dispersal: hydrochory, epizoochory, anemochory, autochory. Life strategy: CS.

Fig. A28. *Carex rostrata* Stokes*Carex viridula* Michx.

Circum-Boreal sub-element (disjunctive range). Frequent in Polesie, Roztocze, the eastern part of the Central Masovian Lowland (Nizina Środkowomazowiecka), and in the central Western Carpathians. In contrast, absent in the North Masovian Lowland, in the delta of the Vistula, and in Warmia. In other parts of Poland scattered. Widespread but infrequent (IV) in most of Pomerania, while absent on the Koszalin Coast. More frequent on the Słowińskie and Kashubian Coasts, in the Charzykowy Plain, and Myślibórz Lakeland (Fig. A29). All-Pomeranian distributional type, *Eriophorum latifolium* subtype. Found in low sedge mires of the orders *Caricetalia nigrae* and *Caricetalia davallianae*, in wet meadows of the order *Molinetalia caeruleae*, and salt-marshes of the order *Asteretea tripolium*. Present also in communities of the classes *Littorelletea uniflorae* and *Isoëto-Nanojuncetea*. Hemicryptophyte. Pollination: wind. Dispersal: hydrochory, epizoochory.

Fig. A29. *Carex viridula* Michx.

Chamaedaphne calyculata (L.) Moench

Circum-Boreal sub-element. In Poland the species reaches the south-western limit of its European range of distribution. Very rare, known only from about a dozen localities in the Masurian Lakeland, Pomerania, Podlasie, Polesie, and Masovian Lowlands. In Pomerania extremely rare (I), recorded in only 2 localities: in the Tuchola Forest and in the Drawa National Park (Fig. A30). These are its westernmost local populations in Europe. The species does not belong to any of the distinguished distributional types. Found mostly in open raised bogs, in the association *Sphagnetum magellanici*, and rarely in wet coniferous forests. Woody chamaephyte. Dispersal: epizoochory.

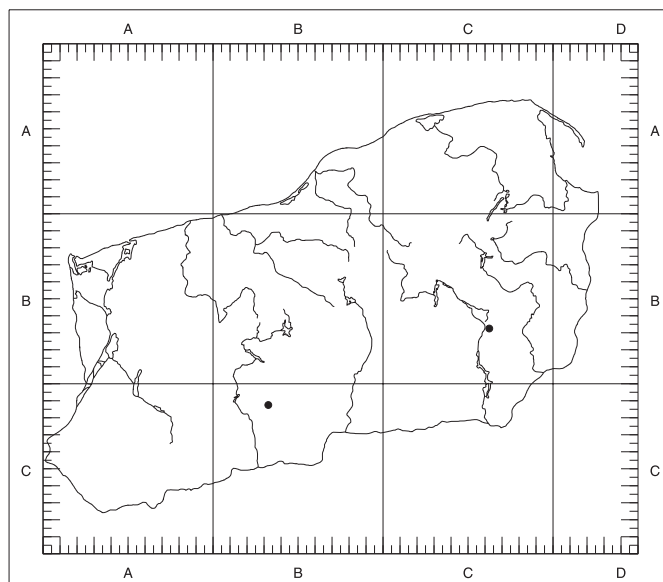


Fig. A30. *Chamaedaphne calyculata* (L.) Moench

Comarum palustre L.

Circum-Boreal sub-element. In Poland common except for the Carpathians, where it reaches the southern limit of its distribution. Less frequent in the central and south-eastern part of the country, and in eastern Germany. In Pomerania frequent (VI) particularly in the north-western and eastern parts, and in the belt of lakelands (Fig. A31). All-Pomeranian distributional type, *Carex nigra* subtype. Often recorded in communities of mires of the class *Scheuchzerio-Caricetea nigrae*, rarely of the class *Oxycocco-Sphagnetea*. Numerous also in wet meadows, tall sedge communities, and sallow thickets. Chamaephyte. Pollination: insects. Dispersal: hydrochory. Life strategy: CS.

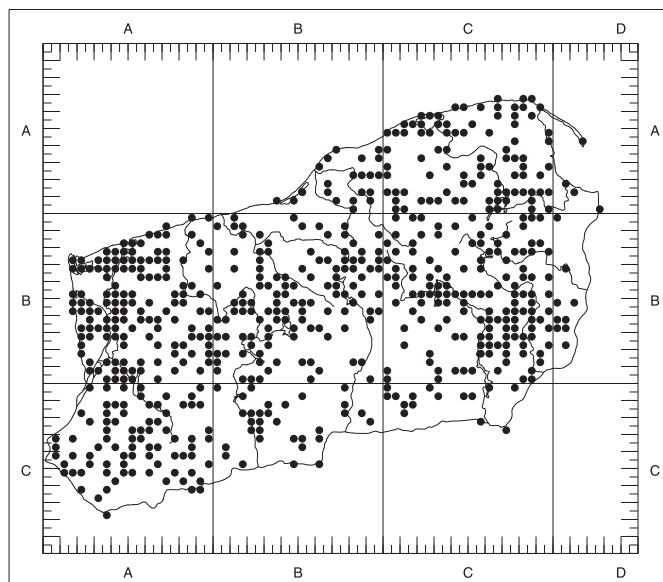


Fig. A31. *Comarum palustre* L.

Dactylorhiza incarnata (L.) Soó

Connective element, linking Euro-Siberian, Mediterranean (northern), and Irano-Turanian (mountains) elements, extending to the Atlantic region of Europe. In Poland distributed mostly in lowlands and in the belt of uplands. Frequent in eastern Poland, while very rare in the mountains and in the south-east. In Pomerania moderately frequent (V), scattered throughout the region, except for the central part of the Baltic coast (Fig. A32). All-Pomeranian distributional type, *Dactylorhiza incarnata* subtype. Associated with low sedge mires, fens, and transitional bogs. Found also in purple moor-grass meadows, rarely in emergent vegetation and alder forests. Geophyte. Pollination: insects. Dispersal: anemochory. Life strategy: CSR.

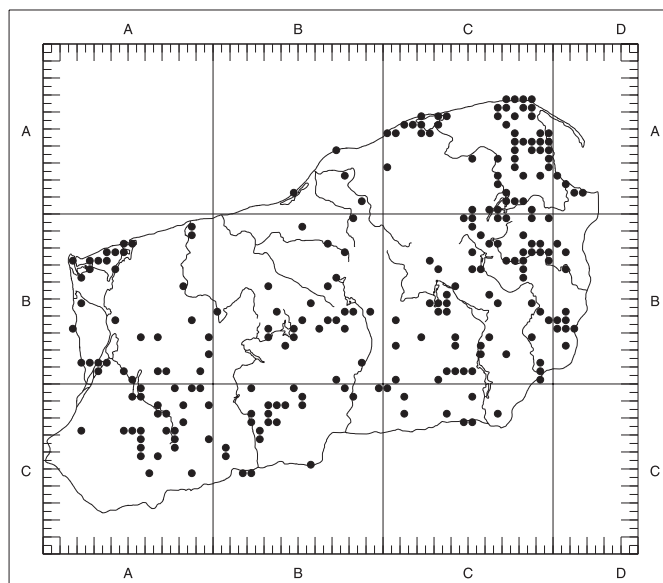


Fig. A32. *Dactylorhiza incarnata* (L.) Soó

Dactylorhiza maculata (L.) Soó

Connective element, linking Euro-Siberian and Mediterranean (northern) elements, extending to the Atlantic region of Europe. Widespread in Poland. Frequent in the Carpathians, while in other parts of Poland recorded less often, except for Polesie and the Masovian Lowlands. In Pomerania moderately frequent (V), concentrated in the eastern and north-western parts of the region, while scattered elsewhere (Fig. A33). All-Pomeranian distributional type, *Dactylorhiza incarnata* subtype. Usually found in fens and transitional bogs, wet and moist meadows, and riparian forests. Geophyte. Pollination: insects. Dispersal: anemochory. Life strategy: CSR.

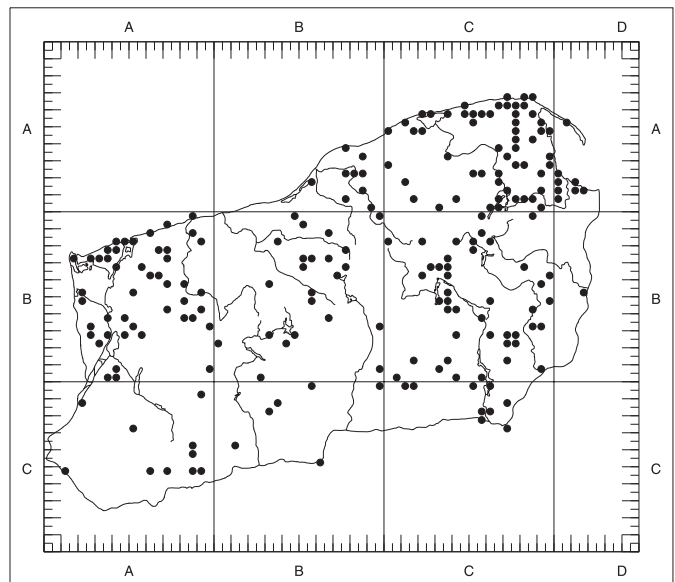


Fig. A33. *Dactylorhiza maculata* (L.) Soó

Drosera anglica Huds.

Circum-Boreal sub-element (disjunctive range), absent from mid-eastern Asia. In Poland distributed mostly in the lakelands, the western part of the South Wielkopolska Lowland, Silesian Lowland, Silesian Upland, Małopolska Upland, Lublin Upland, and Polesie. In Pomerania moderately frequent (V), concentrated in the eastern part of the region. Moreover, recorded in the belt of lakelands and at the north-western margins of Pomerania (Fig. A34). Eastern distributional type in Pomerania, *Drosera anglica* subtype. Recorded usually in communities of transitional bogs of the order *Scheuchzerietalia palustris*. Rare and never abundant in communities of the order *Caricetalia nigrae*, as well as of the alliance *Magnocaricion*. Hemicryptophyte. Pollination: self-pollination, cleistogamous. Dispersal: anemochory. Life strategy: S.

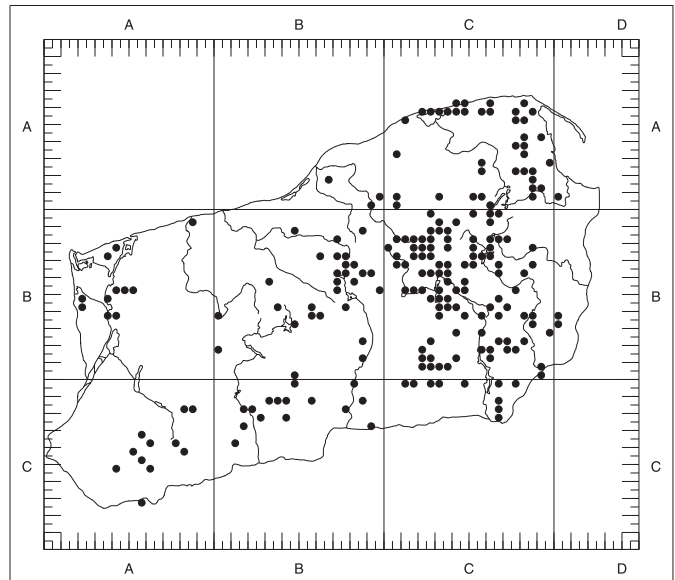


Fig. A34. *Drosera anglica* Huds.

Drosera intermedia Hayne

Amphi-Atlantic sub-element. In Poland the species has the eastern limit of its range. Distributed mostly in Pomerania, the Silesian-Lusatian Lowland, Silesian-Kraków Upland, Lublin Upland, and Polesie. In other parts of Poland absent, or recorded only in scattered localities. In Pomerania infrequent (IV), found chiefly in the Tuchola Forest, Wałcz Lakeland, on the Kashubian Coast, and in the eastern part of the Słowińskie Coast (Fig. A35). Eastern distributional type in Pomerania, *Drosera anglica* subtype. Associated with transitional bogs, especially of the alliance *Rhynchosporion albae*. Moreover, relatively frequent in communities of the classes *Oxycocco-Sphagnetea*, *Utricularietea intermedio-minoris*, *Littorelletea uniflorae*, *Phragmitetea* (Gugnacka-Fiedor 1988). Hemicryptophyte. Pollination: self-pollination, cleistogamous. Dispersal: anemochory. Life strategy: S.

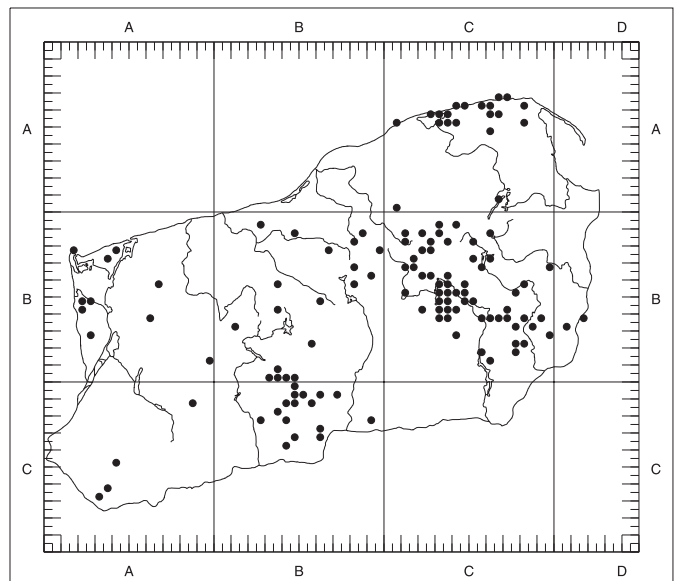
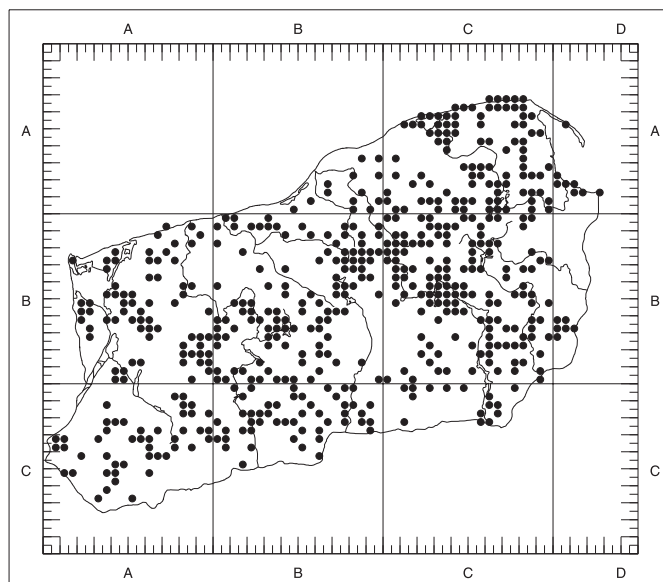


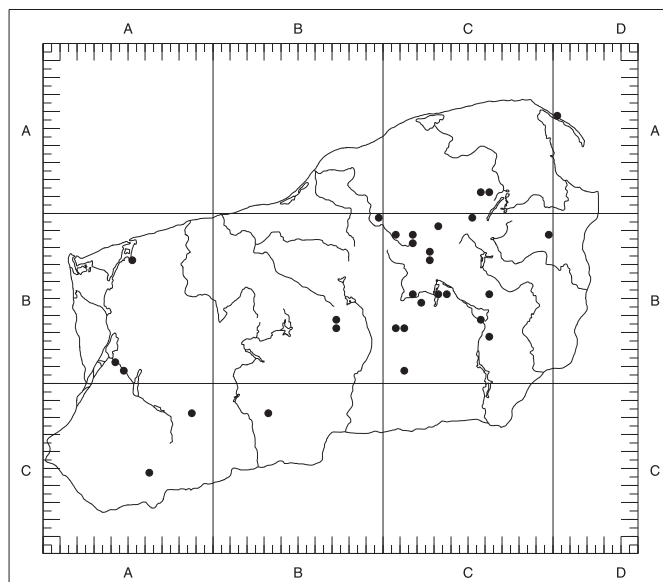
Fig. A35. *Drosera intermedia* Hayne

Drosera rotundifolia L.

