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Vegetation and ecology of black alder (*Alnus glutinosa* (L.) Gaertn.) dominated swamps and mesic forest sites in Finland

Tervaleppäyhdyskuntien ekologia ja kasvillisuus Suomessa

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This study includes all black alder sites (or stands) in Finland in the natural state from wet black alder swamps to fresh black alder -dominated forests. The material is based on 650 sample plots with complete descriptions of vegetation and ecology studied in altogether 200 black alder sites all over the distribution area (59°47′–66°45′N).

The a priori classification of the studied sites is based on field observations during several decades and on DCA-ordination and clustering analysis (Euclidian distance with centroid group averages and the Ward linkage method) using the Finnish "Cajanderian" forest and mire site type classification approach.

Based on this material, 14 black alder community types and several variations are described. Half of them are black alder swamps and the rest herb-rich and alluvial forests. Most of them are situated on lake and seashores where new sites are exposed continuously as a result of land elevation.

The results of the classification are compared with the phytosociology of several Northern and Central European black alder communities. Ecological factors affecting the formation and development of black alder communities in Finland are also discussed. Many of these environmental factors deviate noticeably from conditions in Central Europe and are reflecting the special features of Finnish black alder swamps and forests.

1.1. Introduction

1.1. Black alder as a tree species

The black alder (*Alnus glutinosa* (L.) Gaertn.) is widespread tree species in Europe ranging from the Mediterranean in the south to the Gulf of Bothnia in the Baltic Sea (35°–65°N). In the west-east range it occurs from Ireland to western Siberia (10°W–90°E) (Fig. 1 and Walter 1954, Hylander 1955, Meusel et al. 1965, Hultén 1971, Jalas & Suominen 1987). It is rare in the harsh climatic conditions in the north and in the extreme continental areas in the east. According to Meusel (1943), the distribution of the black alder is boreomeridional, submontan and oceanic. In the east and in the south, the occurrence of the black alder follows the precipitation isohyet of 510 mm, and also elsewhere some correlation with the precipitation and isotherms have been indicated during the growing period (McVean 1953, Hultén 1971 and Hintikka 1963).

Besides geographical characteristics limiting the occurrence of the black alder, climatic characteristics related to the altitude set restrictions. In the north the timberline is at a much lower altitude than in the south: For example, in southern Norway, the timberline can be found at the height of 450 m above sea level, but in Switzerland and in the Kaukasus mountains, the timberline is at a significantly higher level at the height of 1 800 m a.s.l. (Mc Vean 1953, Meusel et al. 1965). In Finland the black alder does not have any altitude limits, because the northernmost black alder trees are situated far away from the mountain areas (fells) (Kujala 1924a, Jalas & Suominen 1987).

The black alder favours wetlands, especially open sea and lake shores, brook sides and wet depressions, where spring brooks or slowly flowing ground water brings nutrients for the plant community. Its moisture tolerance ranges from open water to semidry broadleaf or coniferous forests, but it does not tolerate acidic peatlands with thick peat layer nor shady spruce forests. In minerotrophic mire margins the black alder, however, does grow if there is flowing water.

The area of black alder dominated forests has decreased due to human influence (agriculture, peatland and forest draining, regulation of lake and river systems etc.). The most favourable areas for the growth of black alder are in Russia, Belarus, north-east Poland and in the Baltic States (Linkola 1929, Tessendorf 1921, Regalis 1931, Bodeux 1955, Matuszkiewicz et al. 1958, Ellenberg 1963, Laasimer 1965 and 1975, Traczyk 1966, Jurkevitch et al. 1968, Dierschke 1969, Hainla 1971, Traczyk & Traczyk 1977, Prieditis 1993a,b, 1997a,b). The largest black alder forests may reach an area of 10 km² (Radomski 1962, Glavač 1972).

In Finland, the range of the black alder reaches its northern limits in southern Lapland due to climatic reasons (Fig. 2 and Kujala 1954, Lampinen & Lahti 2013, see also chapter 2.6.). Another limiting factor is the soil characteristics. During the Pleistocene (ice age), the continental ice peeled younger nutrient-rich strata in Finland leaving barrel basic rock behind, which has been covered by water for a long time (the Baltic and its preforms). During the land elevation (up to 1 m per 100 years) occurring in the post-glacial period, many favourable sites for the black alder were formed on the coasts. This phenomenon still continues, but human activity has limited much the area of black alder communities. Most of the sites where the black alder has occurred have been cleared for fields and pastures already hundreds of years ago. Later, the regulation of the water level of lakes has had a great influence on black alder communities especially in the 19th century. Large scale drainage of peatlands (5.2 million hectares) especially at the end of the 20th century (mostly in the late sixties and during the seventies) has destroyed many of the pristine sites suitable for the black alder (chapter 2.7.). The remaining small black alder swamps and forests have been recognized to be threatened, and most of them have been protected in the conservation programs of pristine peatlands and herb-rich forests first in 1979 and 1981 and later in 1996, 1997 and 2014 by the forest and nature conservation laws (Habitats of special importance in commercial forests, as defined in the Forest Act) and Natura 2000 project (Vasander 1996, Ruuhijärvi 1978, Lindholm & Heikkilä 2006a, b).

Because the total area of safeguarded black alder communities in Finland is small and their economic value in forestry is neglible, studies of these forests are few. Only one monograph by Viljo Kujala (1924a), a doctoral thesis, has been published in Finland. It is a complete description of the biology of the black alder in Finland. Similar monographs were written Mc Vean (1953, 1955, 1956 and 1959) in the British Isles, Marek (1965) in Poland and Jurkevitch et al. (1968) in Belarus and Prieditis (1993a, b, 1997a, b) in Latvia. All these studies deal with the black alder in forests, peatlands and wet mineral soils. Besides the monograph by Kujala, local black alder communities in Finland are described more closely in several sources (Hildén 1929, Jaatinen 1950, Skult 1956, Mäkinen 1963, 1964, 1968, 1978a, b). The description of lakeshore vegetation on the Åland (Jaatinen 1950) is also a good reference because black alder is there a dominating tree species and predominantly documented in the study.

The driest black alder communities (which are considered broad-leaved forests) have been discussed formerly in herb-rich grove vegetation studies (Valle 1919, Mäkelä 1936, Mikkola

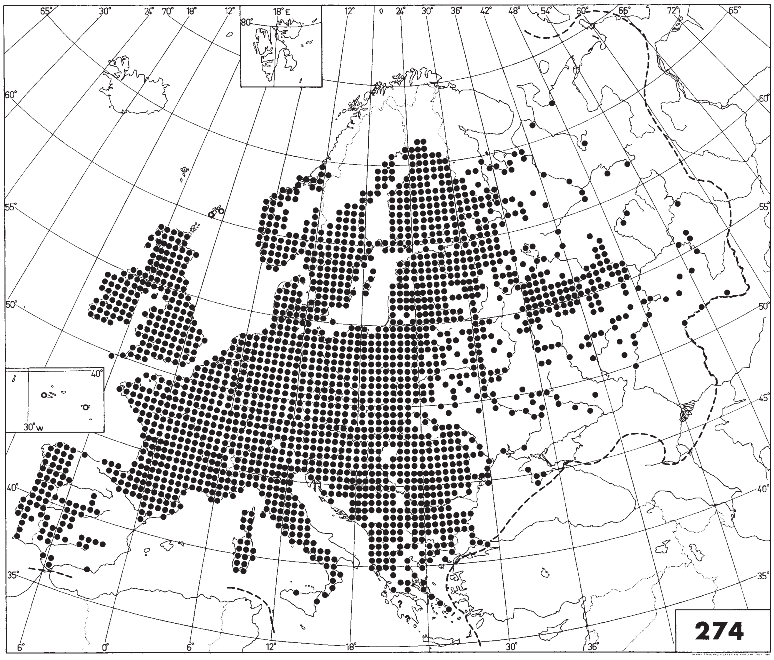

Fig. 1. Distribution of black alder (*Alnus glutinosa*) in Europe according to Jalas & Suominen (1987: Flora Europaea II, Map 274).

Kuva 1. Tervalepän levinneisyys Euroopassa Jalas & Suomisen (1987) mukaan.

1937, Tapio 1951, 1953, Koponen 1961, 1967, Mäkirinta 1968, Alanen et al. 1995, Tonteri et al. 2008, Schulman et al. 2008). These communities have also been discussed in nature conservation programs in Finland (Lehtojensuojelutyöryhmä 1988, Virkkala et al. 2000, Korhonen et al. 2013).

The black alder rich wetland communities in Finland were formerly classified with herb-rich birch-spruce mires, especially in forested mire margin areas (Cajander 1913 and 1916, Ruuhijärvi 1960, Eurola 1962 and Heikurainen & Pakarinen 1982, Ruuhijärvi & Lindholm 2006). Later on, in the site type classifications, swampy mire types were clearly separated from *Sphagnum* rich mires (Tuomikoski 1955 and Eurola 1969) and included in forested swamps. This included all black alder swamps in Finland (Eurola et al. 1984 and 2015).

The third group of black alder communities is alluvial alder forests on mineral soil. Their vegetation is partly the same as in open shore meadows completed with broad leaved forest species. This variable vegetation composition was formerly described in Finland by Kujala (1924a), Aario (1932), Linkola (1937), Brandt (1948), Jaatinen (1950), Skult (1956) and Eurola (1965).

The aims of this study are: 1) to give an overview of the Finnish black alder communities, their vegetation composition and ecology of the sites, taking into consideration their nature conservation value. Many of the black alder forests and swamps are threatened and deviate remarkably from other Finnish peatland and forest communities, and 2) to suggest syntaxonomical improvements and succession development studies of Finnish black alder communities on the basis of the very large data gathered over several decades.

2. Ecological factors affecting the establishment and development of the black alder communities in Finland

2.1. Bedrock

The bedrock in the study area is very old, Archaean Shield of Fennoskandia. On its surface, there have been Paleozoic and younger bedrock layers, which were grinded away by the continental ice. Younger bedrock is found nearest in the Baltic Countries.

In southern Lake-Finland, the dominating bedrock consists of Svecofennian shists and gneiss (Koljonen 1992, Husa & Kontula 2006). In the south, synorogenic and lateorogenic granites as well as porhyric granites (rapakivi) also occur. There are also some small limestone deposits e.g. in Åland.

Most black alder stands are located just in these bedrock areas, but the bedrock alone explains neither the distribution of the black alder nor the appearance of large alder stands. However, in the northern part of Lake-Finland where acidic synorogenic granitoids are dominating, the black alder stands are few in number contrary to the calcitic bedrock areas in Finland, where black alder communities are more abundant (Husa & Kontula 2006, and Fig. 2).

2.2. Topography

After the ice age, a great part of the low-lying study area was covered by water (Tikkanen 2006d). At present, the historical coasts of the Baltic Sea as far as to the distance of 50 km inland are less than at 50 metres above sea level. All black alder stands close to the coasts are situated in this zone, and the rest of the inland stands are at the height of 150 m above sea level at the most. However, the black alder has no altitude limit in Finland (Kujala 1924a).

2.3. Soil and hydrological characteristics

In description and classification of black alder communities, the soil type has to be taken into consideration (Brenner 1916, Ulvinen 1937). The soil types of Finland can be divided into two groups: glacial formations and postglacial deposits. The glacial formations dominate in the study area (Sauramo 1925, Granö 1960, Kujansuu & Niemelä 1990) and they are comprised of tills, which are crushed and accumulated by the continental ice. They are the dominant soil type in central and eastern Finland, where steep and stony shores prevail and are particularly suitable growing sites for the black alder (Häyren 1954). Another group of soil types is the glacifluvial ice river formations (Koljonen & Tanskanen 1992). They are seen as eskers in the direction of ice movement from north-west to south-east or crosswise great eskers (Salpausselkä) running from Hanko Peninsula to north-east (Tikkanen 2002 and 2006b). Their significance in the occurrence of black alder stands is significant. The eskers are groundwater stores and there are generally numerous springs in the lag and marginal areas feeding the alder stands.

For the occurrence of black alder stands, the third group of very significant glacial formations is formed by the fine granular clays and clay layers accumulated in the bottom of the ancient Litorina Sea and lakes. Part of them was formed during the ice age, the rest formed later. These soil formations are occurring on the shores of the Gulf of Finland, south from Salpausselkä eskers and in south-western Finland (Kujansuu & Niemelä 1984 and 1990, Lahermo et al. 1996). In this area, there are plenty of black alder stands but also large cultivated areas. Part of them has been cleared of black alder forests.

Since clay soils retain water well and are rich in nutrients, they often form the substrate for magnificent black alder forests. In clay soils with medium moisture content, which are common in southern Finland, the field layer of black alder forests is dominated by *Filipendula ulmaria.* However, the black alder community of *Urtica* type also seems to favour clay- and silty soils (see chapters 5.6.4 and 5.6.5).

The fourth group of soil formations, which are clearly post-glacial soils, are the organic deposits, mainly slime and peat deposits (Mäkilä 2006). The black alder itself has been a significant factor in the formation of these soils especially during the Atlantic period. Numerous black alder sub-fossils have been found in the bottom layers of peatlands (e.g. Auer 1924, Okko 1960, Vasari 1963 and Nenonen 1995).

In later development of these mires, the thickness of the peat layer has increased and the *Sphagnum* communities have become dominant and nearly totally displaced the black alder communities. In many mires, black alder is growing as a relict in the marginal forested swamps (Vorren 1979, Korpela 2004). They are more common in young mires close to sea shores than in inland bogs (Kujala 1965). Also nowadays black alder may be important for swamp development (Kujala 1924a, Mäkinen 1964 and 1979b, Eurola & Huttunen 2006).

Besides soil quality, also the content of nutrients in the soil has a significant influence on the establishment and growth of the black alder (Holmen 1979). The most productive sites are mesic organic nutrient rich soils, but the black alder also thrives on bare mineral soils obtaining nutrients from moving surface- or ground water (Kujala 1924a, Walter 1960).

An alder stand may establish on bare sandy beach, if ground water is nearby (Mäkinen 1964 and 1979b). Over one hundred years, a tall alder tree produces a ca. 20–30 cm thick layer of decomposed litter and peat (Aaltonen 1932). Rapid growth of peat is possible by the continuous increase of nutrients with moving water and by *Francia* symbiosis (Van Dijk 1978, Van Dijk et al. 1988, Weber 1986). Decomposition of root nodules releases nitrogen into the ecosystem. The alders take up nitrogen and return it to the leaves, which fall as green (Kivinen 1933). The amount of nitrogen in the soil is insignificant for alder (c.f. Malmer 1990).

In wet mires, *Francia* actinomycetes are found only in the aerobic alder root-hummocks. If the pH of the soil is low, the amount of symbiotic *Francia* decreases (Weber 1986, Weber et al. 1987, Smolander & Sundman 1987, Smolander et al. 1988). On such sites, black alders are few or lacking totally. They are replaced by *Betula pubescens* and *Pinus sylvestris* (Ellenberg 1963). Soil acidity may explain the lack of black alder in the shores of oligotrophic lakes. When the ground water is acidic, the amount of micro-organisms decomposing the peat remains small and the mire development leads finally to a nutrient-poor bog (Kotilainen 1927, Ellenberg 1963, Korhola & Tolonen 1996, Huttunen & Tolonen 2006).

Water quality in water courses has smaller influence to black alder than soil quality. For example, in the province of Häme in southern Finland, tall black alder stand are found both on the shores of the oligotrophic lakes (O–Oc) such as in Lake Mallasvesi and Roine, and more nutrient-rich euthonio–eutrophic (Ceu) lakes like Lake Vanajavesi (Järnefelt 1956 and 1963). Besides the river estuaries, the quality of water varies less on the sea shores than on those of lakes.

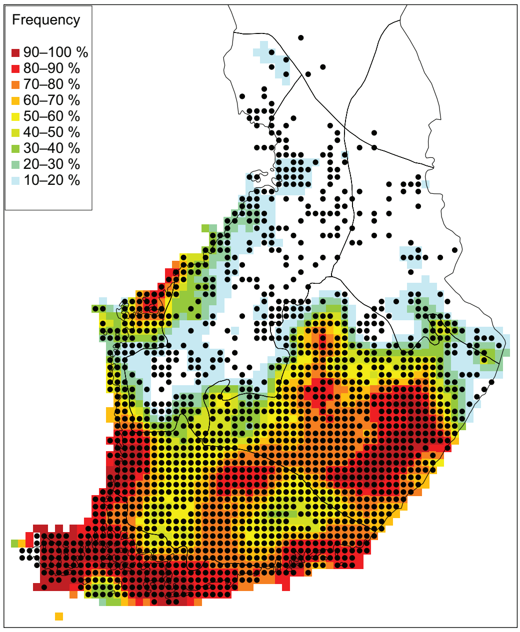

Fig. 2. Distribution of black alder (*Alnus glutinosa*) in Finland. All observations until 2012. Source: Lampinen, R. & Lahti, T. 2013: Kasviatlas. Atlas of the Distribution of Vascular Plants in Finland 2012. Botanical Museum. Finnish Museum of Natural History LUOMUS. University of Helsinki. http://koivu.luomus.fi/kasviatlas/

Kuva 2. Tervalepän levinneisyys Suomessa vuoteen 2012 mennessä.

2.4. Land upheaval

Concerning the establishment of black alder stands on the shores of the Baltic Sea, the land upheaval is one of the most important factors. With a thickness over 3 000 metres, the continental ice pressed down the crust (Kääriäinen 1964, Lisitzin 1964). The greatest depression was born in the Bothnian Bay, where the ice thickness was the greatest. In that area the land upheaval is the greatest nowadays. The upheaval continues all over the Nordic countries, but is becoming gradually slower. The “zero line” crosses the isle of Öland (Cramer 1980).

In the area of this study, the annual uplift varies according to mareographic measurements from 1.7 mm year^{-1} in southeastern Finland to 8 mm year^{-1} in Bothnian Bay (Kakkuri 1985 and 1992, Rehell 2006). On low shores, the land upheaval results in the fast exposure of the sea bottom and in the creation of plenty of new growing sites for the black alder. The upheaval of 1 % slope of the shore seabed results in 17–80 metres of the new growing site for the black alder during a century. In the northern part of the Bothnian Bay, grey alder (*Alnus incana*) is the pioneer and a dominant tree species in the forest succession. Pure black alder stands are rare (Kujala 1954). This first succession stage takes about 50 years (Havas 1967). In south-western archipelago the littoral phase and the influence of shore powers takes about 800 years (Kääriäinen 1964, Lisitzin 1964, Pyökäri 1978).