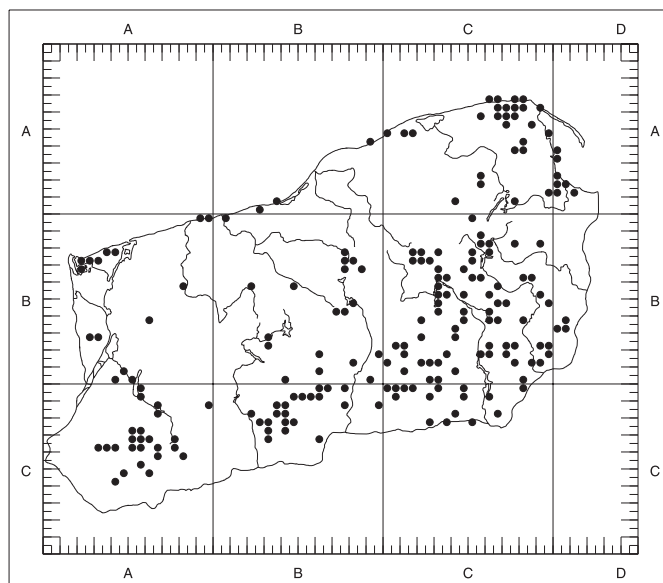
Circum-Boreal sub-element, Circum-Boreal group proper. Found all over Poland, rarely in the Central Polish Lowlands, in the south-west and south-east. Widespread in Pomerania, frequent (VI), found mostly in Pomeranian Lakeland and on the Kashubian and Słowińskie Coasts (Fig. A36). All-Pomeranian distributional type, *Rhynchospora alba* subtype. Associated with raised bogs of the class *Oxycocco-Sphagnetea*, less often with transitional bogs of the alliance *Rhynchosporion albae*. Recorded also in fens and moist depressions between dunes. Hemicryptophyte. Pollination: self-pollination, cleistogamous. Dispersal: anemochory. Life strategy: S.

Fig. A36. *Drosera rotundifolia* L.*Eleocharis mamillata* (H. Lindb.) H. Lindb. ex Dörfel. s. str.

Euro-Siberian sub-element (disjunctive range). Rare in Poland, somewhat more frequent only in the Beskid Niski Mts, at the Carpathian Foothills, and at the south-western margins of the Silesian-Kraków Upland. Moreover, found in scattered localities in Pomerania, the Masurian Lakeland, eastern part of the Central Masovian Lowland, and in the western part of the South Wielkopolska Lowland. In Pomerania very rare (II), recorded chiefly in the Bytów Lakeland, Krajna Lakeland, and Tuchola Forest (Fig. A37). The species does not belong to any of the distinguished distributional types. Found mostly in dystrophic or mesotrophic communities of transitional bogs of the alliance *Caricion lasiocarpae*, less often in tall sedge communities of the alliance *Magnocaricion*. Found also on bare peat and at bare gravelly or mucky margins of lakes. Geophyte, hydrophyte, helophyte. Pollination: wind. Dispersal: anemochory, epizoochory, hydrochory. Life strategy: CS.

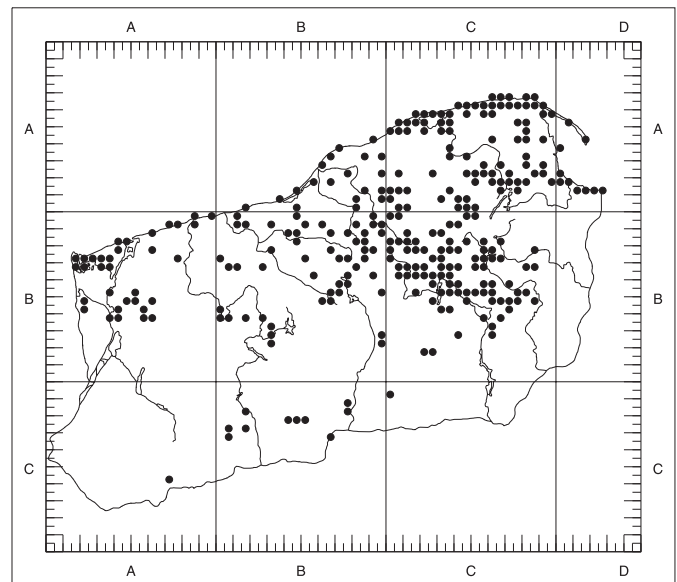
Fig. A37. *Eleocharis mamillata* (H. Lindb.) H. Lindb. ex Dörfel. s. str.*Eleocharis quinqueflora* (Hartmann) O. Schwarz

Circum-Boreal sub-element (disjunctive range). Distributed all over Poland, mostly recorded in the Masurian Lakeland, Pomerania, Kuyavian Lakeland (Pojezierze Kujawskie), and in the mountains: the Tatras and Beskid Żywiecki Mts. In contrast, rarely reported from the Masovian Lowlands, South Wielkopolska Lowland, and the south-eastern part of the country. In Pomerania moderately frequent (V), found mostly in the east and south, rarely in the north (Fig. A38). All-Pomeranian distributional type, *Eriophorum latifolium* subtype. Frequent in calcareous fens and spring-water mires of the order *Caricetalia davallianae*, but also on moist, gravelly or sandy lake shores. Occasionally present in moist meadows, emergent vegetation, and salt-marshes. Hemicryptophyte. Pollination: wind. Dispersal: anemochory, epizoochory, hydrochory. Life strategy: CSR.

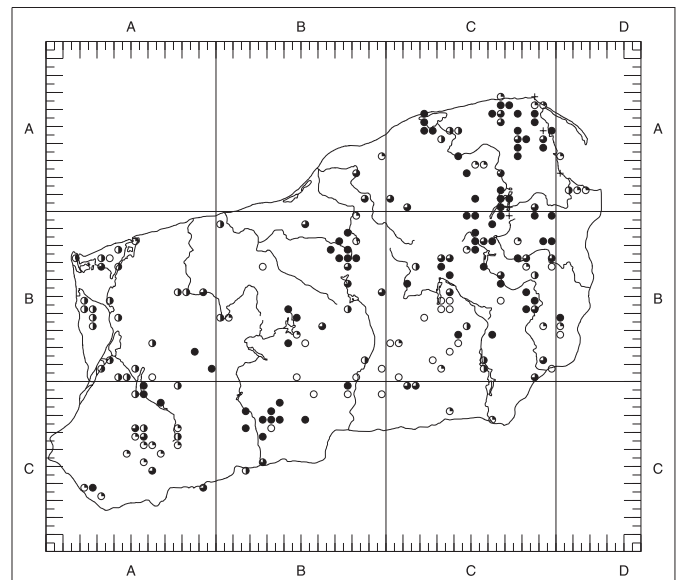
Fig. A38. *Eleocharis quinqueflora* (Hartmann) O. Schwarz

Empetrum nigrum L. s. str.

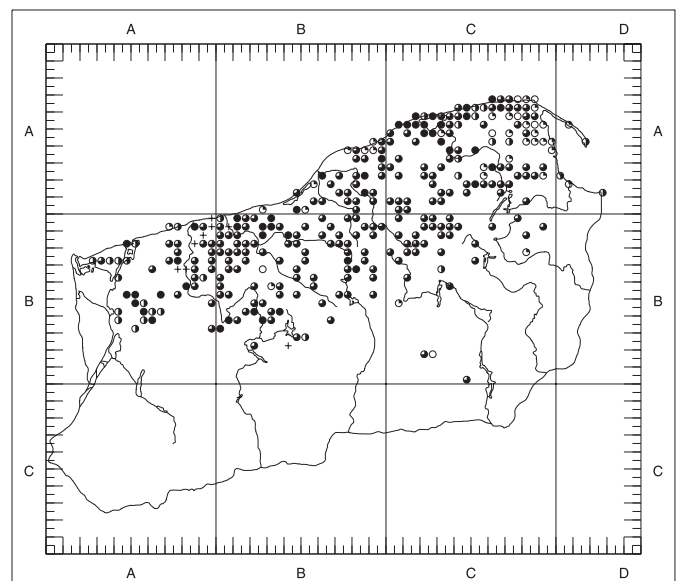
Circum-Boreal sub-element (disjunctive range). In Poland widespread in the north, while infrequent in the Sudetes, Tatras, and Bieszczady Mts. In Pomerania moderately frequent (V), recorded mostly in the northern part of the region, more frequent in the Tuchola Forest, in the Bytów and Kashubian Lakelands, as well as on the Kashubian and Słowińskie Coasts (Fig. A39). Northern distributional type in Pomerania. Associated with coastal crowberry heaths. Found also in raised bogs and in coniferous forests of the alliance *Dicrano-Pinion* (phytocoenotic optimum in coastal pine forests, *Empetro nigri-Pinetum*). Woody chamaephyte. Pollination: insects, self-pollination. Dispersal: endozoochory. Life strategy: CSR.

Fig. A39. *Empetrum nigrum* L. s. str.*Epipactis palustris* (L.) Crantz

Connective element, linking Euro-Siberian, Mediterranean (northern), and Irano-Turanian (mountains) elements, extending to the Atlantic region of Europe. Distributed throughout Poland, rarely in the central and south-eastern part of the country. In Pomerania moderately frequent (V), except for the central part of the Polish Baltic coast (Fig. A40). All-Pomeranian distributional type, *Dactylorhiza incarnata* subtype. Found mostly in fens and in low sedge mires of the order *Caricetalia davallianae*. Recorded also in wet purple moor-grass meadows and in riparian forests. Geophyte. Pollination: insects, self-pollination. Dispersal: anemochory. Life strategy: CSR.

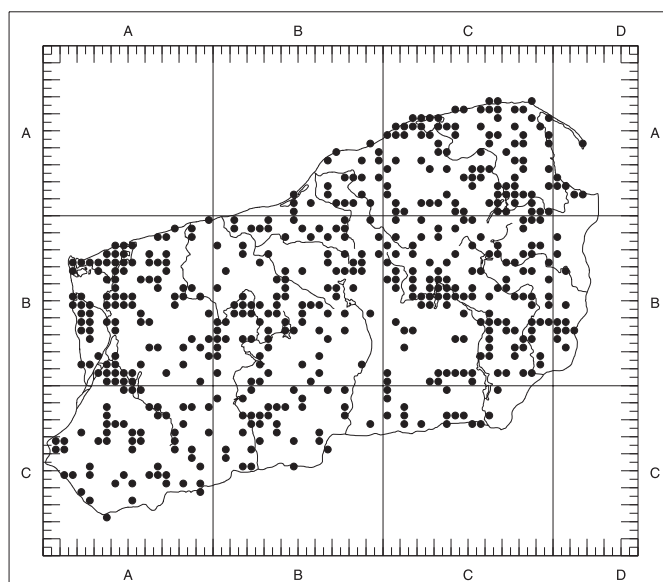
Fig. A40. *Epipactis palustris* (L.) Crantz*Erica tetralix* L.

European-temperate sub-element, European-temperate-lowland group, Atlantic proper distributional type. In Poland distributed not only at the Baltic coast, but also in large parts of the West Pomeranian Lakeland. It reaches to the Gulf of Gdańsk, which is the eastern limit of its main distribution range. Local populations east of the Vistula are outside its main range. Recorded also in the Silesian-Lusatian Lowland and in scattered localities in the Wielkopolska Lakeland, South Wielkopolska Lowland, Silesian-Kraków Upland, and Sudetian Foothills. In Pomerania moderately frequent (V) (Fig. A41). Northern distributional type. Associated with humid heaths, raised bogs, coastal pine forests (*Empetro nigri-Pinetum*), wet coniferous forests, and wet birch forests. Woody chamaephyte. Pollination: insects. Dispersal: anemochory. Life strategy: CS.

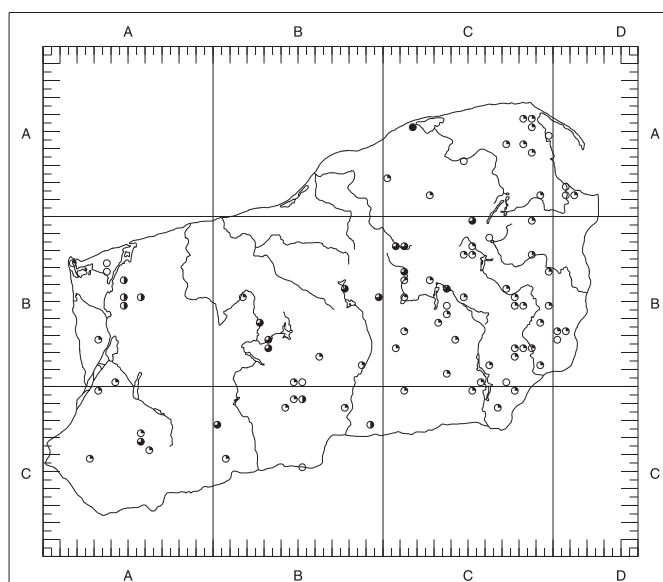
Fig. A41. *Erica tetralix* L.

Eriophorum angustifolium Honck.

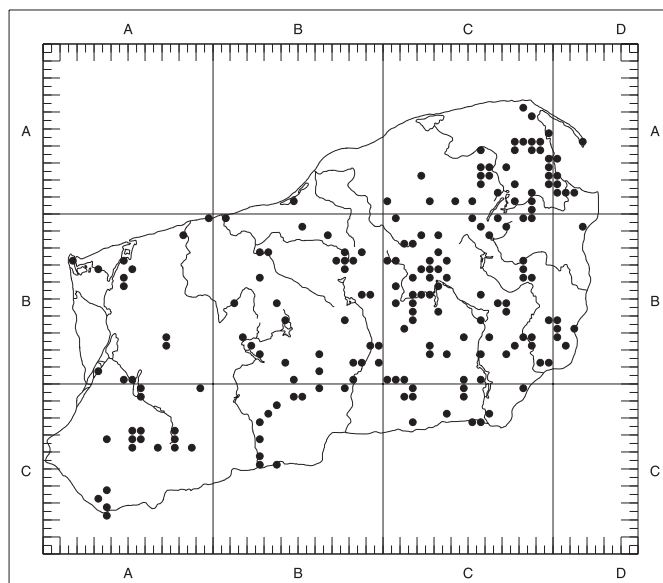
Circum-Boreal sub-element. In Poland frequent except for the alluvial delta of the Vistula. Nonetheless, clearly less frequent in central lowlands and the south-eastern corner of the country. In Pomerania frequent (VI) throughout the region (Fig. A42). All-Pomeranian distributional type, *Carex nigra* subtype. Recorded mostly in communities of mires of the class *Scheuchzerio-Caricetea nigrae*, rarely of the class *Oxycocco-Sphagnetea*. Found also in moist meadows of the alliance *Calthion palustris* and *Molinion caeruleae*, in tall sedge communities, and sallow thickets. Geophyte. Pollination: wind. Dispersal: anemochory. Life strategy: CS.

Fig. A42. *Eriophorum angustifolium* Honck.*Eriophorum gracile* W. D. J. Koch

Circum-Boreal sub-element, Circum-Boreal group proper. Distributed mostly in northern Poland, Polesie, and Roztocze. Absent in central lowlands, rare in other parts of Poland. In Pomerania rare (III), recorded outside the Koszalin Coast, Gryfice Plain, and the western part of the Szczecin Lowland (Fig. A43). All-Pomeranian distributional type, *Hammarbya paludosa* subtype. Found in transitional bogs of the order *Scheuchzerietalia palustris* (phytocoenotic optimum in the association *Caricetum lasiocarpae*), and low sedge mires of the order *Caricetalia nigrae*. Geophyte. Pollination: wind. Dispersal: anemochory. Life strategy: CS.

Fig. A43. *Eriophorum gracile* W. D. J. Koch*Eriophorum latifolium* Hoppe

Connective element, linking Euro-Siberian (disjunctive range) and Mediterranean (northern) elements, extending to the Atlantic region of Europe. Frequent in Poland, particularly in its south-eastern part. In contrast, relatively rarely reported from the Masovian Lowlands. In Pomerania infrequent (IV), widely distributed except for the Słowińskie Coast (Fig. A44). All-Pomeranian distributional type, *Eriophorum latifolium* subtype. Found in peatlands developed on calcareous lake sediments (marl). Associated with low sedge mires of the order *Caricetalia davalliana*. Occasionally appearing in communities of the order *Molinietalia*. Hemicryptophyte. Pollination: wind. Dispersal: anemochory. Life strategy: CS.

Fig. A44. *Eriophorum latifolium* Hoppe

Eriophorum vaginatum L.

Circum-Boreal sub-element. Frequent in Poland, but scattered in the Carpathians, Silesian Lowland, and Central Polish Lowlands. In Pomerania widespread, frequent (VI), recorded mostly in the Charzykowy Plain, the Tuchola Forest, the Kashubian Lakeland, and on the Słowińskie Coast (Fig. A45). All-Pomeranian distributional type, *Rhynchospora alba* subtype. Constant component of raised bogs. Found also in wet coniferous forest and humid heaths, rarely in communities of the alliance *Rhynchosporion albae*. Hemicryptophyte. Pollination: wind. Dispersal: anemochory. Life strategy: CS.

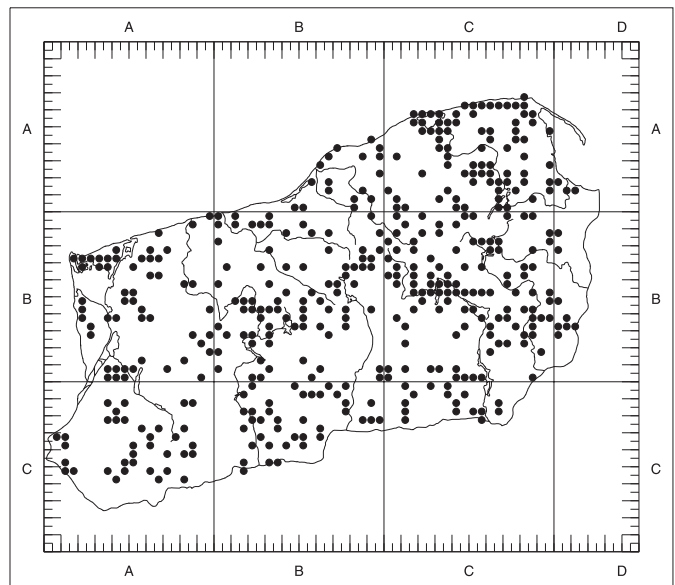


Fig. A45. *Eriophorum vaginatum* L.

Hammarbya paludosa (L.) Kuntze

European-temperate sub-element, European-temperate-lowland group. Very rare in Poland, reaching the southern limit of its distribution range. Reported mostly from the north, chiefly in the belt of lakelands, with a centre of distribution in the Suwałki Region. Moreover, recorded in isolated localities in southern Poland: in Polesie, the Świętokrzyskie Mts, Silesian-Kraków Upland, and Silesian-Lusatian Lowland. Most of its local populations do not exist any more. In Pomerania rare (III), found along the Baltic coast, in the Szczecin Lowland, and in the belt of lakelands (Fig. A46). All-Pomeranian distributional type, *Hammarbya paludosa* subtype. Found in open raised bogs, transitional bogs, and in moist depressions between dunes (phytocoenotic optimum in transitional bogs of the alliance *Rhynchosporion albae*). Geophyte, hemicryptophyte. Pollination: insects, self-pollination. Dispersal: autochory, anemochory. Life strategy: CS.

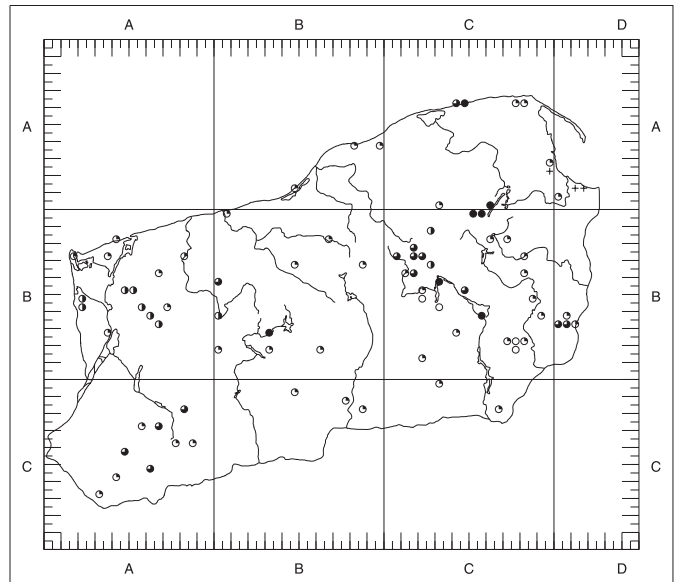


Fig. A46. *Hammarbya paludosa* (L.) Kuntze

Herminium monorchis (L.) R. Br.

Euro-Siberian-Asiatic sub-element (in the mountains). Very rare in Poland (located outside its main distribution range), reported from only 18 localities in the Masurian Lakeland, Pomerania, Lubusz Lakeland, in river valleys of the middle Odra (Oder) and middle Vistula, as well as in the Lublin Upland. At present its only confirmed local population is in the Rospuda river valley, in the Augustów Forest. In Pomerania extremely rare (I), recorded at several sites, which do not exist any more: in the valley of the Brda and on the island of Wolin (Fig. A47). Disjunctive distributional type. In Poland its last local population is found in the mire association *Drepanoclado-Caricetum limosae*. Geophyte. Pollination: insects. Dispersal: autochory, anemochory. Life strategy: CSR.

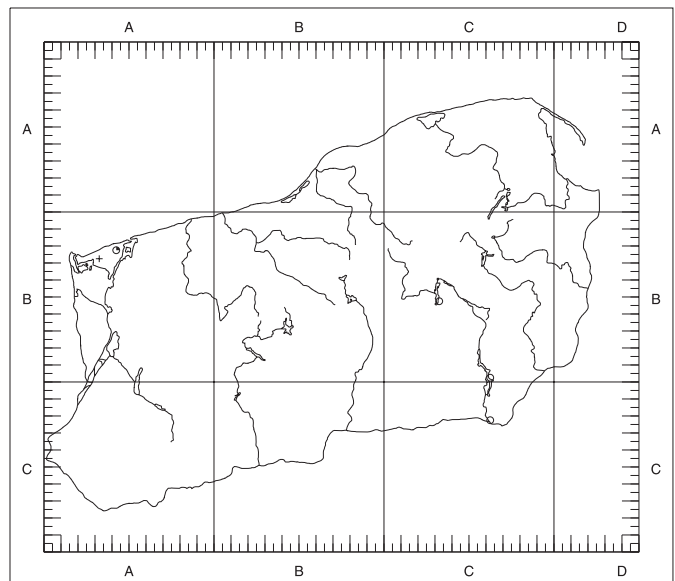
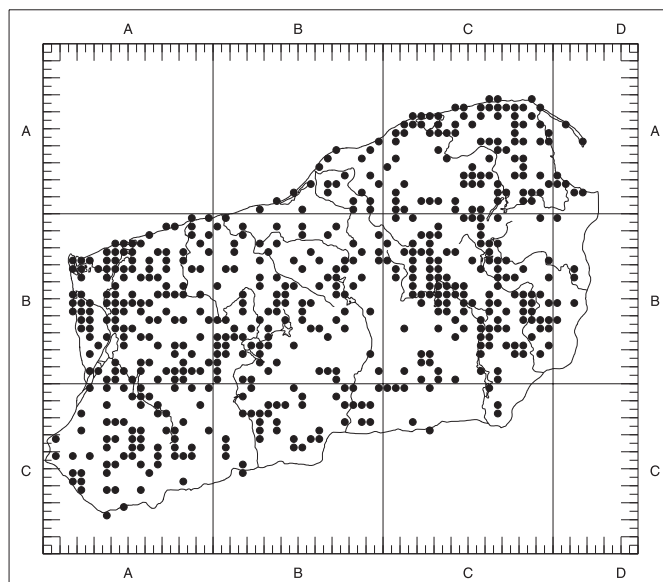


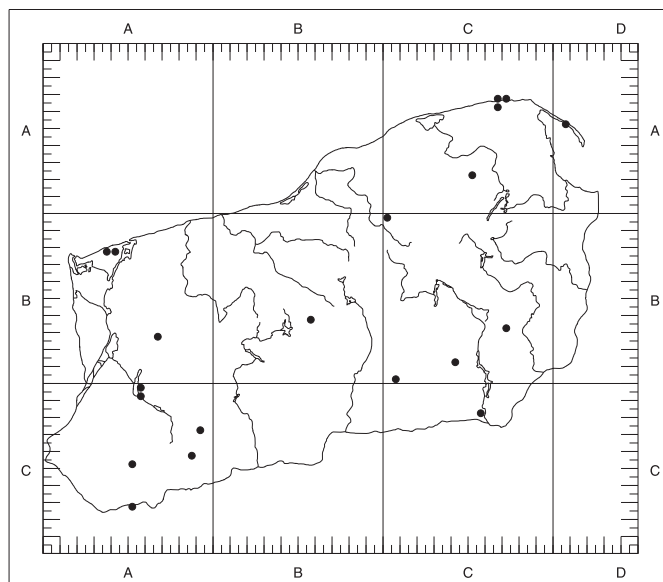
Fig. A47. *Herminium monorchis* (L.) R. Br.

Hydrocotyle vulgaris L.

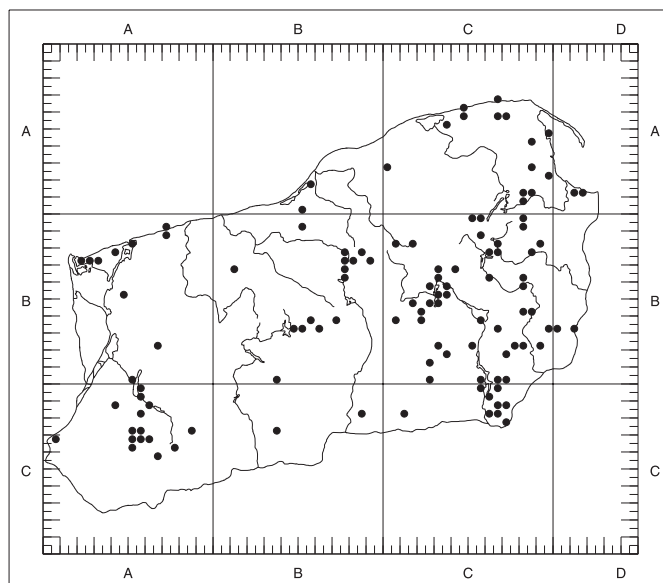
European-temperate sub-element, European-temperate-lowland group, Sub-Atlantic distributional type. In Poland this species reaches the south-eastern limit of its main distribution range. Within the range frequent, while absent in the submontane zone in the Carpathians and Karkonosze Mts, and scattered in the Masurian Lakeland. Frequent (VI) in Pomerania (Fig. A48). All-Pomeranian distributional type, *Carex nigra* subtype. Found in communities of the classes *Scheuchzerio-Caricetea nigrae* and *Litoretetea uniflorae*. Associated mostly with low sedge mires of the order *Caricetalia nigrae*. Found also in tall sedge communities, wet meadows, as well as willow thickets, montane alder forests, and wet birch forests. Hemicryptophyte. Pollination: self-pollination. Dispersal: hydrochory. Life strategy: S.

Fig. A48. *Hydrocotyle vulgaris* L.*Juncus acutiflorus* Ehrh. ex Hoffm.

European-temperate sub-element, European-temperate-lowland group, European-temperate Balkan distributional type, extending to the Atlantic region of Europe. In western Poland the species reaches the eastern limit of its distribution range. In Poland rare, recorded in Pomerania, the Silesian-Kraków Upland, the south-eastern part of the country, and in scattered localities in the Wielkopolska Lakeland. In Pomerania very rare (II), scattered throughout the region (Fig. A49). Disjunctive distributional type. Found in wet meadows of the order *Molinietalia caeruleae*, as well as in acid low sedge mires of the order *Caricetalia nigrae*. Geophyte, hemicryptophyte. Pollination: wind. Dispersal: anemochory, epizoochory. Life strategy: CS.