During time period 1960–1970 the land upheaval in the coastal cities of Finland has been as in the following (mm year^{-1}):

In the Gulf of Bothnia:		In the Gulf of Finland:	
Kemi	8.3	Turku	5.4
Oulu	8.1	Hanko	4.1
Vaasa	9.0	Helsinki	3.5
Pori	7.4	Hamina	3.2

The change in average water level, however, remains up to 1 mm lower due to the rise of ocean surface (Lisitzin 1970).

In the southern part of the Bothnian Bay and in the shores of Gulf of Finland, the black alder is displacing the grey alder in the upper part of the littoral belt (Ericson & Wallentinus 1979, Rehell 2006). A similar exposure of lake bottom is also seen in the north-western shores of great inland lakes in Finland.

2.5. Effect of water level variations in lakes and sea

2.5.1. Sea shores

Because most remaining black alder stands are situated in lake or sea shores, they are under the influence of shore forces, such as the height of the water level and the mechanical press of ice during winter and spring. Black alder communities of the littoral zone suffer or benefit from these factors.

On the shores of the Baltic, variation of the water level is caused mainly by winds, but seasonal variation and variation in air pressure have some influence as well (Mälkki 1986, The Finnish Institute of Marine Research 2007). Large rises of the sea water level are unusual and do not occur every year, but smaller variations may have a great influence on seashore vegetation including black alder communities (Skult 1956). For example, in the middle of January 2007 the seashores were frozen during the episode of high water level (+120 cm above normal level) (The Finnish Institute of Marine Research 2007), and a thick ice layer covered all black alder communities on the shores for two months. In some winters the sea may be frozen for up to four months. Finland is the only country where the whole coast and all lakes are frozen every winter (Jurva 1937, Leppäranta et al. 1987, Kuusisto 1994).

2.5.2. Inland waters

In contrast to the sea, the water level of inland waters may vary considerable due to gales, but the influence of occasional wind episodes is generally small. For example in Lake Saimaa, the seasonal variation has been on average 0.6–5.4 cm (Siren 1950, Kuusisto 1978). Under normal conditions, the surface level of lake water rises by spring floods in April and May after snowmelt and frost (Sallantaus 2006). In the great central lakes, the water table reaches its maximum level in June or later, while the lowest water levels are normally measured in March or April (Kuusisto 1978). The annual fluctuation of the water level is approximately 30–70 cm in regulated lakes comprising about one third of all lakes in Finland (Kuusisto 1986).

In pristine lakes, the long-term fluctuation of the water level may be up to 2.5 m. This has a great influence on the ground water level and on black alder communities close to the shores. All the littoral black alder communities are normally affected by spring floods but dry in June or July. Sometimes the flooding occurs after heavy autumn rains, as in 2006.

If the variation of the water level is irregular, and the water table stays too long in the lower levels of the shore's soil, the seedlings of black alder may dry out and die (Skult 1956). This explains e.g. the lack of black alder on the shores of Lake Ladoga (Linkola 1937, Palmėn 1943). Flooding does not seem to have a negative influence on the survival of the black alder seedlings (Eurola 1965).

A temporary exposure of the shore means new growing sites for numerous plant species. For example, Tuomikoski (1941) found in a formerly water covered shore 35 newcomers in Lake Vesijärvi in southern Finland. Among these plant species, there were black alder seedlings and hemerophile species.

The seeds of black alder fall during winter and early spring. In warm autumns they may fall as early as October (Kujala 1924a, Linkola 1941, Kalela 1961). In good seed years, the yield may be over 100 seeds/100 cm^2, as in 1962. In April 1963, I calculated in Pälkäne under tall trees 52–120 seeds/100 cm^2. At the distance of 50 m from the seed trees, there were on average 22 seeds and at the distance 100 m still 5 seeds /100 cm^2 (Mäkinen 1968). During snowmelt, the seeds are carried by flood waters (Fig. 22 and Kujala 1924a, Mc Vean 1955, 1956 and 1959, Kalela 1961, Shalin 1967, Valta & Routio 1990).

The outermost black alder communities on shores are exposed regularly or temporarily to shore forces. On lake shores the spring floods regularly reach up to the nearest black alder communities in the littoral zone (Hutchinson 1967, Pieczynska 1972 and Tonteri et al. 2008). On sandy soils, especially on the south-eastern shores of large lakes, the erosion by waves may be destructive for the outermost trees (e.g. Fig. 23). The ice pack during a heavy wind or in springtime on riverbanks has also a large erosion effect (Kuusisto 2006). The mechanical rubbing of ice damages the trees leading later to decayed bark and wood. On the shores of large lakes, the expanding ice cover may push high banks and surface waters to the black alder forests.

2.6. Effect of climatic conditions on the distribution of alder

When comparing the climate maps of Europe and the distribution of black alder (e.g. Meusel 1943 and Fig 1), it seems to be that the black alder favours permanently mesic areas rainy in summer times or areas with marine climate, where the mean summer temperature is between 10–20 °C with a precipitation sum of about 500–750 mm such as in southern Finland.

According to McVean (1955) the factors controlling the northern distribution of the black alder are not clear. In Scandinavia, the black alder is absent in areas where the mean daily temperature is below 0 °C for six months of the year. Kujala (1924a) observed that the northern limit of the black alder follows the 0 °C isoterm in Finland.

The black alder is sensitive to frost also during the growing season. I have seen many alder seedlings in clear-felled areas in Lake-Finland injured by spring frost (Geiger 1961). Also night frost during the flowering period may damage the catkins of the alder (Cajander 1917, Kujala 1924a, Metsävainio 1925, Linkola 1941, Kalela 1961, Shalin & Seppälä 1964). One of the most important factors controlling the distribution of the black alder may be the temperature of the winter months. The black alder is absent in continental areas in the east, where winter temperatures are very low (Jalas & Suominen 1987). In Finland, the northern limit of alder seems to follow the −12 °C isotherm of the coldest month and the −17 °C isotherm of the mean minimum daily temperature (Kolkki 1959, Helminen 1987, Solantie 1987 and 2006, Heino 1994, Tikkanen 2006a). Furthermore, the limit of the black alder range seems to follow the isotherm of the duration of thermal winter of 6 months as well as the duration of the growing season of 135 days (Mc Vean 1955 and Kujala 1965). Also Hintikka (1963) has suggested, using his temperature coordinate system, that the northern limit for the black alder in Fennoscandia follows the mean temperature of the coldest and warmest months. Obviously, temperature determines particularly the northern limit of the black alder in Finland, due to its sensitivity to frost (Kujala 1924a, Skult 1956).

Most (over 90 %) of the known black alder stands in Finland are located in frost regions V–VIII, which include the area of large lakes in Lake-Finland, as well as the shores and the archipelago of the Baltic Sea (Solantie 1986, Ollinmaa 1952). In the region of Lake Finland, the length of the growing season without any frost is 130–145 days and on the sea shores and in the archipelago (regions VII–VIII) even longer (Skult 1956). This may be one reason why the black alder stands are concentrated on the shores of large lakes and the Baltic Sea.

The best growing conditions for the black alder in Finland are in the hemiboreal zone, south-western part of Finland, and in southern boreal zone, especially in the so called *Anemone* zone in south-western Finland (Fig. 2 and Jalas 1957, Eurola 1999). The northern-most limit of the black alder follows rather well the border between the middle and the northern boreal zones (Figs. 2and 3, Ollinmaa 1952, Ahti et al. 1968, Valkonen et al. 1995, Eurola & Vorren 1980, Eurola 1999). It has been predicted that climate change, i.e. global warming, may lead to a northward shift of the distribution limit of the black alder (Holten 1990).

Another distribution limit of the black alder lies in the outer archipelago of southern Finland, where rocky islets are rising from the sea (Häyren 1914 and 1931, Eklund 1931, Ulvinen 1937, Skult 1956). There is not enough soil for tree seedlings and the climatic conditions during wintertime are highly unsuitable for the black alder. The alders are also exposed to the damage caused by heavy winds and they remain stunted with winding trunks (c.f. Venho 1963). In the inner archipelago, the growing conditions are better and wide black alder stands with straight trunks are common on the shores of sheltered bays. The vegetation is very similar in the archipelago of Sweden (Du Rietz 1925).

On open shores, winds influence the tree species composition. When the soil is wet, like in black alder swamps, tall spruces and birches fall down in heavy winds, because of their shallower rooting system.

2.7. Human influence

The black alder increases the nitrogen reserves on site, by means of its *Francia* symbiosis, irrespective of the original nutrient content of the soil (Mäkinen 1979a and Weber 1986). Thus, these kinds of sites have been cleared for agricultural purposes for a long time. In Finland, the drainage of peatlands for agriculture begun in the 13th century, but became faster at the end of the 19th century. It has been estimated that totally 0.7–1.0 million hectares of peatlands has been cleared for agriculture, corresponding to about 1/3 of all cultivated land (Alm & Saarnio 2006, Simola 2006, Vasander 2006, Myllys & Soini 2008). The proportion of the organic soils having the content of organic material more than 20 % of its weight is about 13.6 % of all arable area in Finland (Myllys & Sinkkonen 2004, Vasander 2006, Myllys and Soini 2008).

Most of the alder swamps were destroyed in the 1950–1980's because of a program for the drainage of peatlands for forestry (Alm & Saarnio 2006, Kaakinen et al. 2008). In the whole country, the total area of drained peatlands and paludified forests was about 5.6 Mha, i.e. 56 % of all peatlands in Finland (Tomppo 2001). In southern Finland, where most black alder stands are situated, the total area of all peatlands was 3 429 000 ha in the inventory during 1989–1994.

However, only 24.3 % of this area was in an undrained state. Besides this, also about 600 000 ha of wet mineral soil have been drained for forestry (Tomppo 2001). In the 11th forest inventory of 2009–2013, the total area of forested eutrophic herb-rich peatlands in southern part of Finland was estimated to be 60 000 ha and the area of mesotrophic peatlands 401 000 ha (Finnish Statistical Year book of Forestry 2014). Black alder swamps are included to these values, but their proportion is negligible.

The area of black alder -dominated swamps in Finland is small and declining. For example, between the 3rd National Forest Inventory (1951–1953) and the 8th National Inventory (1989–1994), the area decreased from 1.8 % to 0.5 % of the total forest area in Finland (Ilvessalo 1956 and 1960, Kujala 1964a and b, Eurola et al. 1988 and 1991, Tomppo 2001). The present black alder -dominated forest area is smaller than in the Baltic and Central European countries. In Estonia, for example, the proportion of black alder -dominated forests is 1.5 %, in Latvia 2.5 %, in Lithuania 6.3 % and in Belarus 11.3 % of the total estimated forest area (Jurkevitch et al. 1968, Hainla 1971, Prieditis 1993a).

Nowadays in Finland, pristine black alder swamps have been protected based on the Nature Conservation Act and the Forest Act (Virkkala et al. 2000, Kaakinen & Salminen 2006, Kaakinen et al. 2008 Korhonen et al. 2013). However, other black alder communities located on mineral soil sites are mainly outside of any protection. On the other hand, many of them are without intensive human influence, because they are for example too stony for cultivation or for drainage.

Many of the black alder stands have been used for grazing in the Nordic countries. For example, in Finland shore meadows were grazed until the 1950's and in Sweden even until the end of the 1960's (Tyler 1969, Johansson et al. 1986, Jutila 1999). Grazing has had a great influence both on the regeneration of the black alder, on the plant species composition in the field layer, and in the undesrstorey where the abundance of tall herbs decreased, and grasses, especially *Deschampsia cespitosa,* increased (Linkola 1916 and 1921). In Finland, in the Lake Saimaa region, the influence of grazing has led to increased occurrence of *Agrostis canina, A. stolonifera* and *Carex nigra* communities (Eurola 1965, Jutila 1999). However, there are also species resistant to grazing such as *Carex elata, C. rostrata* and *C. vesicaria*. On the shores of Lake Vanajavesi in the province of Häme, grazing has contributed the spread of reed mannagrass *(Glyceria maxima)* (Linkola 1942).

After the withdrawal of grazing, the black alder started to regenerate naturally in many wet shore meadows, because the trees were able to grow without disturbance. At present, many of the past meadows on lakeshores are now dominated by naturally established black alder stands. Old shallow ditches may tell about the usage history of the site. Only very wet black alder swamps have not been used for grazing (Jaatinen 1950).

Other uses of the black alder sites have been less intensive. To some extent, the forests have been used for firewood harvesting. Single tall alder logs have also been used for furniture manufacturing purposes.

3. Historical development

Besides local environmental factors, historical factors have controlled the spread of the black alder in Finland. It is known that the black alder arrived to the area as early as at the end of the Yoldia-stage before the arrival of the spruce and the Ancylus transgression (Hyyppä 1933, Sauramo 1936, Kalela 1949, Vasari 1967). It grew on the shores of the Litorina Sea especially during the warm Atlantic period. For example, in one peatland close to Helsinki, roots of the black alder have been found in the depth of 1.5 m in sand (Sauramo 1936). Their age was determined to be 4 600±115 years using the C-14 radiocarbon method (Okko 1960).

Comparing this age to pollen diagrams, it could be determined that these black alder roots grew at the end of the warm Atlantic period (pollen zone VII) (Sauramo 1934, 1936, 1954 and 1958).

On the basis of subfossil findings, the species *Rhamnus frangula, Iris pseudacorus, Lycopus europaeus* etc. arrived to Finland in the Atlantic period in tandem with the arrival of the black alder (Kujala 1924 a, Hämet-Ahti & Suominen 1986). In those days, the understorey of black alder stands was very similar to today. This demonstrates that during the warm postglacial period, the black alder communities were abundant and rich in species. The black alder swamps have often developed on *Phragmites–Carex* peat. Among the subfossils there are remnants of *Phragmites*, *Carex*, *Equisetum fluviatile, Betula pubescens, Cicuta virosa* and *Viola* sp. (Auer 1924 and 1925, Aario 1932, Vasari 1962, Simola 1963, Aartolahti 1965, Aario 1965, Tolonen 1987, Huttunen & Tolonen 2006). The species are similar as those found on recently formed peat on black alder swamps (see the pollen diagrams in Mäkinen 1966 and 1968) and thus no significant temporal change has taken place in the plant species composition on these sites since thousands of years.

Lush black alder swamps became more frequent during the warm Atlantic period. Their remnants are found at the bottom of many peatlands but are seldom found on upper peat layers contrary to Central Europe (e.g. Radomski 1962).

Examples from northern Sweden show that the black alder arrived there before the spruce along the shores of the lake Ancylus and grows still as a relict in the same places closest to the shores of this ancient lake (Westman 1985). Backman (1918) describes similar communities of the black alder on the shores of small paludifying lakes in Ostrobothnia in western Finland.

The warm Atlantic period was followed by a cooler climatic period when many eutrophic swamps were covered by acidic *Sphagnum* mosses. The black alder disappeared or remains as a stunted relict in the forested mire margins of raised bogs where running soligenic water is available (Kujala 1924b, Eurola 1962, Korpela 2004). The black alder is absent in the north as well as also in the shores of bare small lakes in supra-aquatic areas, where the black alder has never grown. One reason for this may be too low pH of the soil, which restricts the growth of the symbiotic *Francia* (Smolander & Sundman 1987, Weber 1989).

Today, with the grazing of shores ended and the land elevation exposing new growing sites for the black alder especially on the seashores of the Gulf of Bothnia, the amount of pristine black alder forests is increasing. Also the conservation of the remaining black alder swamps has stopped their decline in Finland (Kaakinen & Salminen 2006).

4. Material and methods

4.1. Study region

The study area of the black alder stands covered a great part of Finland as the counry is ranging 1 000 km from south (59°47′N) to north (70°05′N), and 500 km from west (19°20′E) to east (31°35′E). The range of the black alder is, however, smaller and the northernmost latitude, where the black alder has been known to exist is the 66°45′N (Fig. 2). Thus nearly whole Lapland is outside of its natural area of distribution.

The most important area of the distribution of the black alder is the peninsula of Finland, limiting in the south and west to the Gulf of Finland and the Gulf of Bothnia, respectively. Especially the south-western coast is shattered into thousand of islands and rocky islets. The outer archipelago is composed of rocky islets, which are created continuously due to the elevation of the bedrock. On these islets, the black alder exists as a first pioneer tree species together with rowan (*Sorbus aucuparia*).

The maximum area of peatlands in Finland has been over 10 million hectares after the Holocene (Ilvessalo 1960, Turunen 2008, Alm & Saarnio 2006). At present, the area of peatlands is about 8.9 M ha (Tomppo 2001, Finnish Statistical Yearbook of Forestry 2014). The area of the geological peatlands (i.e. those having a peat layer > 0.3 m) is about 7.2 M ha (Vasander 1996). That is about 29 % from the land area in Finland. The proportion of black alder swamps is only about 0.5 % from all mires (Eurola et al. 1991, Tomppo 2001). The total area of forests including forested peatlands is about 86 % and the share of lakes and other water courses is about 10% (Ympäristötilasto 1987, Finnish Statistical Yearbook of Forestry 2014). The third characteristic of the Finnish landscape features is the sandy esker forests. They range from north-west to south-east according to the direction of the withdrawal of the continental ice. Some of these are transverse like Salpausselkä eskers in the southern part of Lake-Finland region and the Central Finland Ice-marginal Formation (Tikkanen 2006 b). The southern costal area of the peninsula of Finland is especially rich in clay soils. In these areas, the black alder forests and swamps are characteristic. In recently elevated shores, competition between species is smaller than in brook valleys surrounded by coniferous forest.

Climate in the study area becomes more suitable for the black alder from north towards south-west and determines the northern distribution limit of the black alder in 66°45′N latitude in Rovaniemi (Fig. 2). The distribution limit of black alder follows approximately 0° C yearly isoterm and the 135 days duration time of the growing season. The most important factor controlling the timberline may be, however, the −12 °C isoterm of the coldest month (normally February) and monthly mean of daily minimum temperature −17 °C. Mean annual precipitation in the study area is 500–750 mm (Tuomenvirta 2004).

The largest part of the study area belongs to the boreal coniferous vegetation zone (Figs. 2 and 3, and Kalela 1958a, b, Ahti et al. 1968). Only south-western Finland, including the Finnish Archipelago and Åland, belongs to the hemiboreal zone (Jalas 1957). Typical to this area is that a proportion of forests are dominated by deciduous tree species, including black alder dominated forests. In this region, black alder forests are larger than in other areas in Finland. However, black alder dominating forests are also found in Eastern Finland (Lake-Finland), and in the southern boreal zone where large lakes milden the air temperature gradients. The black alder grows also in the middle boreal zone, but pure alder stands are rare.

4.2. Sample sites and analysing methods

The study material was gathered at 650 sample sites in 200 separate regions in Finland (Fig. 3, Appendix 1). The selection criteria of the studied black alder stands were: the stand should be black alder dominated, at least 100 m² in size, and naturally established black alder forests or swamps. The stands were chosen since year 1959, using topographic maps and aerial photos, with the help of experts (botanists) and local forest officers. Also many alder stands described by Kujala (1924a) and Jaatinen (1950) were explored again in this study. Comparative observations were done in situ during my excursions in all the Nordic and Baltic states as well as in Great Britain.