Fig. A49. *Juncus acutiflorus* Ehrh. ex Hoffm.*Juncus alpino-articulatus* Chaix

Circum-Boreal sub-element. Distributed throughout Poland, except its south-western margins. Most frequent in Roztocze, Polesie, the eastern part of the Central Masovian Lowland, and in the Silesian Upland and Silesian Lowland. In Pomerania infrequent (IV), concentrated mostly in the east and in the Myślubórz Lakeland, while in other regions generally scattered (Fig. A50). All-Pomeranian distributional type, *Eriophorum latifolium* subtype. Associated with low sedge mires of the order *Caricetalia davallianae*. Recorded also in acid low sedge mires of the order *Caricetalia nigrae* and in tall sedge communities of the alliance *Magnocaricion*. Hemicryptophyte. Pollination: wind. Dispersal: anemochory, epizoochory. Life strategy: CS.

Fig. A50. *Juncus alpino-articulatus* Chaix

Juncus filiformis L.

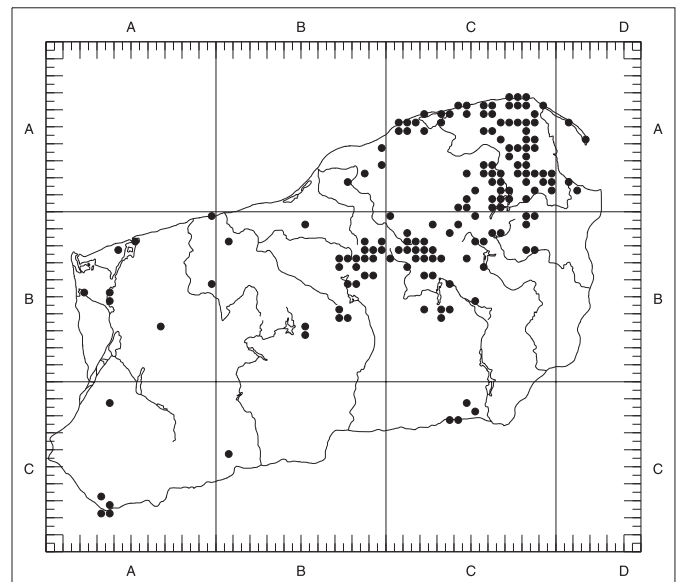
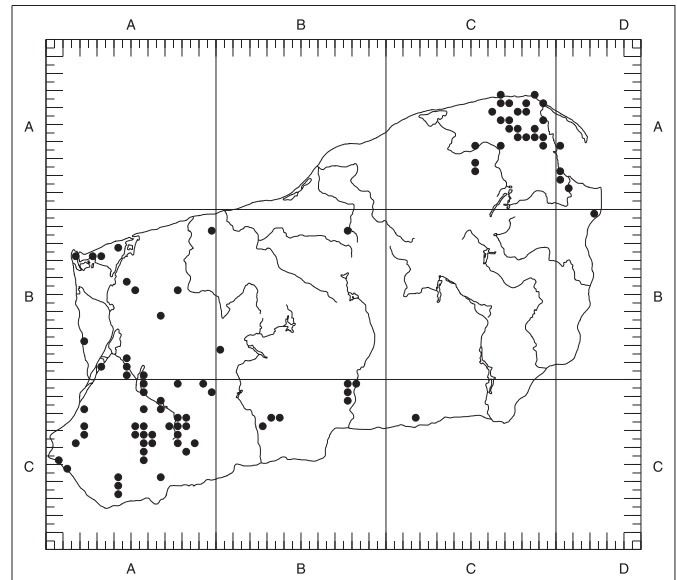
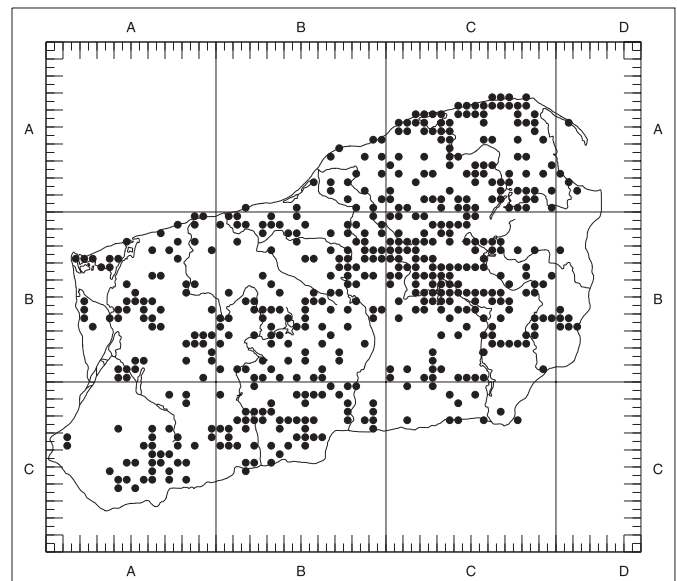
Circum-Boreal sub-element. Rare in Poland, recorded mostly in the north, south-west, in the Tatras, Western Beskid Mts, Silesian-Kraków Upland, and in the eastern part the Central Masovian Lowland. In central Poland probably absent (doubtful records). In Pomerania infrequent (IV), concentrated in the north-east, extending to the Bytów Lakeland and Charzykowy Plain (Fig. A51). Very rare in other parts of the region. Eastern distributional type in Pomerania, *Drosera anglica* subtype. Most frequent in acid low sedge mires of the order *Caricetalia nigrae*. Found also in wet meadows of the order *Molinietalia caeruleae*. Geophyte. Pollination: wind. Dispersal: anemochory, epizoochory. Life strategy: CSR.

Juncus subnodulosus Schrank

Connective element, linking European-temperate (western) and Mediterranean (northern) elements, European-temperate-lowland group, European-temperate Balkan distributional type, extending to the Atlantic region of Europe. In Poland the species has the eastern limit of its distribution range. Reported in Poland from Pomerania, the Lubusz and Wielkopolska Lakelands, and South Wielkopolska Lowland. An isolated stand was noted in the south, in the Opole Plain, while the isolated stand east of the lower Vistula is doubtful. In Pomerania rare (III), more frequent only on the Kashubian Coast and in the Myślubórz Lakeland. Absent on the Kozalin and Słowińskie Coasts, in the Tuchola Forest, and in the Kashubian, Bytów, Drawsko, and Krajna Lakelands (Fig. A52). Disjunctive distributional type. Found in low sedge mires on calcareous deposits, moist and wet meadows (alliance: *Calthion*; phytocoenotic optimum in the association *Juncetum subnodulosi*), and in tall sedge communities. Geophyte, hydrophyte, helophyte. Pollination: wind. Dispersal: anemochory, epizoochory. Life strategy: CS.

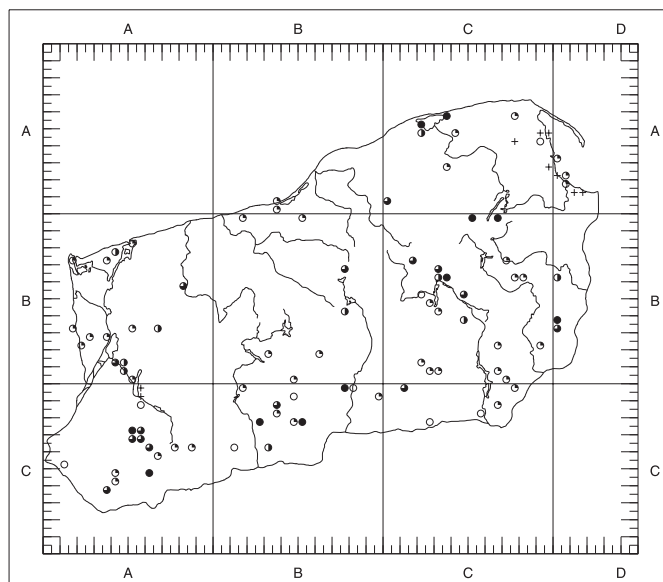
Ledum palustre L.

Circum-Boreal sub-element. South-eastern Poland is the southern limit of the distribution range of this species. Widespread in Polish lowlands, except for the Central Polish Lowlands, where it is absent or found occasionally. In the mountains rare, found in scattered localities. In Pomerania frequent (VI) throughout the region, particularly in the Charzykowy Plain, the Bytów and Kashubian Lakelands, and on the Słowińskie Coast (Fig. A53). All-Pomeranian distributional type, *Rhynchospora alba* subtype. Associated with raised bogs of the class *Oxycocco-Sphagnetea*, and with wet coniferous forests and birch forests of the suballiance *Piceo-Vaccinienion uliginosi* (mostly with the association *Vaccinio uliginosi-Pinetum*). Moreover, recorded in transitional bogs of the order *Scheuchzerietalia palustris*, as well as in spruce stands on peat. Nanophanerophyte, woody chamaephyte. Pollination: insects, self-pollination. Dispersal: anemochory. Life strategy: CS.

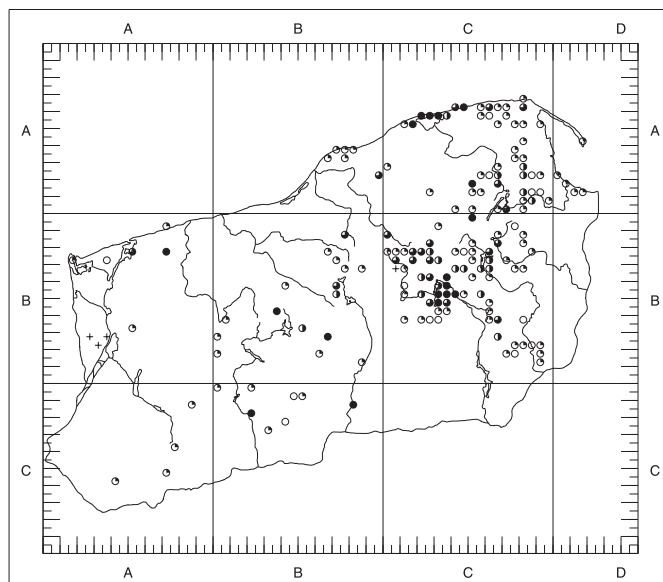
Fig. A51. *Juncus filiformis* L.Fig. A52. *Juncus subnodulosus* SchrankFig. A53. *Ledum palustre* L.

Liparis loeselii (L.) Rich.

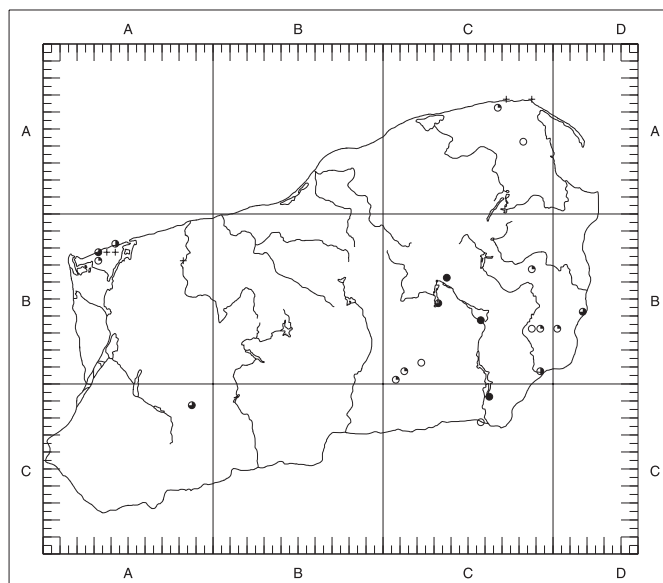
Circum-Boreal sub-element (disjunctive range). In Poland the species reaches the southern limit of its distribution range. Rare, recorded mostly in lakelands and in the western part of the country. Absent in the mountains. In Pomerania rare (III), scattered like in other parts of Poland (Fig. A54). All-Pomeranian distributional type, *Hammarbya paludosa* subtype. Associated with plant communities of the class *Scheuchzerio-Caricetea nigrae*, particularly with those of the alliance *Caricion davallianae*. Frequent also in communities of the alliance *Caricion lasiocarpae*, and very rare in communities of the alliance *Alnion glutinosae*. It is one of the major components of the association *Lipario-Schoenetum ferruginei*, distinguished in Poland by Głazek (1992), and *Schoenetum nigricantis*. Geophyte, hemi-cryptophyte. Pollination: self-pollination. Dispersal: anemochory. Life strategy: CSR.

Fig. A54. *Liparis loeselii* (L.) Rich.*Lycopodiella inundata* (L.) Holub

Circum-Boreal sub-element, Circum-Boreal-Oceanic group. In Poland scattered; absent in the Suwałki Region, the North Masovian Lowland, and in south-eastern margins of Poland. In Pomerania infrequent (IV), most frequent in the Tuchola Forest and in the Kashubian Lakeland (Fig. A55). Eastern distributional type in Pomerania, *Drosera anglica* subtype. Associated with transitional bogs of the alliance *Rhynchosporion albae*, particularly as a component of the association *Rhynchosporium albae*. Found also in acid low sedge mires and less often in raised bogs (e.g. in the association *Sphagnetum magellanici*). Appears also in human-made habitats, e.g. in abandoned sand pits, at the edges of ponds, in mires where peat has been extracted recently, and on moist sandy humus. Woody chamaephyte. Dispersal: anemochory. Life strategy: SR.

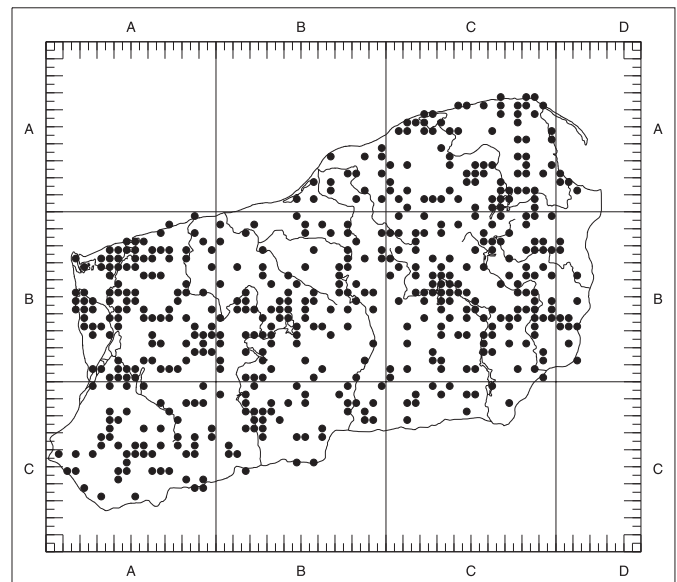
Fig. A55. *Lycopodiella inundata* (L.) Holub*Malaxis monophyllos* (L.) Sw.