Each black alder stand consists of one or more communities. Most alder stands are complexes, where the surface vegetation varies along the soil moisture gradient. The borders of the communities are often clearly visible, but also mixed communities may occur within a stand.

The sample sites were placed randomly within each community in the stands. The number of the sites depended on the area of homogenous community. Each community included at least one sample site and in large communities, several sample sites were chosen.

In each site, the tree and shrub species were surveyed, if possible, from an area of 30×30 m (900 m²) sample plot. The plant species in the undergrowth (field and ground layers) were surveyed from smaller sample plots with 5×5 m (25 m²) of the size. In swamp communities, the species occurring on the surface of microtopographical formations (hummocks and hollows) were recorded separately.

The scientific nomenclature of the vascular plants followed the naming mentioned in Hämet-Ahti et al. (1998). The bryophytes were named according to Koponen et al. (1977).

A proportional abundance scale (+, ½, 1, 2, 3, 5, 7, 10, 15, 20, 25, 30, 40, 50, 60, 70, 80, 90, 100 %) was used to indicate the coverage of the species within the sample plot (5×5 m = 25 m²). From all moss and epiphytic lichen species, samples were taken for microscopic determination by the author and external experts. For identification of the species, the guides by Buch (1936), Nyholm (1954, 1965), Arnell (1956) and Piippo (1990) were used.

After the plant species on each sample plots were identified, the communities were classified in the field. The classification was carried out using a method, where the dominant understorey species have a greater role than in the traditional classification of forest and mire types in Finland (Cajander 1909, 1913, 1925, 1930 and 1949, Kalela 1960 and 1961, Kujala 1961) and in the Braun-Blanquet method (Du Rietz 1936, Braun-Blanquet 1951). However, my classification procedure follows principally the methods of the school of Cajander. The site type was named according to the dominant species, but this classification, made in the field, was based on the floristic composition of the whole plant community including the soil type and hydrological characteristics of the sampling area.

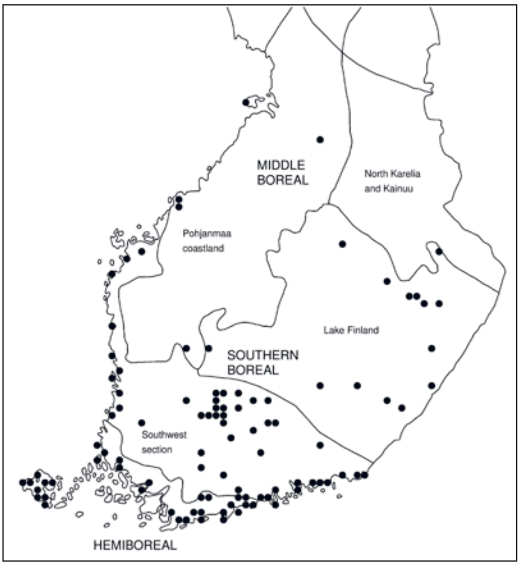

Fig. 3. The location of the studied black alder stands and the vegetation zones of Finland (see Ahti et al. 1968 and Eurola 1999).

Kuva 3. Tähän tutkimukseen sisältyneiden tervelepikoiden sijainti sekä kasvillisuusvyöhykkeet Suomessa (ks. Ahti ym. 1968 ja Eurola 1999).

In the site type classification, if the total area of the observed subcommunities within a stand compartment was less than 100 m^2, the whole compartment was classified to the same site type. Otherwise, several site types may occur within a stand compartment.

The classification of the vegetation is based on the similarities in the understory vegetation and soil type in a large group of black alder stands. A preliminary grouping was based on the observations in the field and was made in the field. Closer grouping was based on clustering and ordination methods commonly used in ecological research. The similarities and differences between the surveyed black alder communities, sample plots, and species were explored using clustering analysis with the Sørensen distance and the Euclid distance measures, group average and Ward linkage methods, as well as DCA ordination (Detrended Correspondence Analysis) using the PC-Ord and CANOCO packages (Sørensen 1948, Gauch 1982, Pakarinen 1984 and Jongman et al. 1987).

Soil type and moisture as well as the ground water level were estimated visually in the middle of summer at the same time with the vegetation survey. Based on the studies by Mäkinen (1968 and 1979a), the following moisture classes were used in the moisture observations: dry, mesic, moist, wet and watery.

5. Results

5.1. Classification method of black alder communities

The range of moisture tolerance of many companion plant species is narrower than that of the black alder. Therefore the frequency of the species common to all black alder communities is small, on average less than 50 % of all study sites. On the basis of the inventories, altogether 11 characteristic species (with more than 30 % mean frequency) could be identified and they are presented in Table 1 (see also Appendix 2).

Species with narrow moisture or nutrient range like *Phragmites australis* or *Thelypteris palustris,* may be very abundant in one community, but are nearly absent in other communities.

Table 1. The character species according to their mean frequency in all studied black alder communities in Finland.

Taulukko 1. Tutkittujen tervalepikoiden kasvupaikkojen tyyppilajit keskimääräisen esiintyvyyden mukaan.

Species	Mean frequency, %
Alnus glutinosa	100
Filipendula ulmaria	51
Viola palustris	47
Peucedanum palustre	46
Galium palustre	43
Lysimachia vulgaris	40
Lysimachia thyrsiflora	40
Sorbus aucuparia	39
Betula pubescens	38
Deschampsia cespitosa	36
Dryopteris carthusiana	35
Rhamnus frangula	30
Solanum dulcamara	29
Calamagrostis purpurea	27
Caltha palustris	27
Brachythecium reflexum	27
Sanionia uncinata	23
Picea abies	18
Plagiothecium denticulatum	17
Carex canescens	15

On the other hand, the species with extensive tolerance, such as *Filipendula ulmaria,* is rather indifferent and can be found in a large variety of the black alder sites.

According to the data analysis, the black alder forests and swamps in Finland fall into three groups, which can further be divided into 14 communities. Permanently wet communities were classified into the black alder swamps. This group differs from the black alder forests growing on dryer soil or on occasionally flood-covered shore forests with mineral soil. Differentiation of these three groups is sometimes difficult e.g. because of annual variation in water table level.

As mentioned earlier, the vegetation descriptions were made mainly in pure and primary black alder forests and in swamp shores, where the competition of coniferous trees is generally weaker than e.g. in brook valleys. In brook valley sites the species composition is different than in the shores and this affects the classification. This difference is clearly seen e.g. when comparing the black alder swamps with Cajander's herb-rich hardwood-spruce fens. The latter have been described as located "in the middle of the coniferous forest", not on shores. Thus, the "biotic effect" of the coniferous forests is visible. The remaining of the black alder swamps, found in brook valleys and mire margins, are no longer pure or "original" as they were during their establishment in the Atlantic period.

Black alder swamps and forest could be classified into the following site type groups (A–C) and communities:

A. Alluvial black alder communities
1. *Carex–Alnus glutinosa* on mineral soil sites
2. *Lysimachia vulgaris–Calamagrostis purpurea–Alnus glutinosa*

B. Black alder swamps
1. *Phragmites australis–Alnus glutinosa*
2. *Paludified Carex–Alnus glutinosa*
3. *Equisetum fluviatile–Alnus glutinosa*
4. *Thelypteris palustris–Alnus glutinosa*
5. *Iris pseudacorus–Alnus glutinosa*
6. *Athyrium filix-femina–Calla palustris–Alnus glutinosa*
7. *Scirpus sylvaticus–Alnus glutinosa*

C. Herb-rich black alder forests
1. *Athyrium filix-femina–Filipendula ulmaria–Alnus glutinosa*
2. *Athyrium filix-femina–Alnus glutinosa*
3. *Filipendula ulmaria–Alnus glutinosa*
4. *Urtica dioica–Alnus glutinosa*
5. *Rubus idaeus–Alnus glutinosa*

5.2. Ordination of the sample plots

DCA-ordination highlights the differences and similarities between the sampled black alder communities better than the mean values of the sites (Fig. 4). In the DCA-ordination analysis of the sample plots, the axes 1–3 reflect the largest differences between the site type groups and the homogeneity of the communities. Based on this analysis, the sample plot groups of the *Phragmites* (A), *Scirpus* (I), *Equisetum* (E), *Rubus* (N) and *Lysimachia - Calamagrostis* (D) communities were most clearly distinct. The rest of the community types partly overlap in the DCA ordination. The most important ecological gradient in the ordination parallels the gradient from the *Iris* (G) to the *Thelypteris* (F) type communities. In addition, the following community groups are evident: *Athyrium–Calla* (H), *Filipendula* (K), *Urtica* (L) and *Rubus* (N) (Fig. 4). This is the same succession order as appears in the field, and reflects both the soil moisture and the fertility gradient of the sites.

The DCA-ordination also captures the homogeneity of the communities. Some sample plots may be very close to each other while others are more dispersed. In this study, the most homogenous black alder communities were the *Urtica* (L), *Equisetum* (E), *Scirpus* (I) and *Phragmites* (A) types. (Appendix 2). The *Filipendula* (K), *Athyrium–Filipendula* (J) and *Athyrium–Calla* (H) communities were small but shared some overlap. Both the *Athyrium* and the *Filipendula* community types are dominated by tall herbs and form a mixed community. The most heterogeneous communities, having a mixture of several type groups, were the *Carex* type (peat) and the *Carex* in mineral soil type (Fig. 4). The *Lysimachia – Calamagrostis* -group is also rather heterogeneous.

5.3. Ordination of the communities

In the DCA-ordination (Fig. 5), the study sites were divided into three groups: black alder forests and swamps, as well as a smaller group of shore forests situated between the first two. The littoral communities share many similarities: They are situated on the shores of sea or lake under the impact of limnogenic waters. In the shore forests, a total of 102 common species were found (Appendix 2).

In the black alder swamps, the following groups could be detected: *Scirpus* (I) and *Phragmites* (A) site types, which differ clearly from each other and the *Iris*- (G) and *Thelypteris*-rich (F) black alder swamps, representing the most eutrophic swamps in southern Finland. The soil moisture and nutrient gradient proceeds from eutrophic *Thelypteri*s (F) and *Iris* (G) swamps via the *Athyrium–Calla* type (H) to *Athyrium filix-femina* dominated black alder forests (M) and then to the *Athyrium–Filipendula* (J) and the *Filipendula* types (K) until the forest types of *Urtica* (L) and *Rubus* (N) (Fig. 5).

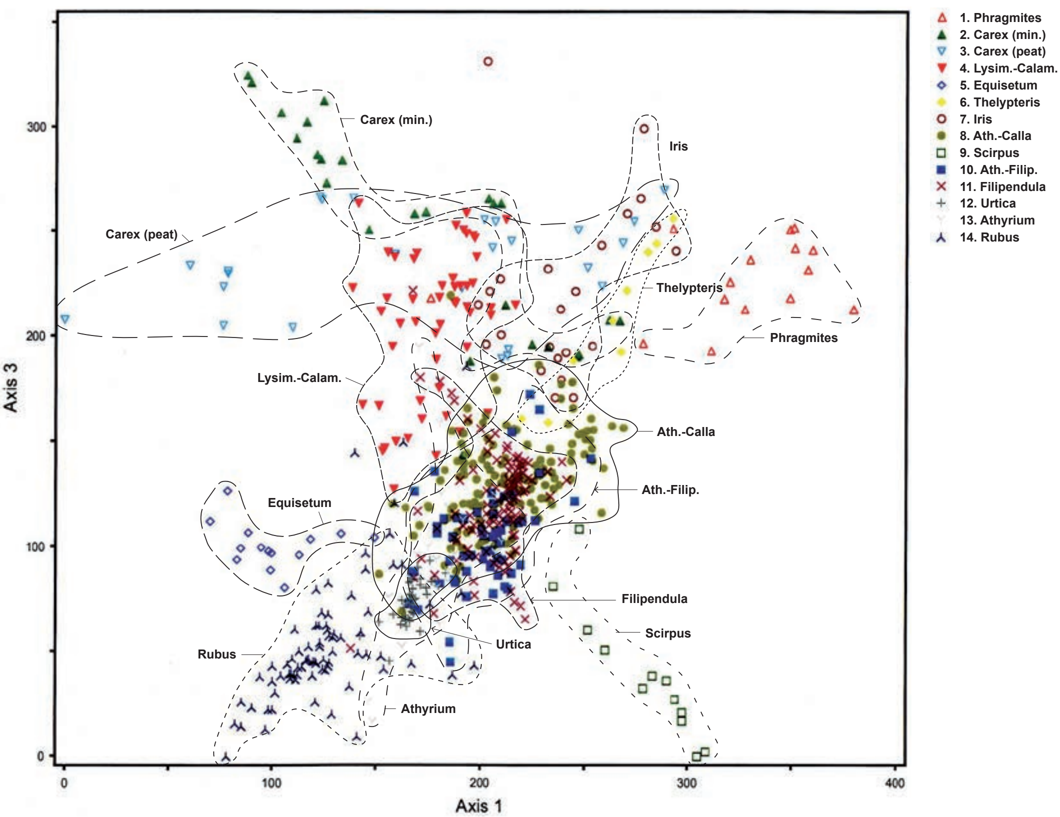

Fig. 4. DCA ordination diagram of the sample plots of black alder stand explored in this study. Different black alder communities are marked with symbols. Rare species are not downweighted. Eigenvalues of axis 1 are 0.510 and eigenvalues of axis 3 are 0.441. The black alder communities: *Phragmites* (A), *Carex* (mineral soil) (B), *Carex* (peat) (C), *Lysimachia–Calamagrostis* (D), *Equisetum* (E), *Thelypteris* (F), *Iris* (G), *Athyrium–Calla* (H), *Scirpus* (I), *Athyrium–Filipendula* (J), *Filipendula* (K), *Urtica* (L), *Athyrium* groves (M), *Rubus* (N).

Kuva 4. Tervaleppäkoealojen DCA-oordinaatioanalyysi. Tervaleppäyhdyskunnat on merkitty eri symbolein.

The results of the cluster analysis showed that the most appropriate analyses for this material seemed to be the Sørensen distance measures with the group average linkage methods (Sørensen 1948). The method gives nearly identical results to the DCA-ordination (Figs. 5 and 6). Among the black alder swamps, the most common type was the *Athyrium–Calla*-type. *Thelypteris* and *Iris* types are infrequent among the southern black alder communities.

Besides these black alder communities, a few others may be found, but they are small in size and often have specific features (e.g. *Menyanthes*-rich vegetation). Within each type, variation occurs, and subtypes or variants can be identified. In most cases, the site types are complex, because both the black alder swamps and black alder forests have a continuum (Appendix 1). This is often a result of the inclination of the shore and variation in topography and soil moisture.

In permanently wet locations, such as on paludifying shores and brook sides, as well as on formerly water-covered shores watered by spring brooks, the succession differs from the forest series. They mainly originate as open nutrient-rich shore meadows. Permanently wet soil attracts wetland species. They stay in the hollows since alders grow with additional roots and make hummocks forming a mosaic-like structure of the microsites. The hummock sites are often dominated by *Athyrium filix-femina*, and the hollows by *Calla palustris, Lysimachia thyrsiflora, Cicuta virosa, Equisetum fluviatile, Iris pseudacorus* or *Thelypteris palustris*. On hummocks, also the shade-tolerant forest species such as *Dryopteris carthusiana*, and on the intermediate lawn levels, many hygrophile mosses (*Mniaceae, Calliergon cordifolium* etc.) may occur.

5.4. Description and distribution of black alder communities

5.4.1. Alluvial black alder forests on mineral soils (A-types)

In the Finnish black alder communities exposed to flooding, the average water table level and the paludification rate of the site were important factors for classification. Based on these factors, the black alder communities growing in littoral and on mineral soil sites were separated from the paludified communities. Some of the paludified communities are however subject to spring floods and limnogenic waters. In given sites, the peat layer is very thin and it is difficult to separate young black alder swamp sites from the mineral soil ones.

For the classification of black alder forest sites on the littoral zone, the approach based on the water table level by Du Rietz (1939) was used. He divided the littoral zone to four categories: 1) Epilittoral belt above high water, 2) Geolittoral belt from mean water to estimated high water level, 3) Hydrolittoral belt from low water to mean water, and 4) Sublittoral belt being permanently submerged area. The sites of alluvial black alder communities occurring on the littoral zone typically range from the elipittoral zone to the upper geolittoral one. These communities can be divided into the following groups: *1. Carex–Alnus glutinosa* community and *2. Lysimachia vulgaris–Calamagrostis purpurea–Alnus glutinosa* community.

In the first group, the name species are either characteristic species or dominant species. *Carex* refers here to the species *Carex vesicaria, C. rostrata, C. acuta* and *C. nigra*. *Glyceria maxima* may dominate over the *Carex* species.

In the second group, the species *Calamagrostis purpurea* may be the most frequent. In many black alder communities, particularly on those used for grazing, *Deschampsia cespitosa* may also be common. The stand canopies on alluvial black alder communities are either closed or sparse and the pioneer forests form a narrow belt on mineral soil nearest to the sea or lake water. The stand on these belts forms the first steps in forest succession. The black alder occurs with the shore vegetation so that their seeds will be present in the water and the beach, germinating in the upper littoral zone (geolittoral) after the water level is lowered. On the shore, there is much light and the competition with other plants is smaller than within dense stands.

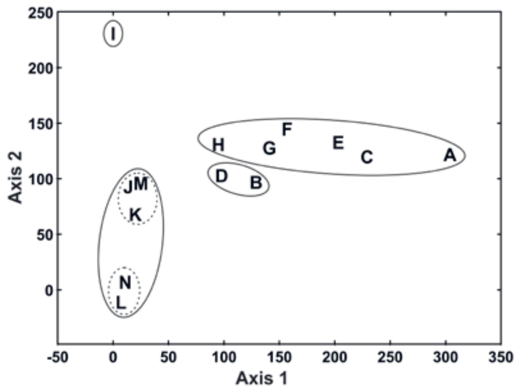

Fig. 5. DCA ordination diagram of black alder dominated communities in Finland (mean releves sensu synoptical table). No downweighting. Axes are rescaled. For symbols, see Fig. 4.

Kuva 5. DCA-oordinaatiodiagrammi Suomessa esiintyvistä tervaleppäyhdyskunnista. Symbolit, ks. kuva 4.