Circum-Boreal sub-element (disjunctive range). Species typical of mountains, but found also in the lowlands. Some of its Polish local populations lie at the western limit of its range. Its records are concentrated in southern and north-eastern parts of Poland, which are separated by a clear disjunction in the Central Polish Lowlands. Its southern range includes the mountain ranges of Sudetes, Carpathians, and in the Silesian-Kraków, Małopolska, and Lublin Uplands as well as in Roztocze. The northern range covers the Masurian Lakeland and Pomerania. In Pomerania very rare (II), its range is discontinued in the central part of the region, while more numerous records are reported from the east (Fig. A56). Disjunctive distributional type. Recorded mostly in fens and transitional bogs, in moist deciduous forests, and in calcareous grasslands. Found also in secondary habitats, in fresh (i.e. moderately moist) pine forests. Geophyte. Pollination: insects, self-pollination. Dispersal: anemochory.

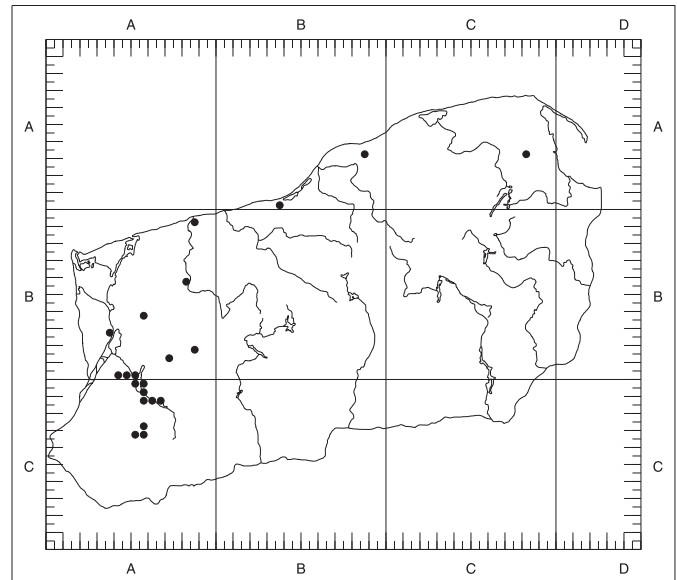
Fig. A56. *Malaxis monophyllos* (L.) Sw.

Menyanthes trifoliata L.

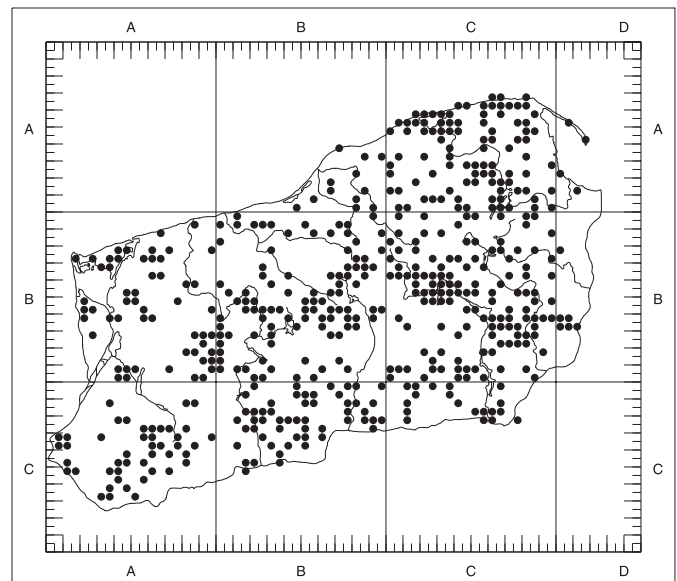
Circum-Boreal sub-element. Frequent throughout Poland, except for the North Masovian Lowland. In Pomerania widespread and frequent (VI). All-Pomeranian distributional type, *Carex nigra* subtype (Fig. A57). Most often found in patches of communities of the order *Scheuchzerietalia palustris* (phytocoenotic optimum in associations of the alliance *Caricion lasiocarpae*). Moreover, recorded in acid low sedge mires and in tall sedge communities. Reported also from wet meadows of the alliance *Calthion* and in willow thickets. Geophyte, hydrophyte, helophyte. Pollination: insects. Dispersal: endozoochory, autochory, epizoochory, hydrochory, anemochory. Life strategy: CS.

Fig. A57. *Menyanthes trifoliata* L.*Orchis palustris* Jacq.

Connective element, linking European-temperate, Mediterranean (northern), and Irano-Turanian (mountains) elements, extending to the Atlantic region of Europe. In Poland the species reaches the north-eastern limit of its distribution range. Very rare, with a centre of distribution in the Szczecin Lowland and Myślubórz Lakeland. Besides, recorded in scattered localities along the Baltic coast, in the Wielkopolska Lakeland and in the south: in the Silesian Lowland, Silesian-Kraków Upland, and at the Carpathian Foothills. Some of its records, including all the southern ones, are now historical. In Pomerania very rare (II) (Fig. A58). Western distributional type. Associated with low sedge mires on calcareous deposits, of the alliance *Caricion davallianae* (phytocoenotic optimum in the association *Orchido-Schoenetum*). Found also in patches of moist and wet meadows and tall sedge communities. Geophyte. Pollination: insects. Dispersal: anemochory. Life strategy: CSR.

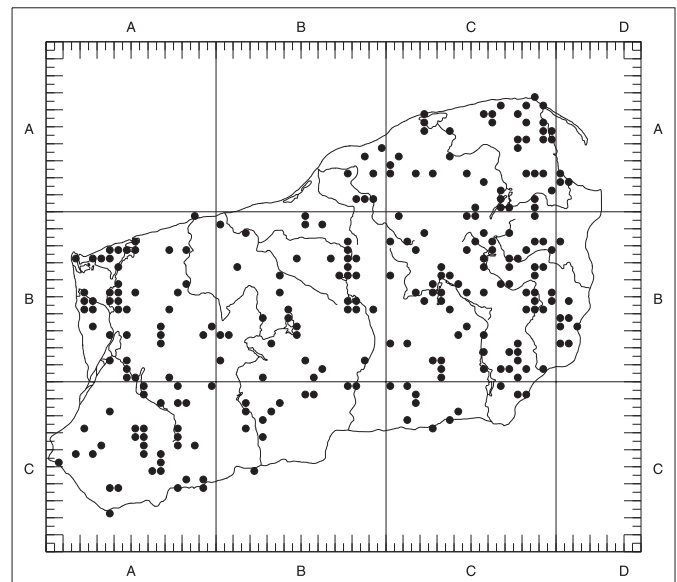
Fig. A58. *Orchis palustris* Jacq.*Oxycoccus palustris* Pers.

Circum-Boreal sub-element (disjunctive range). Scattered in the belt of Central Polish Lowlands and in the Carpathians, while frequently recorded in other parts of Poland. Frequent (VI) all over Pomerania, particularly in the belt of lakelands, the Tuchola Forest, and on the Słowińskie Coast (Fig. A59). All-Pomeranian distributional type, *Rhynchospora alba* subtype. Constant component of moss-dominated communities of raised bogs. Moreover, common in wet coniferous forests, humid heaths, and in communities of transitional bogs of the order *Scheuchzerietalia palustris*. Woody chamaephyte. Pollination: insects. Dispersal: endozoochory. Life strategy: CS.

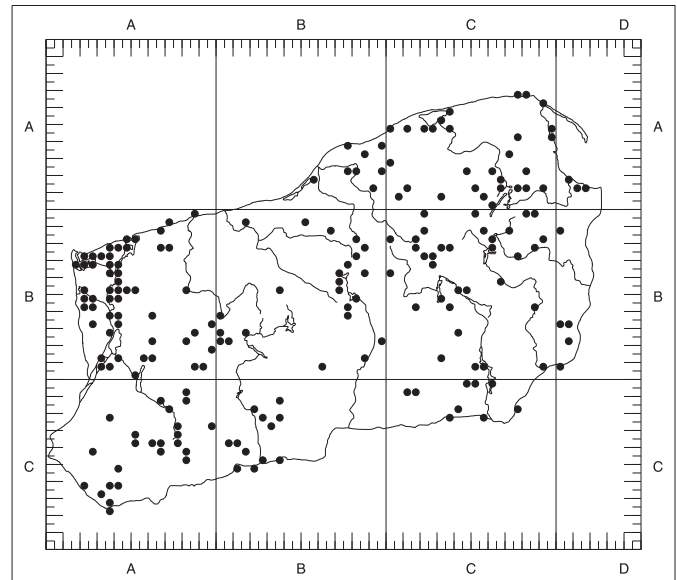
Fig. A59. *Oxycoccus palustris* Pers.

Parnassia palustris L.

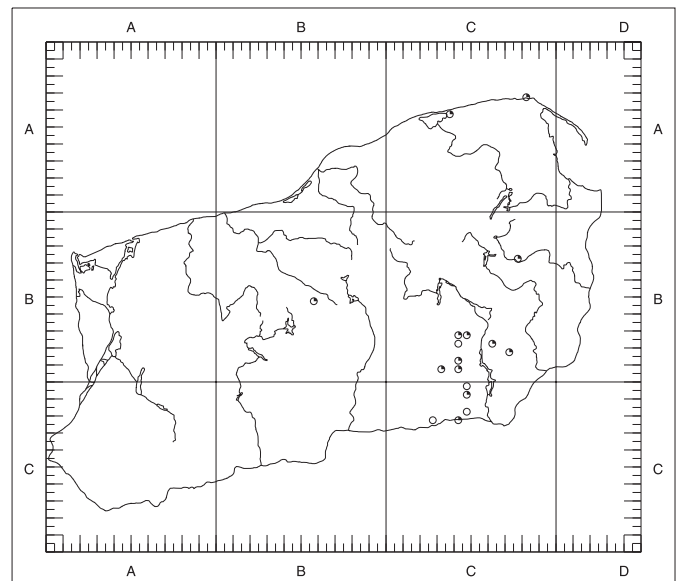
Circum-Boreal sub-element (northern). Frequent in Poland; less often reported only from the Sandomierz Basin (Kotlina Sandomierska), and the North Masovian Lowland. In Pomerania moderately frequent (V), distributed throughout the region but mostly in the east and on the Szczecin Coast (Fig. A60). All-Pomeranian distributional type, *Dactylorhiza incarnata* subtype. Associated with plant communities of low sedge mires, especially of the order *Caricetalia davallianae*. Numerous in communities of wet meadows of the order *Molinietales caeruleae*. Appears also in transitional bogs, tall sedge communities, and sallow thickets. Hemicryptophyte. Pollination: insects. Dispersal: anemochory. Life strategy: CSR.

Fig. A60. *Parnassia palustris* L.*Pedicularis palustris* L.

Euro-Siberian sub-element, extending to the Atlantic region of Europe. In Poland recorded in scattered localities; more frequent in the Western Carpathians, Małopolska Upland, Roztocze, Lublin Upland, and in Polesie. In Pomerania infrequent (IV), its records are most numerous in the Szczecin Lowland and on the island of Wolin, while scattered in other parts, and least frequent on the Koszalin Coast and in the Drawsko and Wałcz Lakelands (Fig. A61). All-Pomeranian distributional type, *Dactylorhiza incarnata* subtype. Associated mostly with sedge mires and transitional bogs of the alliance *Caricion lasiocarpae*. Found also in sallow thickets, tall sedge communities, and wet meadows. Hemicryptophyte. Pollination: insects. Dispersal: myrmecochory, anemochory.

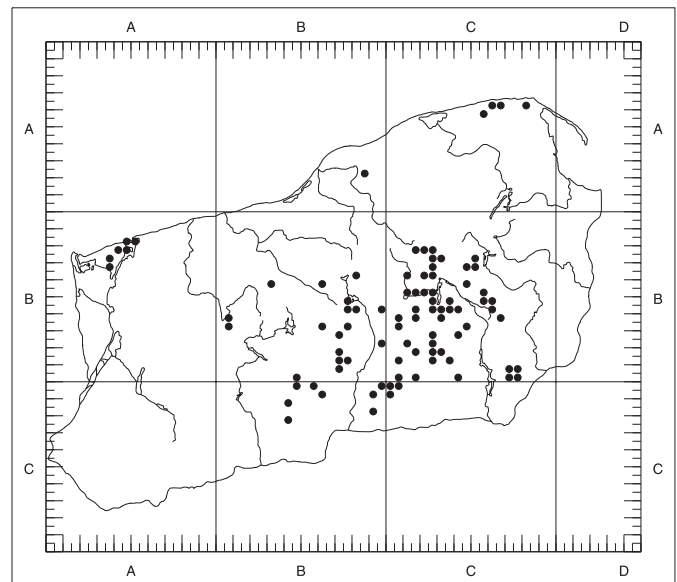
Fig. A61. *Pedicularis palustris* L.*Pedicularis sceptrum-carolinum* L.

Euro-Siberian sub-element. Poland is crossed by the western limit of its main distribution range. Rare west of the river Vistula. Local populations are concentrated in 2 regions: in north-eastern Poland and in Polesie. In Pomerania very rare (II), chiefly in the valley of the Brda (Fig. A62). Eastern distributional type in Pomerania, *Salix myrtilloides* subtype. No phytosociological data are available from Pomerania. In north-eastern Poland found in patches of communities of the order *Caricetalia davallianae*. Hemicryptophyte. Pollination: insects. Dispersal: myrmecochory, anemochory.

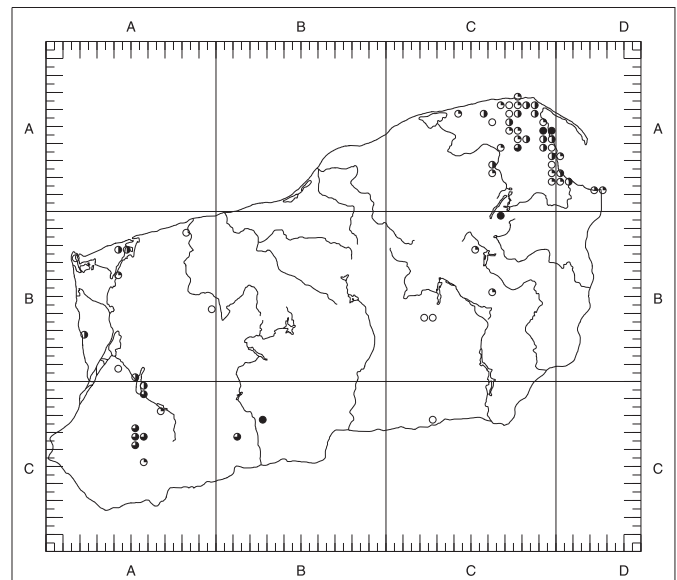
Fig. A62. *Pedicularis sceptrum-carolinum* L.

Pedicularis sylvatica L.

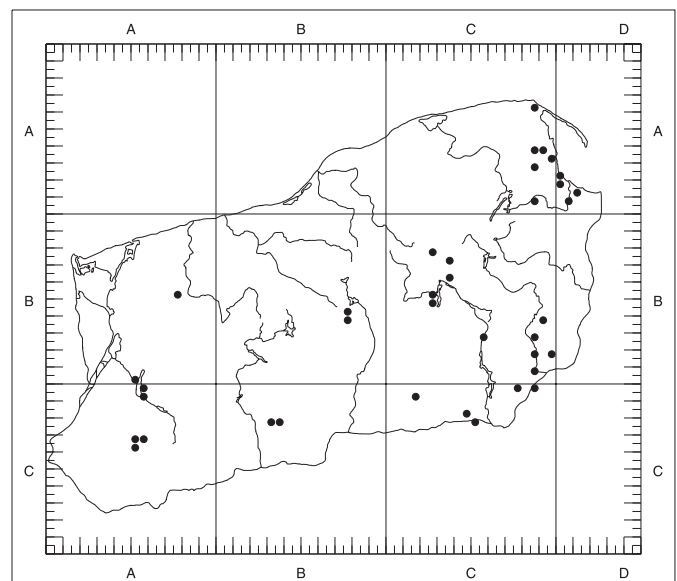
European-temperate sub-element, European-temperate-lowland group, Sub-Atlantic distributional type. In Poland it reaches the eastern limit of its distribution range. Frequent in western and southern Poland, while rare in the east and north-west. In Pomerania rare (III), reported mostly from the island of Wolin, Kashubian Coast, Tuchola Forest, and the Drawsko, Wałcz, and Krajna Lakelands (Fig. A63). The species does not belong to any of the distinguished distributional types. Most often found in *Nardus* grassland. Often reported also from fens and transitional bogs, less often from humid heaths, tall sedge communities, and moist meadows. Hemicryptophyte. Pollination: insects. Dispersal: myrmecochory, anemochory.

Fig. A63. *Pedicularis sylvatica* L.*Pinguicula vulgaris* L.

Circum-Boreal sub-element (disjunctive range). Polish records lie at the eastern limit of the distribution range of this species. They are generally scattered, but more numerous in Pomerania, the western part of the Wielkopolska Lakeland, the valley of the Odra, in the Silesian-Kraków Upland, Lublin Upland, Polesie, and the Carpathians. In Pomerania rare (III), recorded in the west and east, with a centre of distribution on the Kashubian Coast (Fig. A64). Disjunctive distributional type. Frequent on calcareous soils. Associated with fens, wet and moist meadows, springs, and flushes. Hemicryptophyte. Pollination: insects. Dispersal: anemochory, autochory.

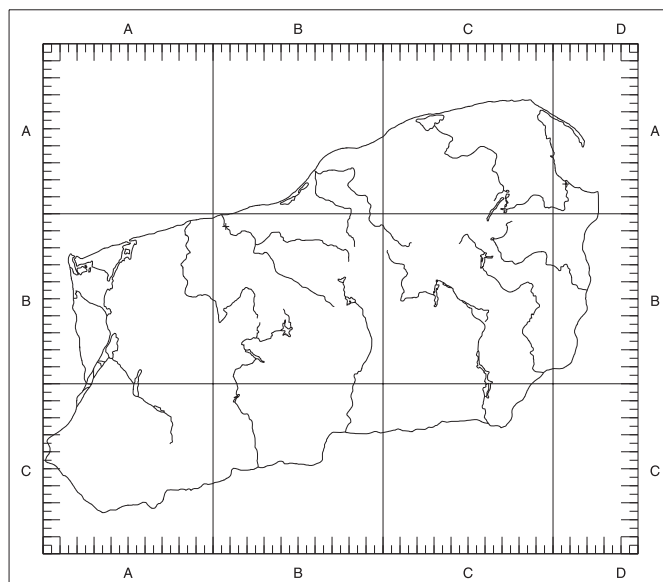
Fig. A64. *Pinguicula vulgaris* L.*Polygala amarella* Crantz

European-temperate sub-element. Frequent in the Wielkopolska Lakeland, Silesian Lowland, Lublin Upland, and Polesie. Less often recorded in Pomerania, central Poland, and at the south-eastern margins of the country. In Pomerania very rare (II), more frequent in the eastern, rare in the southern part of the region, generally scattered (Fig. A65). All-Pomeranian distributional type, *Hammarbya paludosa* subtype. Found in patches of communities of low sedge mires of the order *Caricetalia davallianae*, and wet and moist meadows of the order *Molinietalia caeruleae*. Hemicryptophyte. Pollination: insects. Dispersal: anemochory, myrmecochory. Life strategy: CSR.

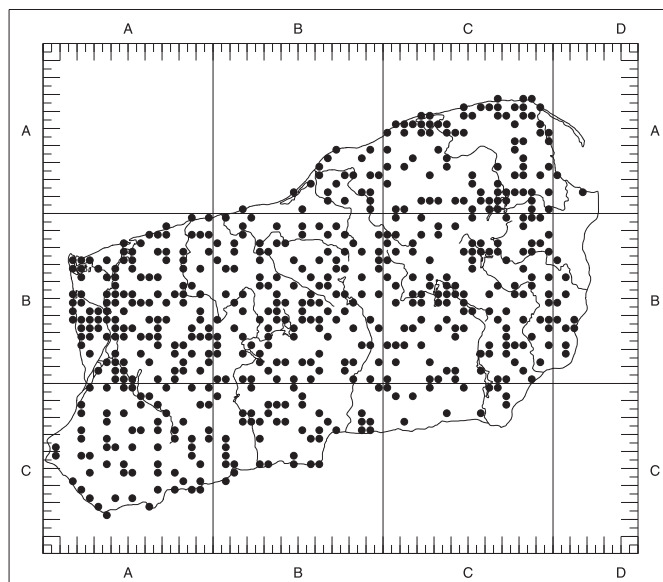
Fig. A65. *Polygala amarella* Crantz

Primula farinosa L.

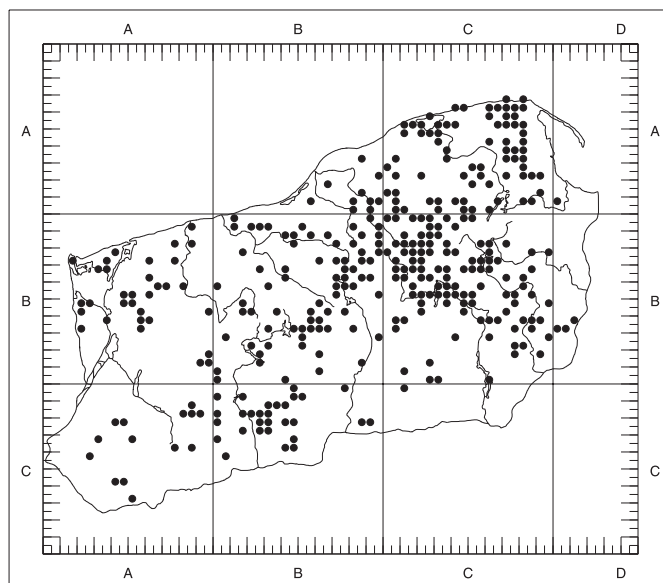
European-temperate sub-element, European-temperate-montane group, Alpic-North-European distributional type. In Poland recorded in the past in scattered, isolated localities, but now only in the Beskid Sądecki Mts. In Pomerania extremely rare (I), found earlier close to Zaspą near Gdańsk and close to Zieleniewo near Kołobrzeg (Fig. A66). Its closest present stands are located in the coastal part of the Mecklenburg region in Germany. The species does not belong to any of the distinguished distributional types. Associated with fens of the order *Caricetalia davallianae*. Hemicryptophyte. Pollination: insects. Dispersal: anemochory, myrmecochory. Life strategy: CSR.

Fig. A66. *Primula farinosa* L.*Ranunculus flammula* L.

Connective element, linking Euro-Siberian (western) and Mediterranean (northern) elements, extending to the Atlantic region of Europe. Frequent in Poland; common in some parts of the country. In Pomerania frequent (VI) throughout the region (Fig. A67). All-Pomeranian distributional type, *Carex nigra* subtype. Found in communities of low sedge mires, wet meadows, and sallow thickets, rarely tall sedge communities. Hemicryptophyte, hydrophyte, helophyte. Pollination: insects, self-pollination. Dispersal: anemochory, epizoochory, hydrochory. Life strategy: CSR.

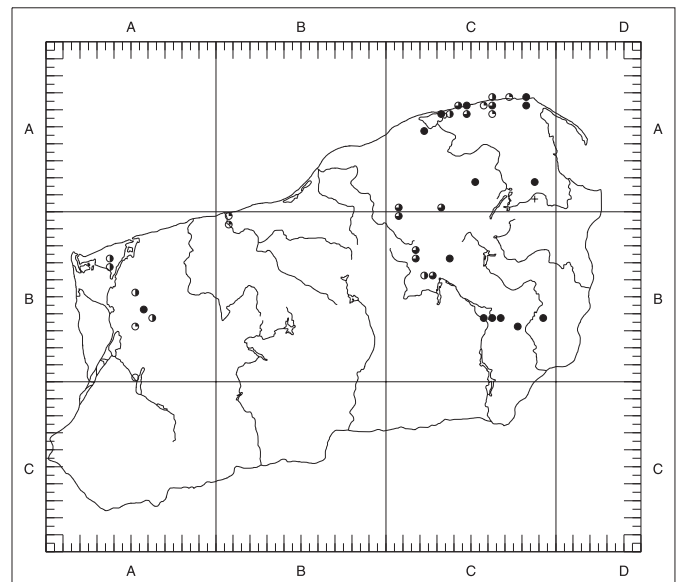
Fig. A67. *Ranunculus flammula* L.*Rhynchospora alba* (L.) Vahl

Circum-Boreal sub-element, Circum-Boreal-Oceanic group. In Poland recorded mostly in the north, west, in Polesie, and in the belt of Polish Uplands. In other parts of Poland absent or scattered. In Pomerania moderately frequent (V), widely distributed, recorded most often in the Charzykowy Plain, Tuchola Forest, on the Słowińskie Coast, and in the Bytów and Kashubian Lakelands (Fig. A68). All-Pomeranian distributional type, *Rhynchospora alba* subtype. Found mostly in hollows and depressions of raised bogs. It participates in plant succession in gradually overgrown dystrophic lakes and flooded pits resulting from excavation. Associated with plant communities of the order *Scheuchzerietalia palustris* (phytocoenotic optimum in the association *Rhynchosporietum albae*). Hemicryptophyte. Pollination: wind. Dispersal: epizoochory. Life strategy: S.

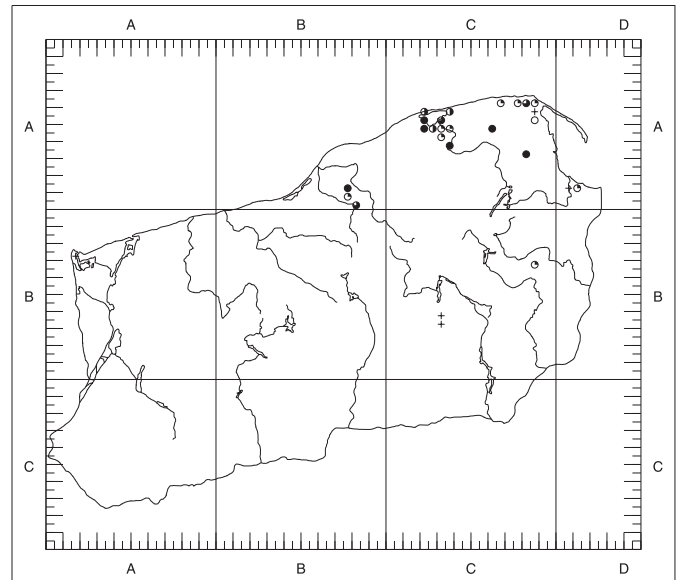
Fig. A68. *Rhynchospora alba* (L.) Vahl

Rhynchospora fusca (L.) W. T. Aiton

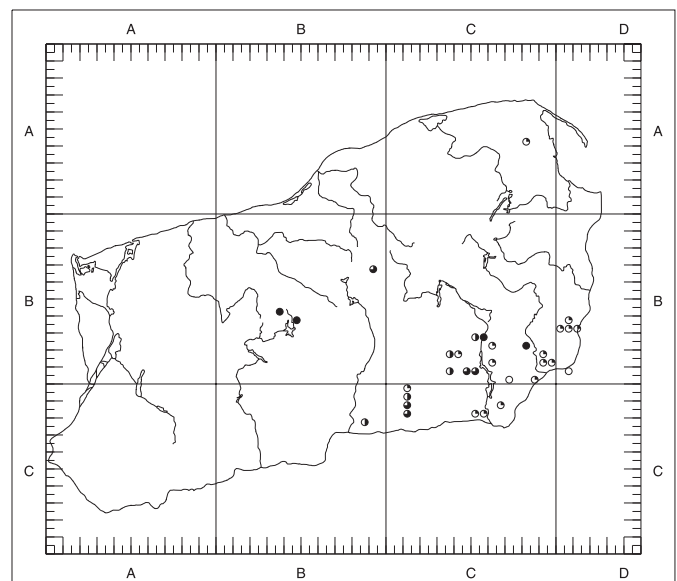
Amphi-Atlantic sub-element. In Poland the species reaches the eastern limit of its distribution range. Rare, recorded mostly in Pomerania, the Lubusz Lakeland, Silesian-Lusatian Lowland, Silesian-Kraków Upland, and in the south-east (the Sandomierz Basin, Roztocze, and Polesie). Its stands in south-eastern Poland are related to an isolated centre of distribution in Volhynia. In Pomerania very rare (II), recorded in scattered localities in the northern part of the region (Fig. A69). Eastern distributional type in Pomerania, *Rubus chamaemorus* subtype. Distinguished by its very narrow phytocoenotic range (optimum in the association *Rhynchosporetum albae*). Hemicryptophyte. Pollination: wind. Dispersal: epizoochory. Life strategy: S.

Fig. A69. *Rhynchospora fusca* (L.) W. T. Aiton*Rubus chamaemorus* L.

Circum-Boreal sub-element, Circum-Boreal-Arctic group. In northern Poland, the species reaches the southern limit of its main distribution range, while is scattered in other parts of the country. Recorded in Pomerania, the Masurian Lakeland, and in the mountains: the Karkonosze and Western Carpathians. Eastern distributional type in Pomerania, *Rubus chamaemorus* subtype. Very rare (II) there, reported from the Kashubian and Słowińskie Coasts, and near Sławno. In the past, recorded also on the Baltic island of Usedom (Polish: Uznam), in the Tuchola Forest, and north-east of the Forest (Fig. A70). Found in raised bogs, in patches of communities of the class *Oxycocco-Sphagnetea*, but also in wet coniferous forests, and wet birch forests. Hemicryptophyte, woody chamaephyte. Dispersal: epizoochory, endozoochory. Life strategy: SR.