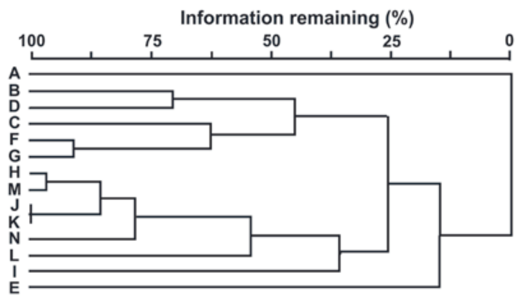

Fig. 6. The cluster dendrogram (Sørensen Group Average), mean values of Finnish black alder communities. The resemblance is indicated in percent scale. For symbols, see Fig. 4.

Kuva 6. Suomen tervaleppäyhdyskunnat esitettynä klusterointipuuna (Sørensenin ryhmittelyanalyysi).

Table 2. The character species according to their mean frequency (MF, %) in the studied alluvial black alder communities in Finland.

Taulukko 2. Yleisimmät kasvilajit tutkituissa tulvarantojen tervalepikoissa. MF = keskimääräinen esiintyvyys, %.

Species	MF
Character species	
Alnus glutinosa	100.0
Galium palustre	75.5
Lysimachia vulgaris	72.0
Peucedanum palustre	55.0
Lythrum salicaria	54.0
Carex vesicaria	51.5
Deschampsia cespitosa	48.5
Climachium dendroides	44.0
Hypnum lindbergii	43.5
Ranunculus repens	41.0
Calamagrostis purpurea	40.0
Myosotis scorpioides	38.5
Scutellaria galericulata	37.5
Agrostis capillaries	34.5
Juncus filiformis	32.0
Lycopus europaeus	30.5
Solanum dulcamara	29.5
Mentha arvensis	24.5
Taraxacum officinale	20.5
Other typical species	
Potentilla palustris	46.0
Sanionia uncinata	43.0
Dryopteris carthusiana	40.0
Betula pubescens	38.0
Sorbus aucuparia	36.0
Lysimachia thyrsiflora	35.5
Brachythecium reflexum	35.0
Calliergon cordifolium	34.5
Caltha palustris	33.5
Viola palustris	33.0
Rhamnus frangula	31.0
Alnus incana	29.5
Calla palustris	24.0
Glyceria maxima	19.0
Cardamine pratensis	18.0
Alisma plantago-aquatica	16.0
Carex rostrata	14.5
Cicuta virosa	15.0
Carex rostrata	14.5
Carex nigra	13.0
Bidens tripartita	11.0

The alder communities where *Carex* species dominate (*Carex – Alnus glutinosa* community) are more common on low clay soils, while the *Lysimachia vulgaris – Calamagrostis* type black alder communities are growing often on stony till soils. Both communities are more under the influence of shore forces (moving ice, flood and the abrasion) than other black alder communities. Their vegetation consists of typical shore plants together with forest species (Tables 2, Appendixes 2 and 3). The black alder is the dominating pioneer tree in the first stage of forest succession. Later, other species such as *Alnus incana, Betula pubescens* in the tree stand, and *Sorbus aucuparia, Rhamnus frangula* and *Ribes spicatum* in the shrub layer, become more abundant. Most common species in the field and ground layers are *Galium palustre, Lysimachia vulgaris, Peucedanum palustre*, *Lythrum salicaria* and *Carex vesicaria* (Table 2). Also *Myosotis scorpioides, Lycopus europaeus, Juncus filiformis* and *Agrostis capillaris* have their highest frequency in the alluvial black alder communities. Their frequency is higher than e.g. in black alder swamps (Appendix 2).

Also some anemochoric species such as *Taraxacum* spp., whose diaspores are dispersed into the littoral zone, are occurring. The most common ground layer species in the alluvial black alder communities are *Climacium dendroides* and *Hypnum lindbergii*.

The geographical distribution of the alluvial black alder communities covers the whole of southern Finland. They can be found both on lake and sea shores, but most of my sampling sites are situated in Lake-Finland (Fig. 3 and Appendix 1). On the shores of the Gulf of Bothnia the occurrence of these sites is rarer than in the site sites in south-western Finland. In steep sloping shores the influence of land upheaval is smaller.

5.4.2. (A1) Carex–Alnus glutinosa community on mineral soil (Carex-type)

The *Carex–Alnus glutinosa* community is often the first stage of succession in the development of black alder forests on mineral soils. It is quite common especially on the shores of large lakes, but also on seashores (Appendix 1) affected by the land elevation after the ice age.

In sheltered bays, thick sediment layers make a good and nutrient rich soil for water and shore plants after lowering of the water level. This is the path for the development of primary shore meadows, which are suitable growing places also for the black alder. The ground water level is high and there is no competition with other tree species except some willows, which tolerate periodical flooding.

Sedge-black alder community on mineral soil is often characterized by tall sedges (Fig. 7a). The most common *Carex* species on lake shores are *C. vesicaria, C. nigra, C. rostrata* and *C. acuta*. On alluvial seashore meadows, the vegetation has similar belts, but the species composition is different (Fig. 7c).

If surface waters are blocked up (e.g. by a shore bank pushed by ice) the paludification starts rapidly. In the beginning there is no great influence on the vegetation and thus similar *Carex–Alnus glutinosa* communities grow both in wet mineral soil and in thin peat. The succession leads to different directions, either to a herb-rich forest or to a swamp. Therefore I split this sedge-black alder community to two groups: mineral soil sites, and thin-layered peat sites. Both are alluvial in the beginning, but the exact limit between these sites is difficult to distinguish.

a. *Carex–Alnus glutinosa* community on alluvial lake shores

These sites typically occur on the low-lying shores of inland lakes where a regular zonation of water and the shore plant species dominate the field layer. On low shores the belts of these sites may be wide, spanning up to several hectares. The most common order of the belts is as following (e. g. Perttula 1958b and Kalliola 1973):

- Epilittoral: 1. *Deschampsia cespitosa, Agrostis capillaris* and *Calamagrostis purpurea* meadow
- Geolittoral: 2. Some dryer *Carex* belt (*C. nigra, C. canescens, Juncus filiformis*, *Eriophorum angustifolium, Calamagrostis neglecta, Agrostis canina)*. 3. A belt of tall sedges (*Macrocaricetum) (Carex vesicaria, C. rostrata, C. acuta).*
- Hydrolittoral: 4. *Equisetum fluviatile* belt, 5. *Phragmites australis* or *Scirpus lacustris* belt

The sedge-black alder communities arise in good alder seed years after the water level has been drawn back. The seeds of black alder germinate quickly on moist mineral soil or on sedge hummocks and continue their growing irrespective of flooding.

If the withdrawal of the water is continuous, such as from land elevation on shallow shores the first alder seedlings are shrub-like and grow in sparse groups, often forming very dense stands (Fig 7a). The canopy and dimensions of the alders increase towards land, while the coverage of the field layer species decreases respectively. Trees compete with each other for light and for the soil resources and may suffocate nearly all ground vegetation. Total number of species in such stands may be less than 10, while it normally is about 20 (Appendix 2).

Besides the black alder, no other trees or bushes grow on such young alluvial shores, except for some *Salix* species such as *Salix phylicifolia*. Once the soil has became drier or the alders have made root-hummocks, some bush species appear: first *Alnus incana, Rhamnus frangula, Sorbus aucuparia, Betula pubescens*, *Ribes spicatum,* and in later stages *Picea abies* begins to occupy the site (Appendix 2). During this late successional stage, sedges start to decline and the site type begins to change.

The vegetation composition of the field layer in sedge-black alder sites is typically helophyte vegetation controlled by the nutrient status of the soil as well as the trophy of the lake. On the shores of nutrient-poor lakes in southern Finland, there are often only two helophyte zones: The outer belt dominated by *Phragmites australis*, and the inner belt dominated by *Carex vesicaria* and *C. nigra*. Usually, the mineral soil is comprised of nutrient-poor clay or silt, but gradually changes to more nutrient-rich soil as the alders increase the nitrogen content and waves accumulate litter in the littoral zone.

If there are springs or brooks on the shore, more nutrients are carried into the community along with running water, and the vegetation becomes lusher during the succession. If the shore waters are surrounded by embankments, paludification begins. In both cases the number of species increases.

Besides tall sedge species, the following common species occur on these sites: *Galium palustre, Lyhtrum salicaria, Myosotis scorpioides, Lycopus europaeus, Agrostis capillaris, Caltha palustris, Scutellaria galericulata, Glyceria maxima, Cardamine pratensis, Stachys*

Fig. 7a. Young black alders on a lake shore (Study site 131, see Appendix 1) in Pälkäne, southern Finland. *Carex vesicaria* dominates in field layer. Photo: Ahti Mäkinen.

Kuva 7a. Nuoria tervaleppiä järven rannalla (Koemetsikkö 131). Pälkäne. Luhtasara (C. vesicaria) on vallitseva kenttäkerroksessa.

Fig. 7b. *Glyceria maxima* displaces tall sedges on a lake shore (Study site 162). Valkeakoski (Sääksmäki). Southern Finland. Photo: Ahti Mäkinen.

Kuva 7b. Isosorsimo (Glyceria maxima) valtaa sarojen kasvupaikat järvien rannoilla (Koemetsikkö 162). Valkeakoski (Sääksmäki).

Fig. 7c. Black alder is spreading on a sea shore meadow. Pyhäranta, southwestern Finland. Photo: Ahti Mäkinen.

Kuva 7c. Tervaleppää merenrantaniityllä. Pyhäranta.

paluster, Alisma plantago-aquatica, *Persicaria amphibia, Taraxacum officinale, Carex nigra* and *Bidens tripartita* (Appendix 2). All of them favour very wet conditions on shores, if the competition is low. In similar conditions, other littoral plants of black alder communities grow, e.g. *Ranunculus repens* and *Juncus filiformis*. *Peucedanum palustre* is also rather common, but typically grows only on shore swamps (Appendix 2).

The number of ground layer species in the *Carex–Alnus glutinosa* community is rather low, because the floods are quite regular and the root-hummocks of alders are low. The most common moss species growing on the roots of alders and on small hummocks are *Hypnum lindbergii and Climacium dendroides* (Appendix 2). *Calliergon cordifolium* also thrives on these sites, even though more common in swamps and herb rich mires. *Sanionia uncinata* and *Brachythecium reflexum* belong to the epiphytic species and grow in the dry butt of alders above the flood limit.

b. *Glyceria maxima–Alnus glutinosa* community

In tall sedge–black alder communities in alluvial soils, some variations can be distinguished according to the species in the field layer. One variant detected is the *Glyceria maxima–Alnus glutinosa* community (Fig. 7b). This community is extremely local, because the reed manna grass *(G. maxima*) was originally planted on those sites and later spread. This classification is based on the findings in four sites on the shores of Lake Vanajavesi in Tavastia (experimental stands 160–164. See Appendix 1), where the reed manna grass was planted in 1767 (Uotila 1971). The reed manna grass thrives in very similar growing conditions as tall sedges (Linkola 1942). However, it is a stronger competitor than sedges, displacing them on shores and forming lush shore meadows even up to two meters tall (Fig. 7b).

Intensive grazing of cattle and muskrats (*Ondatra zibethicus*) enable the natural regeneration of black alder through the thinning of the reed manna grass vegetation. This is the most typical path for the origin of *Glyceria maxima–Alnus glutinosa* communities. When the alder canopy increases, the reed manna grass vegetation declines but some plants can be found in moist gaps and on the intermediate levels in the field layer even in large closed alder stands.

c. *Alnus glutinosa* communities on alluvial seashore meadows

Similar young black alder communities as those on lakeshores are found on the shores of the Baltic Sea, but they are rarer and their species composition is different. Because of land elevation, new growing sites are exposed continuously in formerly water-covered areas, especially on the shores of the Gulf of Bothnia, but they are often stony.

The most common belts and their most typical vegetation in seashores according to Palmgren (1912), Brenner (1916), Kujala (1924a), Borgström (1930), Kalliola (1973), Pyökäri (1978) and Siira (1970) are the following:

- Epilittoral belt: *Deshampsia cespitosa* meadow
- Geolittoral belts: 1. *Agrostis canina, Sesleria coerulea* belt; 2. *Festuca rubra, Carex nigra, C. oederi, Agrostis stolonifera* belt; 3. *Juncus gerardi, Eleocharis uniglumis* belt, 4. *Triglochin maritimum*
- Hydrolittoral belt: *Phragmites australis*

The main growing place of the black alder is the epilittoral belt, but some seedlings may be found in the upper part of the geolittoral belt, as well (Fig. 7c). Especially the *Deschampsia cespitosa–Alnus glutinosa* communities are rather common in many sites on seashores. A large coverage of *Deschampsia* is often connected with grazing.

The appearance of black alder communities on seashore meadows is analogical with the *Carex–Alnus glutinosa* community on lakeshores (Figs. 7a and 7c). The belts are very narrow. Some of these communities are closer to the *Lysimachia vulgaris–Calamagrostis purpurea–Alnus glutinosa* type.

On the shores of the Gulf of Finland, Åland, and the inner archipelago, *Phragmites australis* often displaces sedges and other lower meadow plants especially on silty and clay soils. Thus, in dense *Phragmites australis* and black alder -dominated stands, the main species are often *Filipendula ulmaria*, some willows (*Salix phylicifolia* and *S. nigricans*) or *Hippophaë* belt. If intermediate vegetation occurs at all, the characteristic species on shore meadows are *Phragmites* *australis, Filipendula ulmaria, Hierochloë odorata ssp.baltica, Lysimachia vulgaris* and *Angelica sylvestris* (Jaatinen 1950).

5.4.3. (A2) Lysimachia vulgaris–Calamagrostis purpurea–Alnus glutinosa community (Lysimachia–Calamagrostis type)

Most black alder stands that are characterized by *Lysimachia vulgaris* and *Calamagrostis purpurea* are situated on shores, and less commonly in moist depressions far from the shore. The stands are generally sparse and narrow, rarely wider than 10 meters, on open moraine or silty shores (Fig. 8a). Sometimes their total area may exceed one hectare. The range of tolerated conditions for both species is wide, from barren stony shores to eutrophic swamps and shore groves, but their frequency is often higher in these black alder communities than in other conditions.

Limits of these marginal stands are determined mainly by the height of the ground water and annual flooding. On steep shores, the black alder is incapable of competing with other tree species if the depth of the water table is 0.5 m below the soil surface. In the communities on gently sloping shores, which are under the influence of flooding, the soil is generally silt or stony till with a thin humus layer.

The shrub layer, usually scattered and sparse, and the ground vegetation depend on the tree canopy less than in other types, because of sufficient light. The most common shrub species are *Alnus glutinosa*, *Betula pubescens, Sorbus aucuparia, Rhamnus frangula* and *Alnus incana*, *Salix myrsinifolia* and *S. pentandra* (Appendix 2). In the *Lysimachia–Calamagrostis* type, the field layer species can be divided into three groups: Real shore plants living in the littoral zone, ashore plants and "real forest" plants.

The real shore plants (littoral plants) are adapted to the specific conditions prevalent on shores. Besides the black alder, other such species are*: Lysimachia vulgaris, Galium palustre, Peucedanum palustre, Potentilla palustris, Lythrum salicaria, Juncus filiformis, Scutellaria galericulata* and *Carex vesicaria*. *Phalaris arundinaceae*, *Molinia coerulea* and *Lactuca sibirica* occur occasionally (Fig. 8b).

Ashore plants (i.e.geobionts) are spead by diaspores carried by wind (anemochoric plants). Their seeds also fall into the water and may geminate in the shore litter accumulations. For example the seedlings of *Taraxacum* species, *Tussilago farfara* and *Leontodon autumnalis* are sometimes found on lake shores. Many of them take root permanently, although they are not the original type species (Cajander 1902, Du Rietz 1939, Tuomikoski 1941 and Sjörs 1960).

Real "forest plants" or eugeobionts are e.g. *Calamagrostis purpurea*, *C. canescens, Deschampsia cespitosa, Dryopteris carthusiana, Rubus idaeus* and *Oxalis acetosella* (Appendix 2).

The field layer is typically characterized by *Lysimachia vulgaris, Calamagrostis purpurea* and *Deschampsia cespitosa*. The first one is found in all sampling sites but is seldom dominant. *Calamagrostis purpurea* is more abundant but does not occur at all sites. In some areas it is replaced by *Carex canescens* or *Deschampsia cespitosa*, and sometimes by *Phalaris arundinacea*. Other characteristic species of this type are *Galium palustre, Viola palustris, Juncus filiformis* and *Scutellaria galericulata* (Appendixes 2 and 3).

Because of occasional flooding of the shores, mosses (e.g. *Brachythecium reflexum* and *Sanionia uncinata*) mainly grow on stones or on the base of alders. Species such as *Hypnum lindbergi* and *Climacium dendroides* are able to tolerate temporary flooding and are grow between stones in the upper littoral zone.

The number of all plant species in the *Calamagrostis–Lysimachia* type (230 species in total) is greater than in many other black alder communities (Appendix 2). Some regional variation of species is found, as well as differenes in the species dependence on soil type. Thus, for example, *Calamagrostis purpurea* and *C. canescens* favour moraine soils, while the other name species *Lysimachia vulgaris* and *Deschampsia cespitosa* are distinctly more abundant in sedimentary soils. The latter may sometimes be dominant in the field layer. In these cases, the community may be considered as a variant of the *Lysimachia–Calamagrostis* type or even an independent type. This type is the main one in the littoral zone.

Fig. 8a. Marginal black alder community on a sea shore (Study site 81). Espoo, southern Finland. *Lysimachia vulgaris* is dominating in field layer. Photo: Ahti Mäkinen.

Kuva 8a. Tervaleppäpuustoa meren rannalla (Koemetsikkö 81). Espoo. Ranta-alpi (Lysimachia vulgaris) on vallitseva kenttäkerroksessa.

Fig. 8b. *Calamagrostis* rich black alder community on a lake shore (Study site 194). Joensuu, eastern Finland. Photo: Ahti Mäkinen.

Kuva 8b. Kastikkakasvustoa rantalepikossa (Koemetsikkö 194). Joensuu.

5.5. The black alder swamps (B)

5.5.1. The site types and the vegetation

Black alder swamps are communities situated in wet sites, such as on the shores of sea and lake, on brook or river sides, in peatland margins or in moist depressions. They are rather small in size: as a rule a few hectares or smaller.

Most black alder swamps are so wet that other tree species are not successful in the competition with the black alder.

A typical feature of all black alder swamps is that the water table level is located more or less permanently close to the soil surface. Springs are also frequent. The variation in microtopography, the hummock–hollow mosaic, increases the diversity of plant species. The micrclimate within the stands is often stabile throughout the growing period.

Most black alder swamps grow on sites with a rather thin peat layer, from 5 to 50 cm, which seems to be optimal for the black alder. Slim trees grow up to a height of 25 metres. On thicker peats, the trees remain stunted. At these sites, the dominant communities are the paludified *Carex–Alnus glutinosa* community and the *Phragmites australis–Alnus glutinosa* community in paludified shores and in mire margin areas.