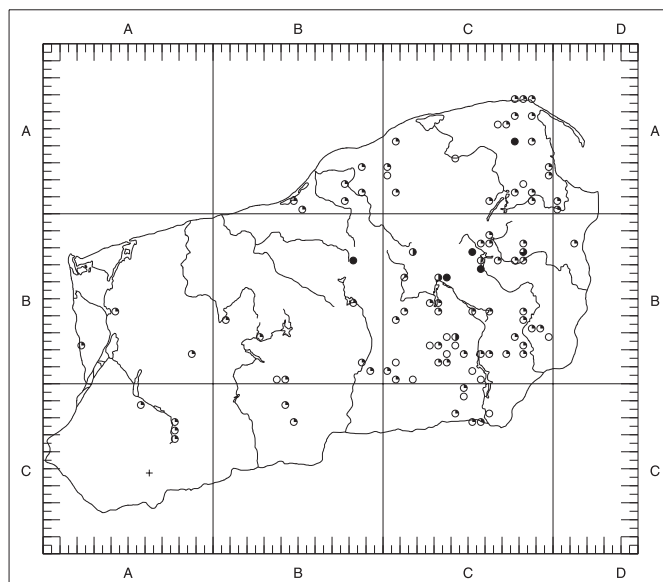
Fig. A70. *Rubus chamaemorus* L.*Salix myrtilloides* L.

Circum-Boreal sub-element. In Poland the species reaches the western limit of its distribution range. Infrequent, distributed mostly on the Lower Vistula, in the Masurian Lakeland, Polesie, and in the belt of uplands in southern Poland. Isolated stands reported from Podlasie, the Masovian Lowlands, Silesian Lowland, and in the Sudetes. In Pomerania very rare (II), its centre of distribution is in the south-eastern part of the region. In other parts of the region scattered, recorded on the Kashubian Coast and in the Drawsko Lakeland (Fig. A71). Eastern distributional type in Pomerania, *Salix myrtilloides* subtype. Found in communities of fens and transitional bogs of the class *Scheuchzerio-Caricetea nigrae*, connected especially with the associations *Caricetum limosae* and *Caricetum lasiocarpae*. Observed also in wet coniferous forest and sporadically in wet birch forest. Nanophanerophyte, woody chamaephyte. Pollination: wind. Dispersal: anemochory.

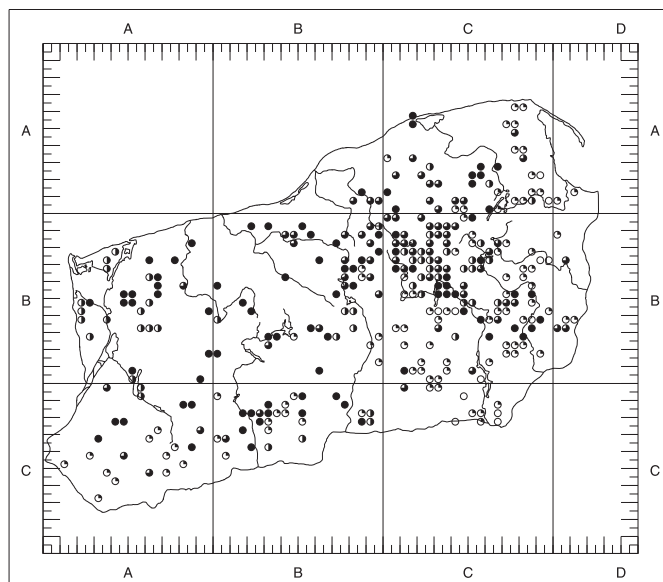
Fig. A71. *Salix myrtilloides* L.

Saxifraga hirculus L.

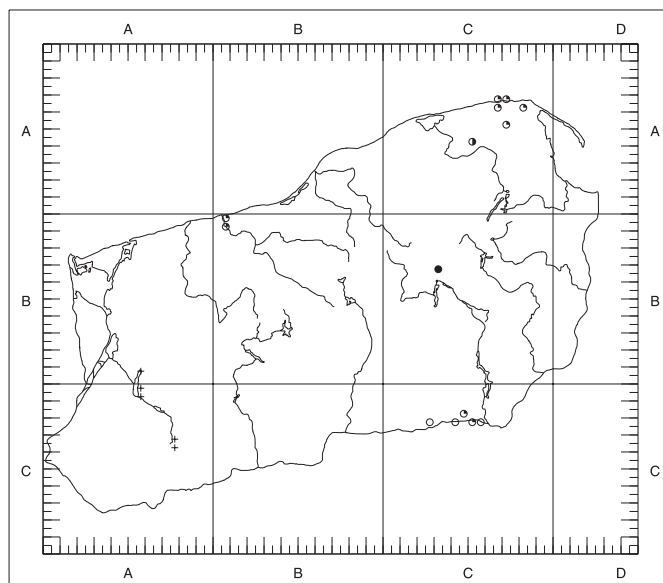
Circum-Boreal sub-element, Circum-Boreal-Arctic group. In Poland the species reaches the southern limit of its main distribution range. Distributed mostly in the Masurian Lakeland and in Pomerania. In other parts of the country scattered, with its frequency decreasing southwards. Recorded in the Wielkopolska Lakeland, Lubusz Lakeland, Podlasie, Polesie, Lublin Upland, Silesia and the Tatras. However, most of its records are historical now. In Pomerania infrequent (IV), recorded mostly in the eastern part of the region (Fig. A72). All-Pomeranian distributional type, *Hammarbya paludosa* subtype. Associated with mires of the class *Scheuchzerio-Caricetea nigrae*, particularly with those of the alliance *Caricion lasiocarpae*, rarely of the alliance *Rhynchosporion albae*. Hemicryptophyte. Pollination: insects. Dispersal: anemochory, autochory.

Fig. A72. *Saxifraga hirculus* L.*Scheuchzeria palustris* L.

Circum-Boreal sub-element (disjunctive range). In Poland recorded mostly in the north, west, in Polesie, the Lublin Upland, and Roztocze. In other parts of Poland absent or scattered. In Pomerania moderately frequent (V), widely distributed, mostly in the Tuchola Forest, the Charzykowy Plain, and in the Bytów and Kashubian Lakelands (Fig. A73). All-Pomeranian distributional type, *Rhynchospora alba* subtype. Found in transitional bogs but also in raised bogs (Atlantic and Baltic types), in patches of the association *Caricetum limosae*. Associated with plant communities of the order *Scheuchzerietalia palustris*. Geophyte. Pollination: wind. Dispersal: hydrochory. Life strategy: CSR.

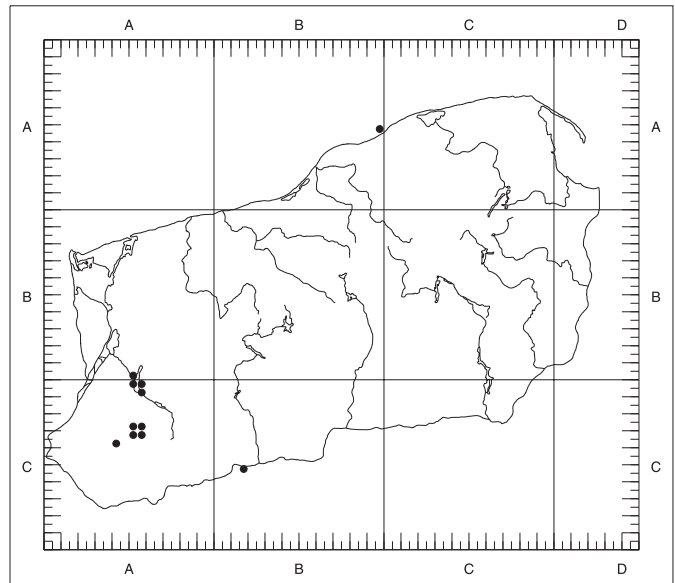
Fig. A73. *Scheuchzeria palustris* L.*Schoenus ferrugineus* L.

European-temperate sub-element, European-temperate-lowland group, European-temperate Balkan distributional type. Rare in Poland, distributed mostly in Polesie and Roztocze. Scattered in other regions: in Pomerania, the Wielkopolska Lakeland and the North Podlasie Lowland. In Pomerania very rare (II), reported from the margins of Lake Miedwie, river valleys of the Płonia and Noteć, Kołobrzeg, and on the Kashubian Coast (Fig. A74). Disjunctive distributional type. Associated with plant communities of calcareous fens of the order *Caricetalia davallianae* (optimum in the association *Lipario-Schoenetum ferruginei*). Hemicryptophyte. Pollination: wind. Dispersal: anemochory, epizoochory, autochory. Life strategy: CSR. It is one of the major components of the association.

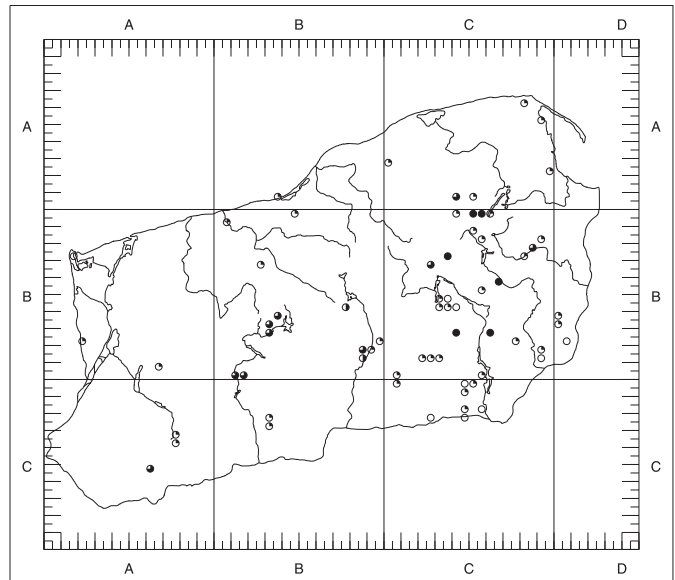
Fig. A74. *Schoenus ferrugineus* L.

Schoenus nigricans L.

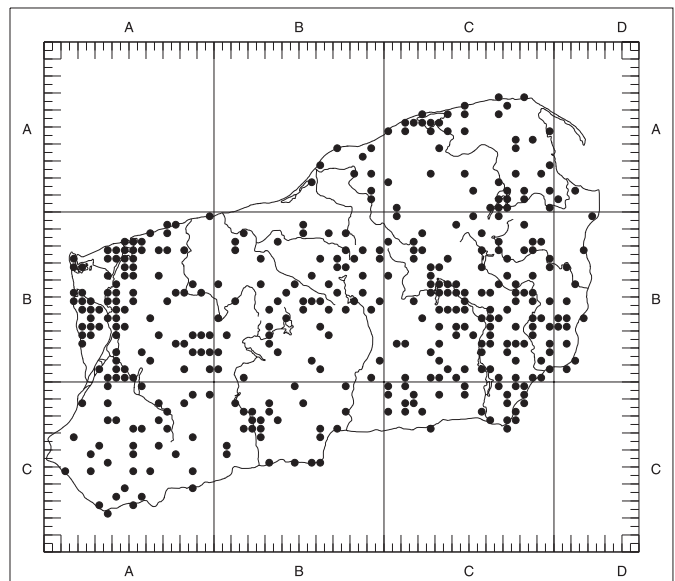
Cosmopolitan element. In Poland recorded in only about a dozen localities, lying at the eastern limit of its European range of distribution. Most of them are concentrated in the Myślubórz Lakeland. Moreover, isolated stands are reported from the Małopolska Upland as well as river valleys of the middle Warta and the upper and lower Noteć. Its record on the Słowińskie Coast is doubtful (Fig. A75). In Pomerania very rare (II), western distributional type. Found in calcareous fens of the alliance *Caricion davallianae* (phytocoenotic optimum in the association *Schoenetum nigricantis*). Hemicryptophyte. Pollination: wind. Dispersal: anemochory, epizoochory, autochory. Life strategy: CSR.

Fig. A75. *Schoenus nigricans* L.*Stellaria crassifolia* Ehrh.

Circum-Boreal sub-element (northern). In Poland it reaches the southern limit of its range. Distributed mostly in the Masurian Lakeland, the Suwałki Region, and Pomerania. Further south, recorded only in scattered localities, never in the uplands. In Pomerania rare (III), generally scattered, but more frequent in the south-eastern part of the region (Fig. A76). All-Pomeranian distributional type, *Hammarbya paludosa* subtype. Associated with communities of waterlogged transitional bogs of the alliance *Caricion lasiocarpae* (phytocoenotic optimum in the association *Caricetum diandrae*). Hemicryptophyte. Pollination: insects, self-pollination. Dispersal: myrmecochory, anemochory. Life strategy: CSR.

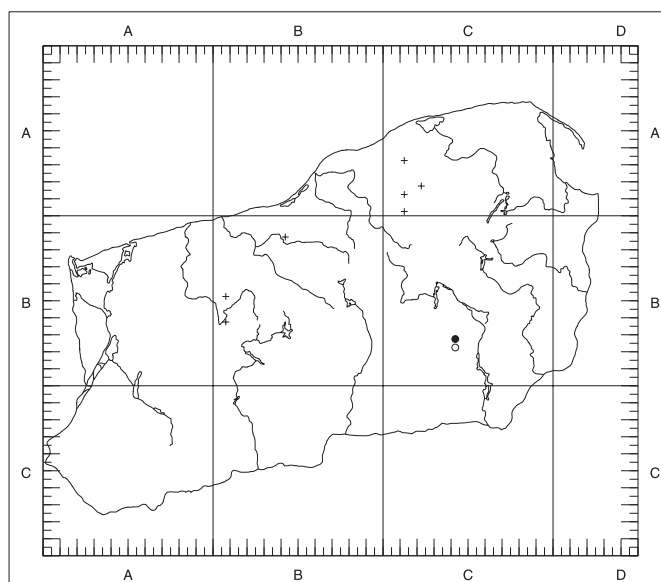
Fig. A76. *Stellaria crassifolia* Ehrh.*Stellaria palustris* Retz.

Euro-Siberian sub-element. Common in Poland, except in the Carpathians, where it is nearly absent; less frequent also in the south-west. Moderately frequent (V) all over Pomerania (Fig. A77). All-Pomeranian distributional type, *Carex rostrata* subtype. Associated with acid low sedge mires. Frequent also in transitional bogs and wet and moist meadows, less often in tall sedge communities and in sallow thickets. Hemicryptophyte. Pollination: insects, self-pollination. Dispersal: myrmecochory, anemochory. Life strategy: CSR.