The ground vegetation of black alder swamps has mosaic-like structure due to the growing strategy of the black alder. On a wet substrate, it makes a conical root hummock by growing adventive roots above the water table level and thus enabling the growth of roots in aerobic conditions (Kujala 1924a, Elveland 1976). This is necessary for the nitrogen processing microbes (*Francia alni*), which live in the fine roots of black alder and do not tolerate anaerobic conditions. The root hummocks of black alder rise generally to 30–50 cm above the wet hollow level. The height of the hummocks depends on the age of the community. In young communities (e.g. close to the shore) the root hummocks are lower than in older swamps, where several successive tree generations have increased the height of the root hummock (Kujala 1924a).

In addition to black alder, other hummock-making plants are great ferns, mostly *Athyrium filix-femina* or *Dryopteris carthusiana*, but also *Deschampsia cespitosa* and *Carex elongata*. They may have originally established on the base hummocks of alder or on an intermediate level e.g. on the surface of the fallen decayed branches of trees.

In pace with the ageing of the black alders, the root hummocks grow both horizontally and vertically and new species may spread over the hummock. These species are e.g. *Filipendula ulmaria, Urtica dioica* and *Rubus idaeus*; mostly also *Calamagrostis purpurea, Equisetum arvense, Oxalis acetosella* and *Trientalis europaea.*

At the intermediate level, ranging from 5 to 20 cm above the hollow level, both swamp and shore plants are present (Eurola et al. 1980). Relatively common species with a frequency over 20 %, are *Galium palustre, Lysimachia vulgaris*, *Lythrum salicaria, Viola palustris*, *Lycopus europaeus*, *Deschampsia cespitosa, Carex canescens* and sparsely *C. elongata* (Appendix 2).

In the lowest level (0–10 cm above the soil surface) i.e. in the hollows, typical wetland species have their largest coverage: *Calla palustris, Lysimachia thyrsiflora, Equisetum fluviatile, Potentilla palustris* and *Peucedanum palustre*, often also *Cicuta virosa, Carex rostrata* and *Solanum dulcamara*. On the most eutrophic swamps, *Iris pseudacorus* and *Thelypteris palustris* also occur sometimes together with *Lemna minor.*

Numerous mosses grow on fallen branches. The most common are *Calliergon cordifolium*, *Pseudobryum cinclidioides, Climacium dendroides* and *Plagiomnium ellipticum*. As well some *Sphagnum* species such as *Sphagnum squarrosum, S. teres, S. angustifolium, S. riparium* and *S. fimbriatum* occur. However, their coverage is normally small indicating, in contrast to other peatlands, their negligible role in peat formation in this site type.

Mosses especially favour high humidity and create the fifth, vertical epiphytic level on the basal trunks of alder. On these microsites, the most common species are *Plagiothecium denticulatum* and *P. laetum, Hypnum cupressiforme* and *Lophocolea heterophylla*. As well *Brachythecium reflexum* and *Sanionia uncinata* can be found in black alder swamps, although their frequency is higher in the mineral soil sites.

The most frequent species in black alder swamps are presented in table 3. For the species typical to different site types of swamps, see Appendix 2.

The regional distribution of black alder swamps varies according to the community. Most of them are concentrated in southernmost Finland (hemiboreal zone) and the southwestern part of country (Eurola and Ruuhijärvi 1961). Out of the studied swamps, the most northerly ones were found in the in the Isle of Hailuoto close to the city of Oulu. The eutrophic types, the *Iris* and *Thelypteris* communities, are only found in the hemiboreal zone and the *Phragmites* and *Carex* communities are more common in the southern coastal area. *Athyrium–Calla* and *Equisetum* dominated black alder swamps are widely spread in the southern coastal area and in Lake Finland (Fig. 3 and Appendix 1).

5.5.2. (B1) Phragmites australis–Alnus glutinosa community (Phragmites type)

Phragmites australis grows on the shores of sheltered bays of the Baltic Sea, on the islands of the inner archipelago, and coastal areas, where it forms large and dense stands ranging from the upper littoral zone as far as into 2 meters deep water (Luther 1951b and Jalas 1958c). The tallest individuals (height over 4 m) and densest stands (300 straws/m²) are situated in gyttja soil, where it is one of the most important peat forming plants during the beginning stage of paludification. However, on nutrient-poor soils, such as on open sandy or till shores, the *Phragmites* stands are sparse and small (Vaarama 1938).

Black alder favours similar sites as *Phragmites* but grows in geo- and epilittoral zones. The land elevation leads to slow moving of all littoral vegetation zones, but not all vegetation zones move simultaneously. *Phragmites* may remain growing on its place after the black alder has spread to the same site (Fig. 9a), giving rise to the *Phragmites–Alnus glutinosa* community.

After rooting of the black alder seedlings, they gradually make low hummocks, where hygrophile herbs can spread, and the succession continues. Because of wet habitat and the great biomass of *Phragmites,* the paludification begins quickly. The increasing shade and decreasing soil moisture make *Phragmites* individuals infertile and thinner. However, because of the deep-extended rooting system and strong vegetative growth, it is a persistent competitor (Luther 1951a and b). It may continue to grow as a relict in mires after the infilling of a lake or a paludified bay.

For vegetation, the reed – black alder community resembles the tall grass savanna with sparsely growing trees (Fig. 9a). Because of the exceptionally high and dense field layer vegetation, their structure differs much from the other black alder communities. For the same reason the species diversity (69 species) is the smallest of all alder communities (Appendix 2).

On these sites, trees are generally short. The tallest trees on the shores were 12 m high and somewhat taller in the mire margin sites. Their mean diameter at breast height (1.3 m) was 5–15 cm and the cover 30–60 % (Table 6, Appendix 1). The trees have bumpy stems with plenty of lichens and small twigs. Sometimes pubescent birch and young spruces may occur, but they do not compete with the black alder.

In the shrub layer, some willow species may occur on shores and on mire margins. *Myrica gale* and *Picea abies* are also common. In mire margin areas, the shrub layer is sparse because of sinking hollows with only some shoots of alder and spruce seedlings growing on low hummocks.

The field layer is characterized by *Phragmites australis*, but as soon as the black alders grow

Table 3. The most frequent species in the studied black alder swamps.

Taulukko 3. Yleisimmät kasvilajit tutkittujen tervaleppäkorpien kasvupaikoilla.

Species	Mean frequency %
<u>In all swamps</u>	
Alnus glutinosa	100.0
Peucedanum palustre	67.4
Calliergon cordifolium	56.1
Viola palustris	55.9
Lysimachia thyrsiflora	55.4
Filipendula ulmaria	50.7
Potentilla palustris	50.6
Galium palustre	48.0
Betula pubescens	44.9
Lysimachia vulgaris	42.7
Calla palustris	40.4
Solanum dulcamara	39.9
*Pseudobryum cinclidioide*s	39.3
Rhamnus frangula	35.4
Sphagnum squarrosum	32.1
Calamagrostis purpurea	30.9
Lythrum salicaria	25.4
Salix phylicifolia	22.9
Carex canescens	18.9
Cicuta virosa	18.4
Menyanthes trifoliate	18.0
Lycopus europaeus	17.9
Carex acuta	17.9
Carex nigra	17.6
Scirpus sylvaticus	17.1
Salix cinerea	16.6
Sphagnum teres	15.0
Lemna minor	12.3
Sphagnum angustifolium	12.3
Sphagnum riparium	11.6
Typha latifolia	11.0
<u>In alluvial black alder swamps</u>	
Equisetum fluviatile	43.3
Iris pseudacorus	43.0
Carex rostrata	25.9
Thelypteris palustris	19.3
Phragmites australis	15.4
Carex vesicaria	9.0
Carex lasiocarpa	6.4
Carex aquatilis	3.6

Fig. 9a. *Phragmites australis–Alnus glutinosa* swamp on a sea shore (Study site 94). Helsinki. Photo: Ahti Mäkinen.

Kuva 9a Phragmites australis – Alnus glutinosa -tyypin korpi meren rannalla (Koemetsikkö 94). Helsinki, Karhusaari.

Fig. 9b. *Phragmites australis* as a relict in a black alder swamp on a mire margin (Study site 56). Raasepori (Tenhola), southern Finland. Photo: Ahti Mäkinen.

Kuva 9b. Järviruoko (Phragmites australis) reliktikasvina tervaleppäkorvessa (Koemetsikkö 56). Raasepori (Tenhola).

higher and their canopy increases, some swamp species like *Potentilla palustris, Peucedanum palustre*, *Lysimachia vulgaris, L. thyrsiflora* and *Carex acuta* occur in the community. Other characteristic species of this type are: *Carex nigra, Agrostis canina* and *C. lasiocarpa*. In mire margin areas, the field layer comprises more species than in younger shore swamps of *Phragmites* type. On the hummocks, there are many bushes and field layer species (e.g. *Carex lasiocarpa* and *Vaccinium oxycoccos),* which are absent in younger successional stages.

Many reed-black alder communities are thinpeated on shores and in the beginning stage of paludification (Fig. 9a). The peat layer is however thicker on mire margins (Fig. 9b).

On shores, because of the very thick *Phragmites* litter and wet soil, the ground layer is fragmentary. Later on when the alders make low root-hummocks, providing a refuge against flood-

Fig. 10. *Carex–Alnus glutinosa* swamp on a sea shore (Study site 90). Helsinki. Photo: Ahti Mäkinen.

Kuva 10. Carex – Alnus glutinosa -tyypin korpea meren rannalla (Koemetsikkö 90). Helsinki.

ing, there are more growing sites for mosses. On hummocks and intermediate levels, *Sphagnum squarrosum* and *Ptilidium pulcherrinum* were the characteristic specie*s* in the studied sites. In the early successional stage, mosses are often absent. In mire margin areas, the ground layer is often dominated by homogenous *Sphagnum* vegetation. Because of great differences, this community on thick peat can be considered as a variant of *Phragmites–Alnus glutinosa* type. (Fig. 9b and Appendix 1).

5.5.3. (B2) Paludified Carex–Alnus glutinosa community (Carex–Alnus glutinosa swamp type)

Black alder is the dominant tree species on these sites (Fig. 10). On sites with a thin peat layer, some birches and willows may grow together with black alder. Other trees require large root-hummocks of alders.

In this study the characteristics of the alders varied according to the depth of the peat layer (see Table 6, Appendix 1). At sites with a deep peat layer, the form of trees typically resembles ”swamp-alders”. They appear very stunted with bumpy stems and curved boughs. Most of the trees grow in dense groups and there is also a large number of dead trees. The number of stems decreases with increasing canopy cover. At sites in the beginning stages of the paludification process, alders have contact with the mineral soil (Päivänen 1988 and 1990). Black alder trees and tree groups spread slowly on a tall sedge fen or on open swamp and the trees develop a root-hummock at their base. In old swamps there are deep flarks covered by water at least during the flood periods between the hummocks. Walking on these sites is possible by stepping only on the hummocks. The stands float on the peat and water and have no more contact with mineral soil. They gain nutrients from moving surface and spring waters.

Tall sedges, particularly *Carex rostrata*, dominate in the field layer (Fig. 10). As well other tall sedges such as *C. lasiocarpa, C. aquatilis* and *C. vesicaria* are characteristic species (Appendix 2). Furthermore, *Peucedanum palustre* and *Vaccinium oxycoccos* have significant coverage (Appendix 2). Other common swamp species are: *Lysimachia thyrsiflora, Potentilla palustris, Galium palustre, Equisetum fluviatile*, *Lysimachia vulgaris* and *Calla palustris*. As a rule, the vegetation of the field layer resembles tall sedge fens and aquatic sedge communities more so than open eutrophic swamps (Fig. 10).

The *Sphagnum* species are not present in greater flarks because of flooding and prefer intermediate levels and the root-hummocks of alders.

Their total coverage, however, is greater than in any other black alder communities (Appendix 2). *Sphagnum squarrosum* is the most common species but does not dominate everywhere. In the younger stages of the community, in open fens the ground layer vegetation is normally closed but also characterized by *Sphagnum spp.* The total number of plant species was 88 (Appendix 2).

The depth of the peat layer varies normally from 20 cm to more than 1.5 m. The surface peat is well decomposed black peat. At deeper levels its color is brown until it turns gradually into blue-grey gytja and bottom sediments. As soon as the black alder grows on the open fen, it makes basal shoots and a small hummock with its adventive roots. In wet sites, the diameter of hummocks varies from 0.5 to 1 m, but on dryer sites it's as large as 1–1.5 m. Their height is usually 5–20 cm in young trees, but 20–30 cm in old trees. The flarks are normally covered with water and are therefore without mosses, but during dry summers they often dry.

These sites mostly occur in the hemiboreal vegetation zone (Fig. 3 and Appendix 1) but are also found elsewhere in southern Finland as small areas in the margins of mire complexes (Eurola 1962). On the base of surface vegetation composition, they resemble tall sedge fens, yet they are more nutrient rich with many swamp species present (Cajander 1913 and Eurola 1962). The occurrence of these sites in paludifying bays and on mire margins closest to soligenic waters indicates that the site type belongs to the same succession series as the alluvial *Carex–Alnus glutinosa* forests site type on mineral soil.

5.5.4. (B3) Equisetum fluviatile–Alnus glutinosa community (Equisetum type)

Equisetum fluviatile is one of the most common helophytes on our lakeshores, especially on sheltered infilled bays of eutrophic lakes (Kujala 1924a, Aario 1933, Vaarama 1938 and Tuomikoski 1958a).

The most typical *Equisetum* type black alder swamps are found scattered in the hemiboreal zone on the lake shores particularly on the coastal area in southwestern and in southeastern Finland, where *Equisetum* and *Equisetum–Phragmites* type lakes are common (Fig. 3 and Appendix 1, Maristo 1941). On seashores, *E. fluviatile* grows only in estuarys to avoid salt waters (Luther 1951a,b). However, it can be found on peatlands close to the shore where it makes wide homogenous communities A good example is Site no. 90 in Helsinki (Fig. 11a). It is a part in a large complex of black alder communities (see Appendix 1).

In this stydy, another typical example of this type is study site 49, on the shore of the small eutrophic lake of Läppträsket in Karjaa in southern Finland, which was formed from an open *Equisetum* swamp about 35 years ago after the lowering of the water table level (Kurtto 1985). Typical to this community is that the underlying vegetation does not deviate largely from the open swamps and permanent flooding is prevailent at the sites. The water table level is commonly 10-30 cm above soil surface and only the small root hummocks (>20 cm in height) occasionally are above the water table level. The depth of the peat layer is 5–35 cm. In older and more paludified sites, the peat layer is much deeper, up to two meters, and the horsetails (*Equisetum sp.*) has to be considered as a relict from the ancient lake era (Fig. 11b and Aario 1932). Large homogenous *Equisetum fluviatile–Alnus glutinosa* communities do not occur on lake shores and mires in the Lake-Finland region, although small stands of this type do occur. In these types of sites, black alder is mostly the sole tree species but also downy birch (*Betula pubescens*) may occur particularly in the later phase of the mire succession promoted by land elevation. Trees grow in sparse stands or in small groups. Little curled trunks and decreasing radial growth occurring over time indicate the increasing depth of the peat layer (Fig. 11b).

The shrubs are few, probably due to the small root-hummocks of the trees and the lack of space for other forest plants. Most of the shrubs are base shoots of the black alder or some *Salix* species as well as downy birch. *Rhamnus frangula* grows in moist places (Appendix 2).

In the field layer, a dense vegetation of about one meter tall *Equisetum fluviatile* dominates. Because of the shade of the alders, it is often sterile but rich in branches (Fig. 11b). In many places however, the *Equisetum* stand is still so dense that there is little space for other species thriving

Fig. 11a. A wide *Equisetum fluviatile–Alnus glutinosa* swamp on a sea shore (Study site 90). Helsinki. Photo: Ahti Mäkinen.

Kuva 11a. Laaja-alainen Equisetum fluviatile – Alnus glutinosa -tyypin korpi meren rannalla (Koemetsikkö 90). Helsinki, Herttoniemi.

Fig. 11b. *Equisetum* rich black alder swamp on a mire margin (Study site 56). Raasepori (Tenhola), southern Finland. Photo: Ahti Mäkinen.

Kuva 11b. Kortevaltainen tervaleppäkorpi (Koemetsikkö 56). Raasepori (Tenhola).

in shallow water sites. Yet some typical swamp species like *Iris pseudacorus*, *Potentilla palustris, Lysimachia thyrsiflora, L. vulgaris, Peucedanum palustre* and *Carex canescens* etc. are found almost in all sites. On low-lying hummocks, there may be a dense cover of fertile *Viola palustris*. On thicker peat sites, *Menyanthes trifoliata* and *Calla palustris* are found as an indicator of long duration paludification. Other characteristic species of this type are *Galium palustre* and *Carex nigra* (Appendix 2).

The total number of species (63 taxa) is similar to that in the *Phragmites* type sites. That is the smallest number of species of all black alder communities. One characteristic in *Equisetum–Alnus glutinosa* swamps seems to be a rich moss cover in spite of permanent flood that is an opposite feature to *Phragmites* type. Particularly the proportion of some *Sphagnum* species is remarkable, up to two thirds of the ground layer (Appendix 2 and 3). The most common *Sphagnum* species in the surveyed stands of this study were *Sphagnum teres* and *S. riparium*. In many other black alder swamps, especially in younger succession stages, the proportion of *Sphagnum* species is small or they do not occur at all. Other characteristic moss species in this type are *Pseudobryum cinclidiopides, Calliergon cordifolium, Plagiomnium ellipticum, Polytrichum longisetum* and *Rhizomnium pseudopunctatum* (Appendix 2).

Equisetum fluviatile favours low lake shores with a gyttja or mud bottom and the communities grow in dense stands with as much as 1 000 shoots/m^2. While the peat layer increases, the proportion of *Sphagnum* spp. increases in all black alder swamps. Simultaneously the soil conditions become less suitable for black alder when e.g. the pH decreases. This results in the gradual decrease in the growth of trees (Mäkinen 1968).

Equisetum fluviatile is a typical companion species or even characteristic species in many black alder swamps (Appendix 2). Sometimes it makes mixed stands with *Menyanthes trifoliata*. This is evidence of a closer relationship between these communities.