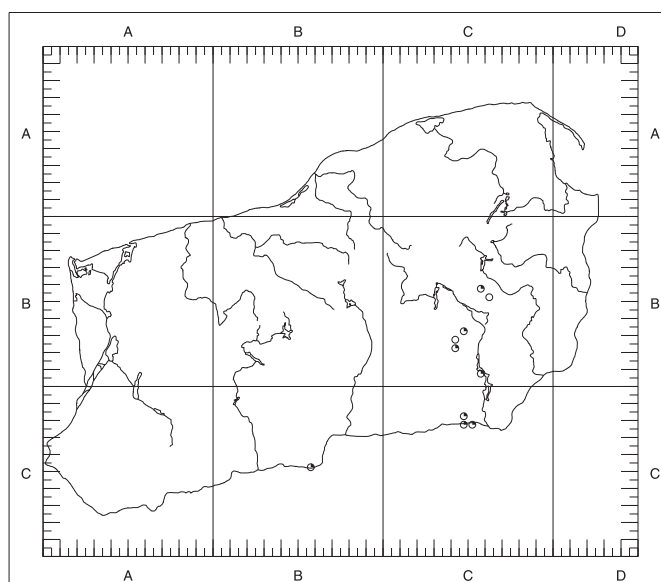
Fig. A77. *Stellaria palustris* Retz.

Swertia perennis L.

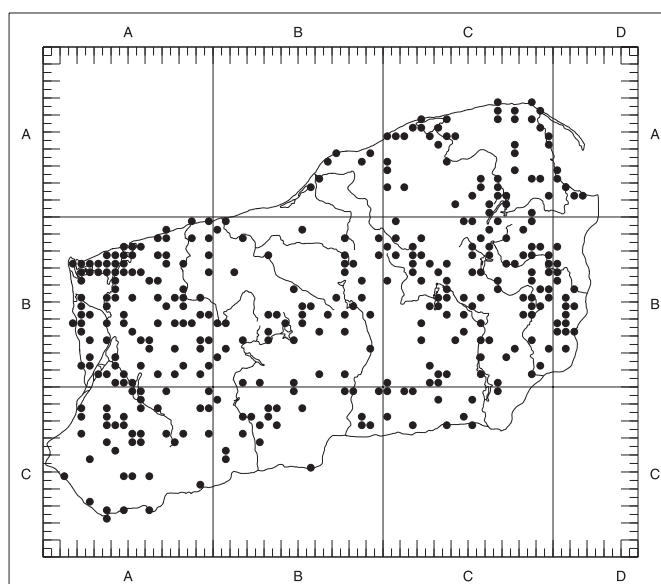
Circum-Boreal sub-element (disjunctive range). The taxon defined in the narrow sense belongs probably to the European-temperate sub-element. Rare in Poland; reaching here the northern limit of its natural range. In the southern part of the country its stands are isolated, distributed mostly in Polesie, Roztocze, the Tatras, and Karkonosze Mts. Its range is disjunct, as the species is absent in central Poland but appears in the north in scattered, often isolated localities. In Pomerania extremely rare (I), known from several localities in the Krajna Lakeland, river valleys of the Rega and Radew, and the catchment area of the Słupia (Fig. A78). The species does not belong to any of the distinguished distributional types. Associated mostly with acid and eutrophic low sedge mires. Hemicryptophyte. Pollination: insects. Dispersal: endozoochory, autochory. Life strategy: CSR.

Fig. A78. *Swertia perennis* L.*Tofieldia calyculata* (L.) Wahlenb.

European-temperate sub-element, European-temperate-montane group, Alpic-Central-European distributional type. Poland is crossed by the northern limit of the main range of distribution of this species. Recorded mostly in the Western Carpathians, Małopolska Upland, Lublin Upland, Silesian Lowland, Wielkopolska Lakeland, Krajna Lakeland, and in north-eastern Poland. In Pomerania extremely rare (I), distributed in river valleys of the Brda and Noteć (Fig. A79). Eastern distributional type in Pomerania, *Salix myrtilloides* subtype. Found in springs and flushes, moist meadows, rock crevices, and fens. Often on calcareous soils. Associated with communities of the order *Caricetalia davallianae*, and with mesotrophic low sedge mires of the order *Caricetalia nigrae*. Hemicryptophyte. Pollination: insects, wind. Dispersal: autochory, endozoochory, anemochory. Life strategy: CS.

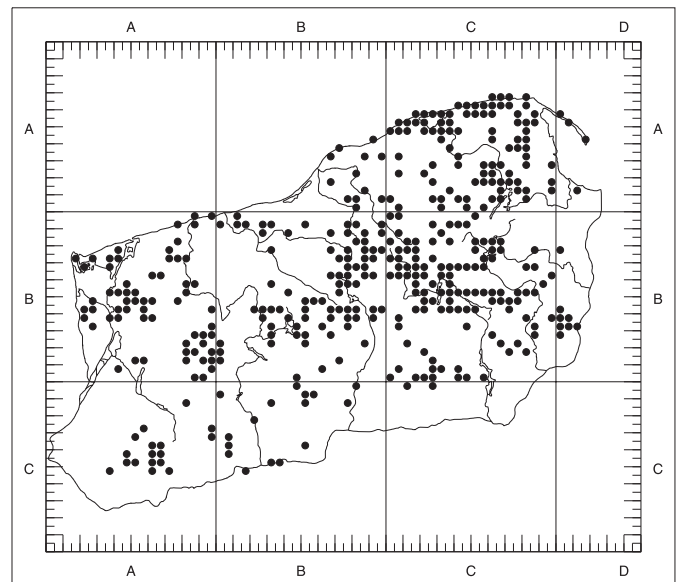
Fig. A79. *Tofieldia calyculata* (L.) Wahlenb.*Triglochin palustre* L.

Circum-Boreal sub-element. Frequent in Poland. Its records are less numerous in the south-east, south-west, and in the South Wielkopolska Lowland. In Pomerania widespread and moderately frequent (V) (Fig. A80). All-Pomeranian distributional type, *Dactylorhiza incarnata* subtype. Associated with communities of fens and transitional bogs of the class *Scheuchzerio-Caricetea nigrae*. Recorded also in wet meadows, tall sedge communities, and among halophytes on sites with a lower salt content of the soil. Hemicryptophyte. Pollination: wind. Dispersal: epizoochory. Life strategy: S.

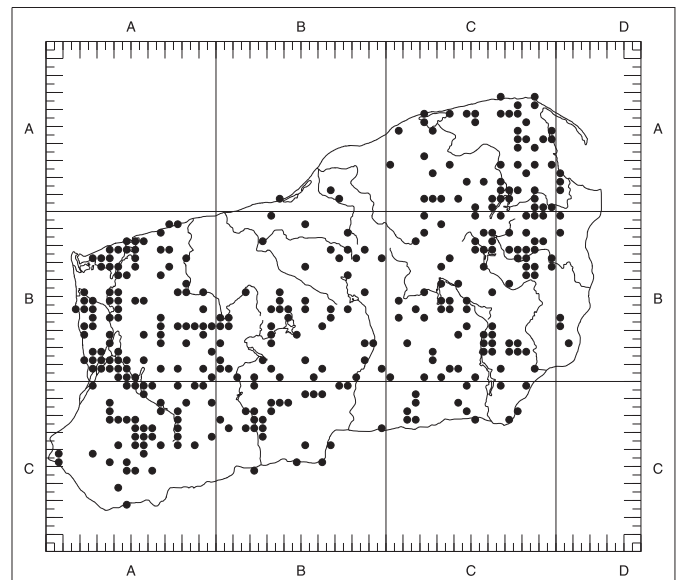
Fig. A80. *Triglochin palustre* L.

Vaccinium uliginosum L.

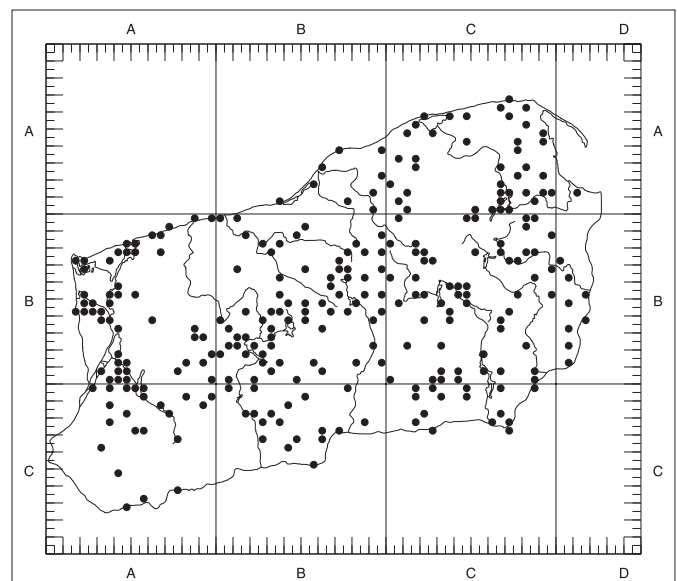
Circum-Boreal sub-element. Frequent in Poland, except for the Central Polish Lowlands and mountains, where it is much rarer. In Pomerania widespread and moderately frequent (V), particularly on the Kashubian and Słowińskie Coasts and in the belt of lakelands (Fig. A81). All-Pomeranian distributional type, *Rhynchospora alba* subtype. Found mostly in acidophilous communities of pine and pine-oak forests of the class *Vaccinio-Piceetea*, and wet heaths and raised bogs of the class *Oxycocco-Sphagnetea*. Less often reported from transitional bogs, moors, and acid grasslands in high mountains. Woody chamaephyte. Pollination: insects. Dispersal: endozoochory. Life strategy: CS.

Fig. A81. *Vaccinium uliginosum* L.*Valeriana dioica* L. s. str.

European-temperate (western) sub-element, extending to the Atlantic region of Europe. In Poland the species reaches the north-eastern limit of its distribution range. Absent or scattered in the east and south-east. In other parts of the country frequent. In Pomerania moderately frequent (V), recorded mostly in western and north-eastern parts of the region, less often in the central part of the Polish Baltic coast (Fig. A82). All-Pomeranian distributional type, *Dactylorhiza incarnata* subtype. Found chiefly in wet and moist meadows, acid low sedge mires, and in tall sedge communities. Hemicryptophyte. Pollination: insects. Dispersal: anemochory, endozoochory. Life strategy: CSR.

Fig. A82. *Valeriana dioica* L. s. str.*Veronica scutellata* L.

Circum-Boreal sub-element (disjunctive range). Frequent in Poland. Distributed all over Pomerania but scattered, moderately frequent (V); more frequent in the north-west and in the belt of lakelands, except for the Myślubórz Lakeland (Fig. A83). All-Pomeranian distributional type, *Carex rostrata* subtype. Associated mostly with acid low sedge mires. Found also in transitional bogs of the alliance *Caricion lasiocarpae* and in tall sedge communities of the alliance *Magnocaricion*. Hemicryptophyte. Pollination: insects, self-pollination. Dispersal: anemochory, hydrochory, myrmecochory, autochory. Life strategy: CS.

Fig. A83. *Veronica scutellata* L.

Viola epipsila Ledeb.

Circum-Boreal sub-element, Circum-Boreal group proper. Northern Poland is crossed by the southern limit of the natural range of this species. Very rare, distributed mostly in north-eastern Poland. Moreover, single localities recorded in Pomerania, Polesie, Lublin Upland, and north-west of the Małopolska Upland. In Pomerania extremely rare (I), known from 3 localities in the north-eastern part of the region (Fig. A84). Eastern distributional type in Pomerania, *Rubus chamaemorus* subtype. Found in riparian forests, alder forests, and low sedge mires. Hemicryptophyte. Pollination: insects, self-pollination, cleistogamous. Dispersal: myrmecochory, autochory. Life strategy: CSR.

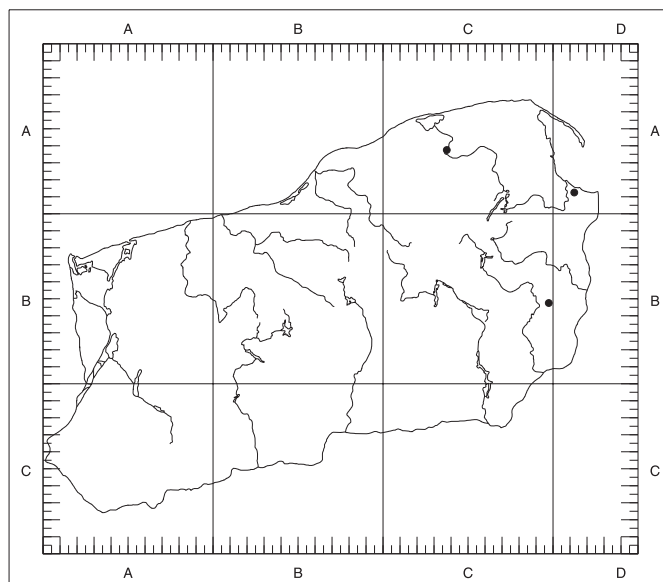


Fig. A84. *Viola epipsila* Ledeb.

Viola palustris L.

Circum-Boreal sub-element, Circum-Boreal-Oceanic group. In Poland widely distributed except for the south-east; less common in central lowlands. In Pomerania frequent (VI) (Fig. A85). All-Pomeranian distributional type, *Carex nigra* subtype. Associated with mires of the class *Scheuchzerio-Caricetea nigrae* and with alder forests. Moreover, found in tall sedge communities, wet meadows, and sallow thickets. Hemicryptophyte. Pollination: insects, self-pollination, cleistogamous. Dispersal: myrmecochory, autochory. Life strategy: S.

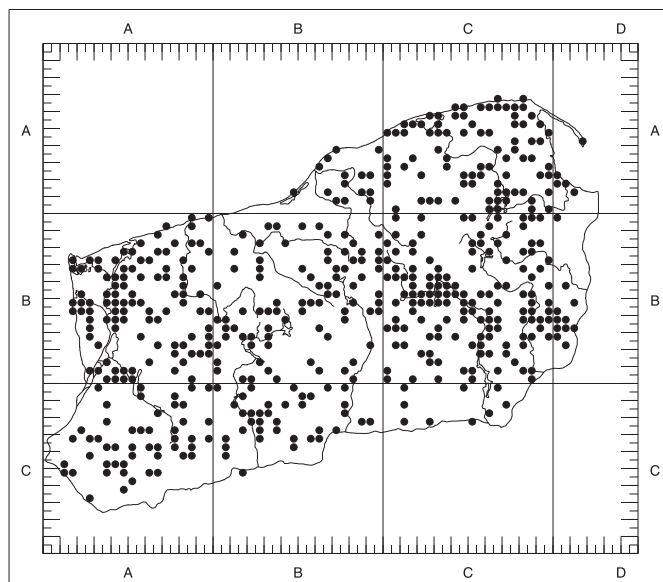


Fig. A85. *Viola palustris* L.