5.5.5. (B4) Thelypteris palustris–Alnus glutinosa community (Thelypteris type)

Most of the *Thelypteris palustris–Alnus glutinosa* communities are located in southernmost Finland in the hemiboreal vegetation zone (Fig. 3 and Appendix 1). They grow on the shores of shallow eutrophic lakes as a result of their paludification by infilling (Tuomikoski 1958b and Fig. 12a). The peat float is fastened by tree roots but the youngest alders closest to open water lean towards the lake. In the middle of the float the older alders gradually sink through the peat float due to their weight so that the trees are surrounded by a depression filled with water. On margin areas, low hummocks (1×1 m, height < 20 cm) occur. This kind of vegetation where black alder takes part in the paludification of lakes is exceptional in Finland (Jaatinen 1950 and Hinneri 1965).

In the shrub layer, willows (*Salix cinerea* and *S. phylicifolia*) are quite common, but no clear willow margin is found. In the field layer, the most common species is *Thelypteris palustris* that is a mire plant. Its typical growing sites are humifying shores of eutrophic lakes and their brook estuaries (Tuomikoski 1958b). In Åland, and in Kirkkonummi (Sites 27 and 76), where this kind of black alder stands are found, *Thelypteris* grows furthest out in the peat float. In Åland it grows together with *Rumex hydrolapathum*, *Solanum dulcamara* and *Calla palustris* (Fig.12a). Also mixtures of vegetation with *Carex acuta, Calla palustris*, *Iris pseudacorus*, *Carex pseudocyperus* and *C. aquatilis* occur. Other characteristic species are *Peucedanum palustre, Viola palustris, Typha latifolia, Carex nigra, Rumex hydrolapathum* and *Lemna minor* (Appendix 2).

Because of the rich litter crop, the ground layer is poor especially in flarks (Jaatinen 1950). If there are suitable elevations, species such as the *Mniaceae* species like *Pseudobryum cinclidioides* and *Plagiomnium ellipticum* grow, but no homogenous ground layer can be found (Appendixes 2 and 3).

The depth of the peat layer varies according to the depth of water and the age of the community. Peat-floats may have a thickness of 0.5 m or less.

5.5.6. (B5) Iris pseudocorus–Alnus glutinosa community (Iris type)

This community, which is characterized by iris and black alder, is rare in Finland and occurs only in the southern hemiboreal zone (Fig. 3 and Appendix 1). Although the characteristic species, *Iris pseudacorus* grows nearly as far north as black alder, it is more common in southern Finland on the muddy shores of small eutrophic lakes. It often grows in dense stands together with other swamp plants (Perttula 1958a).

Some regional variation is found in *Iris* type as well as in other black alder communities, but most characteristic species are found in nearly all the sites (Appendix 2). A typical hummock-flark mosaic, like in all forested swamps, is also a typical feature in this type, except in the surface floating part of the community. The trees are stunted and grow in sparse stands.

Particularly shoots of alder and some willows (*Salix phylicifolia* and *S. cinerea*) as well as seedlings of *Betula pubescens* and *Sorbus aucuparia* are common on hummocks. In later succession stages some spruce seedlings are also found.

Usually there are two field layers in this community. On flarks, the upper layer is made by *Iris pseudocorus* together with tall sedges (Fig. 13a). The lower one is often occupied by *Calla palustris* or some other short vascular plant species and small floating plants like *Lemna minor*. On hummocks, the vertical layers are not so conspicuous. More common is a mosaic-structure where each species, such as *Gymnocarpium dryopteris* and *Calamagrostis purpurea,* occupies their own

Fig. 12a. Vernal aspect of *Thelypteris palustris–Alnus glutinosa* swamp floating on the surface of a small eutrophic lake (Study site no. 27). Åland. Photo: Ahti Mäkinen.

Kuva 12a. Keväinen näkymä pinnanmyötäisesti rehevälle järvelle muodostuneesta Thelypteris palustris – Alnus glutinosa -tyypin korpisuosta (Koemetsikkö 27). Ahvenanmaa.

Fig. 12b. *Thelypteris palustris–Alnus glutinosa* swamp (Study site 49). Raasepori (Karjaa), southern Finland. Photo: Ahti Mäkinen.

Kuva 12b. Thelypteris palustris – Alnus glutinosa -tyypin suo (Koemetsikkö 49). Raasepori (Karjaa).

hummock. Other characteristic field layer species are *Peucedanum palustre, Galium palustre, Equisetum fluviatile, Cicuta virosa* and *Dryopteris carthusiana*. Characteristic moss species are *Calliergonella cuspidata* and *Mnium hornum*. The role of *Sphagnum* spp. is insignificant.

The amount of epiphytic lichens is greater than normal in black alder stands because of suitable growing conditions such as permanently high humidity and slow growth of trees.

The black alder swamps of *Iris* type can be classified to smaller systematic units according to the field layer species (Jurkevitch et al. 1968). In Finland, two variants should be particularly mentioned. Their characteristic species are either tall sedges *Carex vesicaria* and *C. rostrata* or *Calla palustris* (Appendix 2):

***a. Carex* variant**

One typical example of *Carex* site type variant was found in Åland (Site no. 30). On these sites, black alder trees grow on large hummocks surrounded by tall sedge vegetation (*Carex rostrata* and *C. vesicaria*) as well as fertile iris vegetation forming “a park-like” swamp community (Fig. 13b). The flarks are covered by 20–40 cm deep

Fig. 13a. Eutrophic *Iris pseudacorus–Alnus glutinosa* swamp is rare and "exotic" in Finland (Study site no. 76). Kirkkonummi, southern Finland. Photo: Ahti Mäkinen.

Kuva 13a. Rehevät Iris pseudacorus – Alnus glutinosa -tyypin suokasvupaikat ovat harvinaisia Suomessa (Koemetsikkö 76). Kirkkonummi.

Fig. 13b. Wide and luxuriant *Iris pseudacorus–Alnus glutinosa* swamp in Åland (Study site 30).

Kuva 13b. Laaja-alainen rehevä Iris pseudacorus – Alnus glutinosa -tyypin korpi Ahvenanmaalla (Koemetsikkö 30).

water during the whole growing season. Besides the dominant species, *Lemna minor* and *Lysimachia thyrsiflora* also occur in the flarks.

Alders make great hummock-like root collars. These "hummocks" arise 50–60 cm above the water level. Freezing processes also play an important role in their establishment. The oldest trees have an age over 100 years but their height is usually only 9–10 m.

The ground vegetation on hummocks differs greatly from that of flarks and consists mainly of typical forest species such as *Gymnocarpium dryopteris, Dryopteris carthusiana*, *Maianthemum bifolium* and *Oxalis acetosella*. Also *Vaccinium vitis-idaea* and *V. myrtillus* can be found on the hummocks. Close to the water level in the hummocks (on intermediate level sites) *Mnium hornum* can be found.

b. *Calla* variant

This second variant type differs from the previous one by the flark vegetation. *Calla palustris* forms wide vegetation patches between the *Iris* dominated tussocks. Furthermore, *Calamagrostis purpurea* is characteristic on the hummocks.

In this work, one of the best examples of this variation is the Site no. 76 in Kirkkonummi municipality in southern Finland (Fig. 13a). The "type community" is located in brook estuary on the southwest shore of a small humifying lake.

In these sites, the black alder stand has been established after the paludification of the lake shore. The black alder together with *Iris* and other swamp plants are dominant species. Trees are stunted and grow in small groups in flat root-hummocks together with some willow bushes.

In the field layer, the eutrophic-like habitus of the sites is completed by *Lemna minor, Carex pseudocyperus, Thelypteris palustris* and *Solanum dulcamara*. For mosses, favourable growing sites are few due to the luxuriant field layer vegetation and continual flooding. The thickness of the peat and detritus layer varies from about 0.5 m to >2.0 m

5.5.7. (B6) Athyrium filix-femina–Calla palustris–Alnus glutinosa community (Athyrium–Calla type)

In this black alder community, *Calla palustris* and *Athyrium filix-femina* were selected as the name species, because they often grow together and are characteristic in most of the typical black alder swamps in Finland.

Calla palustris favours flarks and often forms dense stands both in open swamps (Jaatinen 1950) and in wet flarks of treed swamps (Tuomikoski 1958c). Although other swamp plants may be more common in this type, they usually form more sparse vegetation than *Calla palustris*.

On hummocks, the most common species is *Athyrium filix-femina*. It favours wet conditions with high humidity during the growing season but does not occur in sites having a thick peat layer or in young alluvial soils (Kalliola 1958). Thus it is absent in many black alder communities (Appendix 2).

Typical black alder swamps with *Athyrium filix-femina* and *Calla palustris* as the dominant species are often located in formerly water covered soils irrigated by spring brooks. In most cases such places are found inland at the base of the glacial eskers close to oligotrophic lakes.

The spring waters discharge continuously from the esker through the forest to flat areas support permanent soil moisture and high nutrient levels (Mäkinen 1964).

The *Athyrium filix femina–Calla palustris–Alnus glutinosa* community is the most common and luxuriant of all the black alder swamps in Finland, and it is widely spread, especially in the Lake-Finland region (Fig. 3 and Appendix 1). In this work, 40 stands with 145 sample sites belonged to this type.

Although many of these sites are situated on shores, they are also found above the highest water level of lakes, where the fluctuation of limnic waters has no influence on the vegetation.

The competitiveness of the black alder in wet soil is distinctly stronger than that of other trees. Spruce (*Picea abies*) can be found in brook valleys surrounded by spruce forests. As well *Betula pubescens* and *Alnus incana* can be found in pristine, intact *Athyrium–Calla–Alnus glutinosa* swamps, and their proportion increases after drainage or other human influence.

The growth of the black alder is moderate; a maximum annual growth has been found to be 6.4 m^3/ha (Päivänen 1988) (see also Glavač 1972, Mäkinen 1964, 1968, 1978a, 1979b). Here the highest tree measured was 27 m (Mäkinen 1968 and 1979b). The length of the living canopy is typically about 1/3 of the tree height and the lower trunk is without twigs and leaves. Generative regeneration of black alder is impossible, because of the harsh competition for light in dense stands (Kujala 1924a).

If the alder canopy becomes sparser through the mortality of single trees or tree groups caused by self-thinning or disturbances, a shrub layer will become established on the root-hummocks of the alders. The upper shrub layer, with a mean height of about three meters, consists of *Sorbus aucuparia* and *Rhamnus frangula* species, often together with *Betula pubescens* and *Prunus padus*. The lower shrub layer (mean height of 70 cm) is mainly dominated by *Ribes spicatum* and young bare shoots of black alder together with shrub saplings.

The field and bottom layers of the vegetation have a mosaic-like structure (see Kalela 1949, Kalliola 1973), where *Calla palustris* and *Oxalis acetosella* appear in the bottom and *Athyrium filix-femina* in the upper layer. For the most important plant species in this type, see table 4.

In flarks, the dominant species are *Calla palustris, Cicuta virosa* and *Equisetum fluviatile*. As well *Lemna minor* may grow in flarks. Because

Table 4. The most frequent species of *Athyrium filix femina–Calla palustris–Alnus glutinosa* community. For vertical position of the species; h = hummocks, i = intermediate level and f = flark level.

Taulukko 4. Yleisimmät kasvilajit Athyrium–Calla tyypin tervalepikoissa. Lyhenteet; h = mätäspinta, I = välipinta, f = rimpipinta.

Species	Vertical position	Frequency %	Abundance %
Alnus glutinosa	h	100.0	63.8
Athyrium filix femina	h	94.5	20.7
Lysimachia thyrsiflora	f	82.1	9.8
Viola palustris	i	82.1	7.5
Calliergon cordifolium	f	66.2	3.2
Calla palustris	f	65.5	22.2
Betula pubescens	h	62.1	4.6
Sorbus aucuparia	h	55.2	1.9
Prunus padus	h	52.4	3.3
Ribes spicatum	h	52.4	1.2
Galium palustre	i, f	50.3	0.7
Dryopteris carthusiana	h	50.3	3.6
Equisetum arvense	h, i	49.7	1.8
Impatiens noli-tangere	i, f	44.1	1.7
Potentilla palustris	i, f	49.7	0.8
Solanum dulcamara	i, f	49.7	5.3
Rhamnus frangula	h	48.3	2.5
Pseudobryum cinclidioides	i, f	47.6	6.0
Caltha palustris	i, f	46.2	1.8
Peucedanum palustre	i, f	42.8	0.4
Carex canescens	i, f	36.5	0.5
Rubus idaeus	h	35.9	0.4
Deschampsia cespitosa	i, f	35.2	3.1
Carex elongata	i, f	23.4	0.9
Cicuta virosa	i, f	20.0	1.2

of the extreme wetness of soil where water flows slowly, and the shady conditions, only very few mosses survive on these micro sites. Only some *Sphagnum* species, if occurring at all, grow in hollows. The depth of peat layer is typically 20–30 cm.

Between the flark and the hummock levels, there is an intermediate zone with specific species (Eurola et al. 1984). This zone includes also the humifying twigs and trunks of trees. The intermediate levels are moist and therefore very suitable germinating and growing places for many plant species. They are above the water level nearly the whole summertime, but the plants growing on these elevations have sufficiently water and nutrients. High air humidity supports hygrophile plants.

The intermediate levels are favoured by e.g. *Lysimachia thyrsiflora, Galium palustre, Caltha palustris, Potentilla palustris, Peucedanum palustre, Viola palustris, Equisetum arvense, Impatiens noli-tangere* and *Carex elongata*. According to Bodeux (1955), the latter is a type species of all European black alder swamps. As well *Solanum dulcamara, Carex canescens, Deschampsia cespitosa* and *Filipendula ulmaria* grow on the surface of intermediate level (Table 4).

Most mosses also grow on the intermediate levels, and only there, because the hummocks are too dry and the flarks too wet. Most common moss species are *Calliergon cordifolium, Pseudobryum cinclidioides* and *Brachythecium reflexum* (Table 4). Their coverage is, however, sparse.

The most important hummock-forming plants are the black alder and *Athyrium filix-femina* (Table 4). Other typical field layer species on root-hummocks are *Dryopteris carthusiana, Rubus idaeus, Oxsalis acetosella* and *Trientalis europaea*. Also many other plants growing typically in forests on mesic mineral soil sites grow in nutrient-rich black alder hummocks (Kujala 1924a, Brandt 1933, Jaatinen 1950, Almquist 1965 and Laasimer 1965). Because of rich litter the cover of mosses is small, but some epiphytic species such as *Climacium dendroides, Brachythecium reflexum, Sanionia ucinata* and some *Plagiothecium* species can be found.

5.5.8. Variants of Athyrium–Calla site type

The *Athyrium–Calla* site type can be divided into smaller subtypes or variations according to the swamp species growing on the flarks and on the intermediate levels. Most typical species that make wide pure stands in flarks are: *Calla palustris, Lysimachia thyrsiflora, Solanum dulcamara* and in the beginning of paludification also *Caltha palustris*.

a. *Calla* variant

The most common variant is characterized by *Calla palustris*. In this study material it dominated in flarks of 26 sample plots. In this variant, *Athyrium* is rare or absent. Small hummocks are found only around black alders, and there is no space for other hummock plants (Fig. 14b).

Fig. 14a. Mosaic like vegetation in *Athyrium filix-femina–Calla palustris–Alnus glutinosa* swamp (Study site 143) in Pälkäne, southern Finland.

Kuva 14a. Athyrium filix-femina – Calla palustris – Alnus glutinosa -tyypin korven mosaiikkimaista kasvillisuutta (Koemetsikkö 143). Pälkäne.

Fig. 14b. *Calla* variant of *Athyrium–Calla* type (Study site 56) in Raasepori, southern Finland.

Kuva 14b. Athyrium–Calla-tyypin Calla-variantin kasvupaikkaa (Koemetsikkö 56). Raasepori (Tenhola).

b. *Lysimachia* variant

On these sites, *Lysimachia thyrsiflora* dominates in flarks. Its maximum coverage may approach 100 % in flarks where *Calla palustris* is absent. Difference with the main type (var. typicum) is small. On the hummocks, *Athyrium filix-femina* and *Dryopteris cartusiana* are common.

c. *Solanum* variant

The third variant is characterized by *Solanum dulcamara*. It grows well in dryer flarks and on the intermediate levels.

d. *Caltha* variant

The fourth variant is characterized by *Caltha palustris*. It favours wet open shore meadows and brook valleys in mineral soils. It often reflects an intermediate successional stage from open swamps to the *Athyrium–Calla* type. A good example of this type is the study site 162 located in Valkeakoski on formerly water-covered land. In 1963 there was a large and tall, 18 m high grazed black alder forest. The field layer was a mosaic-like, large complex consisting of *Ranunculus repens, Impatiens noli-tangere, Myosotis palustris, Urtica dioica, Caltha palustris, Solanum dulcamara, Filipendula ulmaria* and *Scirpus sylvaticus*. Forty-five years later, large areas were occupied by *Athyrium filix-femina* vegetation and the paludification had begun. However the flarks were still dominated by *Caltha palustris* and *Impatiens noli-tangere*.

The preconditions to the establishment of the *Athyrium–Calla–Alnus glutinosa* community is stabile hydrological conditions troughout the year. Formerly water-covered lakeshores and brook valleys offer suitable conditions if they receive nutrients from running surface waters or springs.

As long as the alders have contact with mineral soil, the thickening of the peat layer has very little effect on the vegetation composition and growth (See Kujala 1924a and Mäkinen 1979b).

5.5.9. (B7) Scirpus sylvaticus – Alnus glutinosa community (Scirpus site type)

Scirpus sylvaticus favours similar biotopes as black alder but forms only seldom pure communities with black alder. It is well known that *Scirpus sylvaticus* grows as scattered stands with other swamp plants (Jalas 1958). It tolerates well a seasonal flood and is an indicator of minerotrophy (Eurola et al. 1984). If the brook has a wide estuary, pure *Scirpus* stands with an area of more than 0.5 hectares may be found (e.g. study site 108 in Virolahti). Most of the 12 *Scirpus*-dominated sites surveyed in this study are located in inland of southern Finland (Appendix 1). The total area of *Scirpus* type is very small in the study area, probably smaller than the area of *Equisetum* type.

In typical *Scirpus*-type sites, there is usually a spring brook with nutrient- and oxygen-rich waters. Depending on the age of the community, the soil consists either of wet alluvium or thin peat layer and the mineral soil beneath these is usually clay or gytja.

After the stand ages, the peat layer becomes deeper and many mesic vascular plants and heather mosses are replaced by mire plants. Beneath the tree canopies, the number of shrubs may be remarkable although in most sites their coverage is scattered. In addition to base sprouts of alder, also *Rhamnus frangula* and *Sorbus aucuparia* can be found.

In the field layer, *Scirpus sylvaticus* is a sovereignly dominant species. Other characteristic species are *Deschampsia cespitosa, Carex elongata, Chrysosplenium alternifolium, Cardamine pratensis* and *Crepis paludosa* (Appendix 2). The physiognomy of the community resembles the *Glyceria maxima* variant in *Carex – Alnus glutinosa* community (Figs. 7b and 15).

Both *Scirpus sylvaticus* and *Glyceria maxima* start growing on mineral soil, but their great biomass accumulates organic matter soon. In dense stands tall herbs and their litter impede the growth of smaller plants. On hummocks, the most frequent species are *Lysimachia thyrsiflora*, *Potentilla palustris, Galium palustre* and typical hummock species such as *Calamagrostis canescens* and *Viola palustris*. In older stands, the proportion of *Athyrium filix-femina* may be remarkable (Appendix 2).

The species composition in the ground layer is poor, because of the shade of trees and particularly the abundance of litter on the soil surface. Dead leaves of *Scirpus* cover most of the shallow flarks in autumn. Thus, there are very few free growing sites for other plants and e.g. only a few moss species find their places in the community; mainly on the root hummocks of alders (Kujala 1926).

5.6. Herb-Rich Black Alder Forests (C)

5.6.1. Sites and vegetation

Black alder forests are moist sites dominated by the black alder, but they cannot be considered as swamps, because mire plants do not usually dominate in the field and bottom layer and form peat. The surveyed herb-rich black alder sites are fertile ones, whose development is tightly bound to the development of black alder stands. Most of them are established on formerly water-covered land, which was a grazed shore meadow or a hayfield about 100 years ago. The succession has progressed step by step from open shallow water and shore vegetation zones to herb-rich forests. This stage of development is caused by land upheaval. Often the black alder is the only plant species surviving through the succession (Kujala 1924a). When the black alder starts to grow on shore meadow, some shore plants may remain in forest openings or in mesic depressions, but after soil drying their amount decrease and the mesic forest plants of upland sites occupy the site.

The thickness of the humus layer often correlates with the age of the stand and the nutrient status. Thus, the thickness gradient of the humus layer increases from the shore.

According to the study material, the herb-rich black alder forests can be grouped in to five separate communities i.e. site types:

Fig. 15. *Scirpus sylvaticus* is often sterile when growing in black alder swamp (Study site 53). Lohja, southern Finland. Photo: Ahti Mäkinen.

Kuva 15. Korpikaisla (Scirpus sylvaticus) kasvaa usein steriilinä tervaleppäkorvissa (Koemetsikkö 53). Lohja.

1. *Athyrium filix-femina–Filipendula ulmaria–Alnus glutinosa*
2. *Athyrium filix-femina–Alnus glutinosa*
3. *Filipendula–Alnus glutinosa*
4. *Urtica dioica–Alnus glutinosa*
5. *Rubus idaeus–Alnus glutinosa*

As all black alder communities, these site types are named according to the dominating field layer species. Typical for these sites, the tall herbs are often so dominant and conspicuous that the communities are possible to identify even in wintertime when covered by snow.

In fresh silty or clay soils, *Filipendula ulmaria* or *Urtica dioica* are the most common site types, where large homogenous communities in black alder forests occur. On the other hand, the *Filipendula ulmaria–Alnus glutinosa* community is the most common especially on the shores of the Baltic Sea. *Rubus idaeus–Alnus glutinosa* communities are often situated on sandy soils. In low-lying shores, the stand gradient starts from pure black alder forests to mixed coniferous and deciduous tree stands.

For the most frequent plant species on these sites, see Table 5.

Table 5. The most frequent plant species in the mesic herb-rich black alder upland forests.

Taulukko 5. Yleisimmät kasvilajit tutkituilla ravinteikkailla kangasmaiden tervalepikoiden kasvupaikoilla.

Species	Mean frequency %
Alnus glutinosa	100.0
Filipendula ulmaria	62.8
Ribes spicatum	61.6
Prunus padus	61.4
Sorbus aucuparia	58.6
Urtica dioica	58.2
Rubus idaeus	58.0
Athyrium filix-femina	56.4
Dryopteris carthusiana	47.6
Deshampsia cespitosa	45.2
Oxalis acetosella	39.2
Trientalis europaea	30.8
Brachythecium salebrosum	26.4
Geum rivale	24.6
Hypnum cupressiforme	17.2
Sambucus racemosa	16.2
Anemone nemorosa	16.0
Paris quadrifolia	14.0
Silene dioica	11.2
Viola palustris	39.4
Brachythecium reflexum	35.4
Equisetum arvense	29.8
Alnus incana	29.6
Sanionia uncinata	21.6
Ranunculus repens	20.8
Brachythecium oedipodium	19.2

Fig. 16. Luxuriant undergrowth is characteristic for *Athyrium filix-femina–Filipendula ulmaria–Alnus glutinosa* forest (Study site 140). Pälkäne, southern Finland. Photo: Ahti Mäkinen.

Kuva 16. Rehevä alikasvos on tyypillistä Athyrium filix-femina – Filipendula ulmaria – Alnus glutinosa -tyypin metsissä. (Koemetsikkö 140). Pälkäne.

5.6.2. (C1) Athyrium filix-femina–Filipendula ulmaria–Alnus glutinosa community (Athyrium–Filipendula type)

The *Athyrium filix-femina–Filipendula ulmaria–Alnus glutinosa* community can be considerd as an intermediate type between the black alder swamps and black alder forests on the basis of the plant species composition. The name species, *Athyrium filix-femina* is not only a mire plant but it also favours mesic fertile sites in upland forests. *Filipendula ulmaria* grows on similar sites, especially on moist shore meadows and the banks of brooks (Jalas 1965).

In black alder communities on mineral soil sites, these species can even appear alone forming separate communities such as *Athyrium–Alnus glutinosa* and *Filipendula–Alnus glutinosa* communities, which both belong to the group of herb-rich black alder forests. The "mixed" type is a result of the succession between the *Athyrium–Calla* and *Filipendula* types. In this study material, the fequency of indicator species of herb-rich black alder forests was larger than that observed on the swamps, and the peat layer was very thin and scattered. Therefore I include this type to the group of herb-rich black alder forest and not to the mire group.

Most of these sites are located inland (Appendix 1). The micro-topography on this type is very similar to that of *Athyrium–Calla* swamps, where the mosaic-like structure of hollows and hummocks exists (Fig. 16). The difference in moisture between hummocks and intermediate levels, especially in young forests, is not as large as in the *Athyrium–Calla* type swamps.

The hummock levels belong to the same category as those in *Athyrium–Calla* swamps. In younger communities the height of the *Athyrium* hummocks and alder hummocs is often smaller than 30 cm. The most important "hummock plant" is the black alder, but the proportion of grey alder (*Alnus incana*) may also be considerable (mean frequency 45 %) and larger than in black alder swamps (10 %) (Appendix 2). In older stands, the black alder regenerates from sprouts and the height of the hummock is 60–80 cm. So, the differences in soil moisture between hummocks and hollows are a key factor enabling the establishment of more diverse vegetation than in swamps.

Besides the black alder, the most common tree and shrub species are *Prunus padus* (mean frequency 73 %), *Sorbus aucuparia* (62 %), *Ribes spicatum* (62 %) and *Betula pubescens* (42 %). In this material, *Rhamnus frangula* was distinctly rarer (25 %) than in *Athyrium-Calla* swamp, but the proportion of Norway spruce was larger (32 %) (Appendixes 2 and 3).

The root-hummocks of the black alder are suitable growing sites for many species of the herb-rich black alder forests. Especially zoochoric plants, such as e.g. *Rubus idaeus, Ribes spicatum, Prunus padus, Sorbus aucuparia, Sambucus racemosa*, sometimes also *Ribes nigrum, Cornus alba* and even *Fragaria vesca* and *Vaccinium myrtillus,* spread easily with birds into black alder forest, which providing shelter and berries for the birds.

Other plant species growing on hummocks are *Oxalis acetosella, Trientalis europaea, Paris quadrifolia, Maianthemum bifolium* and *Geum rivale,* partly the same as in the *Athyrium–Calla* type (Appendix 2). Among the hummock plants there may also occur species common in deciduous forests, such as *Acer platanoides, Fraxinus excelsior, Anemone nemorosa*, *Adoxa moshatellina, Circaea alpina, Calystegia sepium, Humulus lupulus* etc. *Athyrium filix-femina*, *Dryopteris cathusiana*, as well as *Deschampsia cespitosa* create hummocks on the site.

The characteristics of the intermediate levels of the *Athyrium–Filipendula* type resemble the young and shallow hummocks (= intermediate elevations) in *Athyrium–Calla* swamps. In April, when the snow melts, the intermediate levels may be covered by floodwater. In May, the flooding pools dry up and the typical spring aspect with flowering *Caltha palustris* or *Anemone nemorosa, Chrysosplenium alternifolium, Paris quadrifolia, Viola palustris* and *Circaea alpina* emerges.

If moisture comes continously from springs and brooks, the same species as in the *Athyrium–Calla* swamps grow here too, but in smaller extent*: Impatiens noli-tangere, Caltha palustris, Lysimachia thyrsiflora, Viola palustris, Equisetum arvense* and *Calliergon cordifolium* are common (Appendix 2). The best-growing species, often tall herbs, make sometimes small very dense sub-communities so that the herb layer takes a mosaic-like form. Sometimes tall herbs such as *Equisetum silvaticum* and *Impatiens noli-tangere* may be very abundant. These communities are described as variants of *Athyrium–Filipendula* type:

a. ***Impatiens* variant**
On this site type, the dominant plant species is *Impatiens noli-tangere*. It favours sheltered brook banks or shady nutrient-rich shore marshes. Most abundant *Impatiens* vegetations (height of 150 cm) occur in “semiopen” inland brook estuaries, where it produces big fruits. In shady places and in dryer soils *Impatiens* remains smaller and reproduces by means of cleistogamy i.e. automatic self-pollination.

Besides the type species, also *Alnus incana, Prunus padus*, and *Ribes spicatum* are quite common, but not abundant. In the field layer, *Urtica dioica* may be conspicously abundant (Appendixes 2 and 3). Also *Scirpus sylvaticus* favours the same brook estuaries as *Impatiens noli-tangere*. This indicates a close relationship between these communities (chapter 6.2.8.). Both *Impatiens* and *Scirpus* grow on flooded mineral soil sites, but *Scirpus* thrives in thin nutrient-rich peat soils, too.

In the ground layer, the only species worth noting is *Brachythecium reflexum*. It grows on hummocks and intermediate levels, but also as epiphytic moss on the butts, logs and fallen twigs of trees.

b. “Swampy” variant
This is another variant of the *Athyrium–Filipendula* type, which is similar to the *Athyrium–Calla* type described earlier, but with *Calla palustris* absent. *Calliergon cordifolium, Viola palustris* and *Lysimachia thyrsiflora* are common.

***c. Equisetum silvaticum* variant**
These sites are characterized by the horsetail, *Equisetum silvaticum*. Other characteristic species are *Caltha palustris* and *Geum rivale* (Appendix 2). Also, the frequency of *Oxalis acetosella, Trientalis europaea, Climacium dendroides* and *Anemone nemorosa* may be high.

5.6.3. (C2) Athyrium filix-femina–Alnus glutinosa community (Athyrium type)

The *Athyrium* type is similar to the *Athyrium–Filipendula* black alder forests and the *Athyrium–Calla* black alder swamps described earlier. However, in contrast to these types, *Athyrium* is more frequent, forming only small hummocks, and no

Fig. 17. Luxuriant black alder forest of *Athyrium* type. The cover of ferns (near 100 %) is often impeding the growth of other species (Study site 90). Helsinki. Photo: Ahti Mäkinen.

Kuva 17. Rehevää tervalepikkoa Athyrium-tyypin kasvupaikalla. Tiheä saniaiskasvusto usein rajoittaa muiden lajien kasvua (Koemetsikkö 90). Helsinki.

Fig. 18. The last stage in succession of black alder forests starts when the spruces reclaim the site and the alders die in their shadow (Study site 81). Espoo, southern Finland. Photo: Ahti Mäkinen.

Kuva 18. Tervalepikoiden kasvillisuussukkession viimeinen vaihe alkaa kuusten syrjäyttäessä tervalepät (Koemetsikkö 81). Espoo.

wet hollows occur in the soil surface. The soil in the *Athyrium* type is mesic but aerobic and rich in nutrients. Also for the black alder the growing conditions are optimal.

In the lower tree layer and in the shrub layer the following species are abundant: *Prunus padus, Sorbus aucuparia* and *Ribes spicatum*. As well *Betula pubescens, Alnus incana* and *Rhamnus frangula* are quite common. *Sambucus racemosa* and *Acer platanoides* have their highest frequency in this type (Appendix 2).

The rich field layer is characterised by tall ferns (Fig. 17). Besides the name species, *Athyrium filix-femina*, and *Dryopteris carthusiana* also *Viola palustris*, *Oxalis acetosella* and *Trientalis europaea* are present.

Other perennial species, such as *Rubus idaeus* and *Urtica dioica,* grow with ferns and may be abundant (Appendix 2). Spring-flowering species such as *Anemone nemorosa* flower in May before the ferns grow and the leaves of the alders burst. In the black alder forests of the *Athyrium* type, nearly all swamp species are absent. This is an important difference between the *Athyrium*-rich black alder forests and black alder swamps of the *Athyrium–Calla* type.

Because of the leaf litter and the shade caused by ferns, the number of species in the bottom

Fig. 19. Black alder forest of *Filipendula* type in Helsinki. *Filipendula ulmaria* dominates wide areas of formerly sea shore meadow (Study site 89). Photo: Ahti Mäkinen.

Kuva 19. Filipendula-tyypin tervalepikkoa (Koemetsikkö 89). Helsinki. Mesiangervo vallitsee laajoja aiemmin rantaniittyinä olleita kasvupaikkoja.

layer is very small; only 29 species were observed (Fig. 17 and Appendix 2). In this study material the most common species were *Calliergon cordifolium* and *Plagiomnium ellipticum*. Both of them favour rather mesic growing conditions.

Most of the sites of the *Athyrium* type belong to the largest inland black alder complexes of Finland in the municipalities of Pälkäne, Valkeakoski and Tammela (Appendix 1). In ancient times, the number of *Athyrium*-rich black alder forests was probably larger. However, most of them have been claimed for agricultural use. Furthermore, the natural vegetation succession towards Norway spruce -dominated sites has decreased the area of this site type.

5.6.4. (C3) Filipendula ulmaria–Alnus glutinosa community (Filipendula type)

The *Filipendula ulmaria–Alnus glutinosa* community is typically found on low-lying shores of the Gulf of Finland (Appendix 1), but also on the shores of inland lakes or in brook valleys. On the shores of the Gulf of Bothnia, *Filipendula ulmaria* is a dominant plant species, but it is worth noting that the black alder is absent above the latitude of Kokkola (63°50′N). North of this limit, *Filipendula* forms communities together with *Alnus incana* on coastal areas (Havas 1967).

The soil in the *Filipendula ulmaria–Alnus glutinosa* community is humus-rich mineral soil in the surface. At deeper levels the humus layer turns into clay or gyttja sediments, sometimes into sandy soils or till.

The coverage of *Filipendula ulmaria* is usually more than 50 % (Fig. 19). Their shade gives little room for other species in the field and ground layers (Appendix 3). Most alder stands studied were young and the trees were in their best growing phase in the beginning of the succession development (Table 6, Appendix 1). Their growth rate is one of the best in natural forests in Finland (Mäkinen 1978a, Björklund 1984). Tallest trees are slim and may reach the height of 25 meters at the age of 50 years (Glavač 1972). *Alnus incana* and *Betula pubescens* grow on these sites. When both *Alnus* species grow together, hybrids sometimes occur. In addition, *Prunus padus*, *Sorbus aucuparia,* Norway spruce and *Ribes spicatum* are common.

In the field layer, *Filipendula ulmaria* is a dominant species (Fig.19). The next common species are *Angelica sylvestris*, *Paris quadrifolia, Urtica dioica, Deschampsia cespitosa, Rubus idaeus* and *Geum rivale.* In certain sites, *Urtica dioica* as well as *Rubus idaeus* may even dominate the vegetation over *Filipendula. Anemone*

Table 6. Mean characteristics of black alders on the studied sites in Finland. For, the full names of the site types/communities, see text in chapter 5.1. and Table 7. H = mean stand height (m); DM= mean stand diameter (cm) at the breast height (1.3 m); A = mean stand age (years).

Taulukko 6. Tervalepikoiden puustotunnukset tutkituilla kasvupaikoilla kasvupaikkatyypeittän (kasvupaikkatyyppien täydelliset nimet esitetty tekstissä, kappale 5.1). H =puuston keskipituus (m); DM = puuston keskiläpimitta (cm) rinnankorkeudelta (1,3 m); A = puuston keskimääräinen ikä (vuotta).

Site type	H	DM	A
Carex (mineral soil sites)	14.9	16.4	28.4
Lysimachia–Calamagrostis	15.3	18.2	33.5
Phragmites	12	15	38
Carex (peatland)	8.5	7.2	38
Equisetum	14	20	31
Thelypteris	8	14	22
Iris	15.5	23.5	52.5
Athyrium–Calla	21	23.8	49.3
Scirpus	18	18	32
Athyrium–Filipendula	17	23	47.4
Athyrium forest	18.5	26.2	42
Filipendula	15	21.5	37.4
Urtica	16.2	23	50
Rubus	17.2	26.1	73

nemorosa makes often a conspicuous vernal aspect together with *Filipendula ulmaria* and in mesic depressions, also with *Caltha palustris.*

Because of the extremely shady conditions, only a few species occur in the ground layer. Most common mosses are the *Brachythecium* species *(B. reflexum, B. rutabulum* and *B. salebrosum)*, which can be found especially on the butts of alders. In this study material their mean coverage was less than 1 %. The total number of species in this community was 165 (Appendix 2).

5.6.5. (C4) Urtica dioica–Alnus glutinosa community (Urtica type)

Urtica dioica favours above all nitrogen-rich soil with human influence, but its natural and obviously original sites are herb-rich forests and swamps at lake shores and brook banks (Pettersson 1965 b). The black alder grows on similar sites and thus they often form communities together. Pure stands may be more than one hectare in size (e.g. in Lempäälä (study site 169), Valkeakoski (study site 163), Mäntsälä (study site 99) and Kangasala (study site 121)), and altogether 41 sites of the *Urtica* type were found in the survey.

Small *Urtica* stands can be found in many black alder forests. However, in those cases, they often occur only around decaying alder stumps, where the nitrogen content is high, and form a mosaic-like structure with *Filipendula ulmaria* on *Filipendula* type sites.

Considering only the trees, the black alder forest of *Urtica* type does not differ much from the other black alder forests on flat mineral soil sites. The mean coverage of the black alder (67.7 %) is somewhat higher in the *Urtica* type, than in other black alder forests and varies between 60–90 %. The most abundant tree species in addition to the black alder is the grey alder (*Alnus incana*, mean cover 2.2 %). According to the study material, on these sites, *Picea abies* was rarer than in any other black alder sites on mineral soils.

In the shrub layer, the most common species are *Ribes spicatum* (frequency 68.3 %) and *Prunus padus* (53.7 %). Other zoochoric shrub species are *Sambucus racemosa* and *Sorbus aucuparia*. The total number of shrub species (15) is a bit smaller than in other black alder communities (Appendix 2).

A dominant species of the field layer is *Urtica dioica*, which in flat areas forms homogenous stands (Fig. 20). In fertile soil sites, the dense *Urtica* vegetation may reach up to the height of 170 cm, impeding the growth of smaller plants and having coverage as high as 76.7 % (Appendix 3). In many sample plots there were only less than 10 species in the field layer. These were e.g. *Dryopteris carthusiana, Ranunculus repens* and *Filipendula ulmaria*. In the ground layer, *Brachythecium salebrosum*, *Amblystegium serpens*, *Plagiomnium ellipticum, Brachythecium reflexum, Sanionia uncinanta* and *Plagiothecium laetum* may occur especially on decaying tree trunks, stumps, root hummocks of black alder and as epiphytes on the bases of the alders. The total number of moss species (31) is smaller than in many other black alder site types.

Fig. 20. Nitrophile *Urtica dioica* favors fresh black alder forests, where the root nodules of alder increase the nitrogen content of the soil. (Study site 94) Helsinki. Photo: Ahti Mäkinen.

Kuva 20. Nokkonen suosii reheviä tervalepän kasvupaikkoja, joissa lepän juurinystyrät lisäävät maaperän typpipitoisuutta (Koemetsikkö 94). Helsinki, Karhusaari.

Fig. 21. *Rubus idaeus* makes wide stands in black alder forests on sea and lake shores (Study site 64). Raasepori (Tammisaari), southern Finland. Photo: Ahti Mäkinen.

Kuva 21. Vadelma muodostaa laajoja kasvustoja järven ja meren rantojen tervalepikoissa (Koemetsikkö 64). Raasepori (Tammisaari).

5.6.6. (C5) Rubus idaeus–Alnus glutinosa community (Rubus type)

Rubus idaeus often forms a community together with black alder, especially on drier sandy soils and in later successional stages of shore forests on mineral soil sites (Fig. 21). Its range of moisture tolerance is narrower than that of black alder, but it also grows in drier sites on forest margins and in stone stacks. It thrives on warm sites and clear-cut areas were the cutting residues have been left on site providing shelter for raspberry plants. Vaarama (1965) suggests that *Rubus idaeus* is a plant that favours nitrogen-rich sites. That may be one reason why it grows on many black alder sites. It demands very similar growing conditions as *Urtica dioica*. Therefore these species often compete for the same growing sites such as the surroundings of decaying alder stumps and openings, where enough nutrients and light with moderate moisture are available.

In this study material, in total 49 *Rubus*-type alder stands were included. They are situated both in seashores and in the shores of lakes all over the

Fig. 22. The seeds of black alder are carried by melt water on ice and waves. The seeds accumulate and germinate in littoral belt of lakes and sea (Study site 137). Pälkäne, southern Finland. Photo: Ahti Mäkinen.

Kuva 22. Tervalepän siemenet kulkeutuvat jään päällä sulavesien mukana sekä aalloilla. Siemenet kasautuvat ja itävät helposti järvien ja meren rantojen litoraalivyöhykkeessä. (Koemetsikkö 137). Pälkäne.

southern part of the country. In Åland this type is less common.

When considering the black alder stands on sites of this type, in contrast to the trees in other black alder communities, the trees are older and their diameter is larger in unmanaged stands. The *Rubus* type can be seen to represents one kind of climax community i.e. the final stage of the succession of black alder forests. In the littoral zone, land rises 25–30 cm during one tree generation (chapter 2.4.). After this stage, if succession proceeds without disturbance, the Norway spruce will occupy the site and starts to dominate the stand structure.

The number of tree and shrub species increases with increasing dryness of the soil. Most common species are *Sorbus aucuparia*, *Prunus padus, Betula pubescens, Alnus incana* and *Picea abies*. Also *Ribes spicatum* is very common (average frequency 65 %). *Juniperus communis* is also often present (21 %) particularly in grazed areas.

Besides *Rubus idaeus* and black alder, other characteristic species are *Oxalis acetosella, Trientalis europaea, Maianthemum bifolium* and *Dryopteris carthusiana*. Other important vascular plant species in the field layer are *Deshampsia cespitosa* and *Silene dioica* (Perttula & Jalas 1965) The frequency of *Deschampsia cespitosa* was as high as 67 % and mean coverage 9 % (Appendix 2 and 3). This species is found in nearly all black alder site types, but favours especially grazed black alder stands. *Humulus lupulus* and *Anemone nemorosa* were found only in few sample plots and considered temporary plants in this type (Suominen 1987 and 1990).

However, where the black alder stands of the *Rubus* type border against other herb-rich deciduous forests, also *Anemone nemorosa* may be abundant in the lower field layer and conspicuous in the spring (Jalas & Perttula 1965). It, however, grows better together with *Filipendula ulmaria*. It is known that the soil in the *Filipendula* and *Athyrium* types is more mesic than that in the *Rubus*-type sites. The sites of *Anemone nemorosa* are limited mainly to the southwestern part of Finland, where also *Filipendula ulmaria* is frequent (c.f. Kujala 1961). Both *Anemone nemorosa* and *Silene dioica* -rich black alder forests may be considered as a variant of the *Rubus* type. According to this study material, the most common moss species in the *Rubus* type is *Brachythecium reflexum.* It is found in 50% of the sample plots mainly on the base of the alder trunks. Other frequent species, such as *Sanionia uncinata* and *Dicranum scoparium,* are often found on stone surfaces. *Hypnum cupressiforme* and *H. pallescens* prefer moister places but grow also on stumps and alder trunks.

The *Rubus* type can be regarded as the last stage of the succession series and gradually changes to other deciduous or coniferous forests on mineral soil sites (Fig. 18).

Fig. 23. Erosion may destroy black alders during high water on the shores of large lakes. Köyliö, southwestern Finland. Photo: Ahti Mäkinen.

Kuva 23. Eroosiovoimat voivat irrottaa tervalepät kasvualustastaan rannoilla korkean veden aikaan. Köyliö.

6. Discussion

6.1. (A) The alluvial black alder forests

6.1.1. Occurrence of the sites

During the land elevation process new growing sites for the black alder are created. Most of them are in gently sloping seashores, but also the inclination of great inland lakes from northwest to southeast exposes new growing sites for shore plants (compare with section 2.4.). In steep shores the significance of land elevation for black alder site formation is negligible.

In recently formed shore meadows the black alder is a pioneer species. In gently sloping shores, the meadow vegetation consists of parallel "belts". In Baltic seashores the characteristic species of these belts differ from inland lakeshores, but they also have many similarities (e. g. Palmgren 1912, Brenner 1916, Kujala 1924a, Kalliola 1973, Pyökäri 1978 and Eurola 1999). The most common species are *Phragmites australis, Lysimachia vulgaris, Deshampsia cespitosa, Agrostis canina* and *Carex nigra.* Furthermore, some halophytes in seashores such as *Juncus gerardi* and *Triglochin maritimum* are frequent (Cramer 1980). Typical lakeshore plants also found in alder sites are e.g. *Juncus filiformis, Equisetum fluviatile* and many *Carex* species (*C. rostrata* and *C. vesicaria).*

The black alder may spread on the shore meadows generatively. In seashores, a lot of seedlings are present in the so-called *Sesleria* meadows (Palmgren 1912, Kujala 1924a) but young black alder seedlings can be found also in the *Phragmites* belt in the hydrolittoral zone (Häyren 1902, Kujala 1924a).

In inland sites, I have seen a lot of alder seedlings in the *Carex* tussocks in the macrocaricetum. Because young black alders often grow in these sedge meadows, it is relevant to classify them according to the characteristic species as the *Carex–Alnus glutinosa* community on mineral soil.

In steep sloping shores, a similar zonation of vegetation is established as in the gently sloping shores, but the belts are narrow and fragmentary (e. g. Perttula 1941, Toivonen 1981a and Tonteri et al. 2008). One reason to this is that the soil in steep sloping shores is often till. The content of nutrients in lake water does not have a large influence on the shore vegetation (Lohammar 1938). The *Lysimachia vulgaris–Calamagrostis purpurea–Alnus glutinosa* community is the main type in this area. In spite of the large species diversity, there are few common characteristic species. The occurrence of both name species varies widely from barren stony shores to eutrophic swamps and shore groves. However, their frequency is often higher in these black alder communities than on other site types (Appendix 2).

6.1.2. (A1) Carex–Alnus glutinosa community on mineral soil sites

Most *Carex* species grow on wetlands. Tall sedges (macrocariceta) occur as dense communities in shores as well as in minerotrophic mires (Vaarama 1938, Ruuhijärvi 1960, Eurola 1962, 1965 and 1999, Kalliola 1973, Toivonen 1981b). The charcteristic species occur on various sites: in open fens, shore swamps and in mesic mineral soil sites. *Carex rostrata* prefers swamps and rich fens but occurs also on shores (Jalas 1958b). *Carex acuta* occurs sometimes as dense vegetation covering an area of more than one hectare. It favours clay soils on shallow the shores of large lakes but occurs also in flooded fens. *Carex vesicaria* is also common in clayey shores and flooded meadows but occurs very often on herb-rich mires and swamps (Perttula 1958b). Sometimes the communities consist of one *Carex* species only, but especially on shores, mixed communities are common (see also Tikkanen 1967).

Certainly, there is regional variation in the species composition of this site type. In this study, *Carex vesicaria* and *C. nigra* are typical characteristic species (Appendix 2). Also in some shores of lakes in Åland and in Uppland in Sweden, *C. nigra* forms together with *Alnus glutinosa* communities in non-paludified mineral soil sites (*Alnus glutinosa–Carex nigra* community)(Jaatinen 1950, Almquist 1929).

Both hydrological and edaphic conditions affect the direction of the succession of these communities i.e. whether a shore meadow develops towards a black alder forest or a black alder swamp. The paludification may start in gentle sloping shores where ice compresses an embankment in the littoral zone blocking the surface waters. Sometimes also foreign species, such as *Glyceria maxima,* may displace the original sedges in inland lakeshores (Linkola 1942, Erkamo 1949, Perttula 1953 and Uotila 1971).

Carex–Alnus glutinosa communities on mineral soil in Finland have previously received very little attention (Jaatinen 1950, Mäkinen 1978a and 1978b), but on mires the literature is more frequent. Kujala (1924a) describes in his monograph many lakeshore meadows, where black alder seedlings occur together with *Carex rostrata* and *C. nigra* vegetation, but he does not discuss newly established communities. Most of his inland descriptions are about dryer black alder groves away from the meadow sites.

Open shore and water vegetation has been described frequently in the literature (Teräsvuori 1926 and 1927, Maristo 1935 and 1941, Vaarama 1938, Eurola 1965 and 1999, Tikkanen 1967, Siira 1970, Kalliola 1973 and Toivonen 1981a), but little information on shore forests has been presented.

Elsewhere in Europe pure sedge–black alder communities are rare also on alluvial shores (Ellenberg 1963). This is partly due to the nutrient-rich soil. On these sites, paludification is common (e. g. Pieczyńska 1972, Pigott & Wilson 1978). The Finnish *Carex–Alnus glutinosa* community is reminiscent of the East European *Carex vesicaria* subtype of the *Dryopterideto cristatae–Alnetum* community (Bodeux 1955). The species of this subtype community, *Carex vesicaria, Potentilla palustris* and *Betula pubescens,* are abundant also in Finland, but the species of the main type community, *Thelypteris palustris, Dryopteris cristata* and *Calamagrostis canescens,* are absent.

The Finnish *Carex–Alnus glutinosa* community also resembles the *Carici–Fraxinetum angustifolia typicum* community decribed by Berta (1970), but the dominating species *Fraxinus angustifolia* and *Carex acutiformis* or *Carex elongata* are unknown in the Finnish *Carex*-dominated site types As well Jurkevitch et al. (1968) have described the *Alnus glutinosa–Carex* type in Belarus and divided it to four community types. All of them, however, occur on peaty sites, where the depth of peat layer is 20–150 cm, as does the paludified *Carex–Alnus glutinosa* community presented in this study.

6.1.3. (A2) Lysimachia vulgaris–Calamagrostis purpurea–Alnus glutinosa community

The name species of this collective community were selected according to their high frequency (60 % and 100 %). Among the characteristic species of this site type, there are species with a high frequency such as *Deschampsia cespitosa* (F 65 %), *Galium palustre* (F 63 %), *Peucedanum palustre* (F 53 %) and *Viola palustris* (F 54 %)

(Appendix 2). They seldom form uniform stands on their own. In some cases, only *Deschampsia cespitosa* may be dominant but often the abundance of this species indicates former grazing and its abundance decreases gradually with time. On the shores of the Bothnian Bay, black alder is replaced by grey alder, but *Calamagrostis purpurea* remains as a characteristic species (Havas 1961 and 1967, Vartiainen 1980).

The abundance of the name species and that of *Deschampsia cespitosa* varies considerably. In most cases, all of them grow together on the same site, but sometimes only one species may dominate. Thus, I consider this type to be collective, but it can be divided into three separate subtypes or types according to the frequency of the name species and *Deschampsia cespitosa*. *Calamagrostis* species favour stony and steep shores, *Lysimachia vulgaris* and *Deschampsia cespitosa* prefer gently sloping sedimentary sites (Jalas 1958d).

The borders of this vegetation type are inside the geo- and epilittoral zones such as the *Carex*-belt on the shores (See Du Rietz 1950 and Luther 1951a, b). In open shores, these borders are located at higher elevation than in sheltered shores (Brenner 1916 and 1921, Ulvinen 1937, Du Rietz 1939 and Du Rietz et al. 1939, Kielland-Lund 1981 and Fremstad 1983). Most of the black alder forests of the *Lysimachia–Calamagrostis* type are located on the shores of lakes and in the inner archipelago (c.f. Cajander 1902, Linkola 1916, Palmgren 1915 and 1917, Kujala 1924a, Ulvinen 1937, Jaatinen 1950, Perttula 1950, Häyren 1954, Luther 1961 and 1964, Kalela 1961, Mäkinen 1964, 1968 and 1978a, Koponen 1967 and Havas 1967). They form narrow vegetation belts and are controlled by the hydrological characteristics such as flooding (Leka et al. 2008). There are also large important alder seed reserves on these sites. Most marginal black alder forests growing on barren sites belong to the *Lysimachia–Clamagrostis* type. Palmgren (1915–1917 and 1961) and Jaatinen (1950) consider *Lysimachia vulgaris* as a characteristic species of non-paludified shore forests in Åland. *Calamagrostis purpurea* and *C. canescens* are usually mire plants (Kalliola 1973, Jaatinen 1950), but they grow well in shores and in flooded meadows, as well (Kalliola 1973).

Similar marginal black alder stands are described also in Scandinavia and in Central Europe (e.g. Warming 1906, Kujala 1924a, Almquist 1929, Sjörs 1958a, b, Ellenberg 1963). However, the bare stony shores are rare in Central Europe (Ellenberg 1963). The name species are more common in black alder swamps. Bodeux (1955) mentioned that *Calamagrostis canescens* is a characteristic species everywhere in Europe, but in spite of high frequencies, *Lysimachia vulgaris* is generally only a companion species. Prieditis (1997a) regards *Lysimachia vulgaris* as a diagnostic species in many black alder swamps in Latvian forested wetlands, such as in the associations of *Carici elongatae–Alnetum* and *Sphagno squarrosi–Alnetum*, both of which have a counterpart in the Finnish black alder swamps.

Also Fremstad (1983) describes very similar black alder forest communities in West Norway: The *Lysimachia vulgaris–Alnetum glutinosae* community is similar to the Finnish *Lysimachia vulgaris–Calamagrostis purpurea–Alnus glutinosa* type. In Norway these black alder forest types form narrow belts behind salt marshes and in sheltered places close to the sea (Fremstad 1983). The list of the species is nearly identical with the type presented here. According to Kielland-Lund (1981) this black alder community is common also in the southeastern Norway.

6.2. (B) Black alder swamps

6.2.1. About the occurrence and classification of the swamp sites

The Finnish classification of mire site types is based on the system by Cajander (1913, 1916). He describes four main site type groups of mires: pine mires (including bogs), spruce mires, fens and rich fens. According to his classification system, the black alder -dominated sites are spruce swamps. For single site types, the black alder dominated-spruce swamps can be further classified into eutrophic paludified hardwood–spruce forest (LhK), herb-rich hardwood-spruce swamps (RhK), herb-rich sedge hardwood spruce fens (RhSK), eutrophic pine fens (VLR) and drained herb-rich hardwood spruce peatlands (Rhtkg) (Cajander 1916, Kivinen 1948, Ruuhijärvi 1983, Laine & Vasander 1990 and 1996). Black alder is, however, very seldom a dominating tree species in any of these site types. Spruce is a stronger competititor and generally occupies the black alder sites along with stand succession on swamps (Kaakinen et al. 2008).

In Cajander's classification system, the forest site types are mainly named according to the dominating plant species such as *Calluna* type (CT), *Myrtillus* type (MT) etc. In my opinion, Cajander's method is more suitable for classification of the black alder communities in Finland than other European floristic-ecological systems (e.g. Braun-Blanquet, Hult-Sernander and Du Rietz), which use too small and local units. However, they have counterparts in Cajander's classification system (Dierssen 1982 and 1996). The closest similarities with my classification method can be found in the classification method of mires used in Belarus (Jurkevitch et al. 1968).

Kujala (1924a, b) has classified black alder swamps and forests using Cajander's site types (Cajander 1909 and 1913). He presents that those fern-rich black alder sites, which are watered by ground water are fern dominated herb-rich forests (germ. Erlenfliess) and can be classified into the *Filices* type (FT) described by Cajander (1909), or to eutrophic paludified hardwood-spruce forests (LhK) (germ. Heinartige Bruchwälder, Cajander 1913, Kujala 1965). The distinction between black alder forests and black alder swamps is thus not clear.

According to Kujala (1924a), the inland alder forests, which are flooded for long times, are herb-rich hardwood-spruce swamps (RhK). He further claims that these black alder swamps are the most characteristical alder sites in inland areas and they can be classified into mesic fern-dominated herb-rich forests and eutrophic paludified hardwood-spruce forests. According to Kaakinen et al. (2008), these sites can also be classified into thin-peated rich spruce mires. Only the wettest swamps (germ. Erlensumpfe) on the paludified shores of sea and lakes, are excluded, but according to Kujala (1924a) they are pretty rare site types in Finland, and more common in central Europe. However, in my study material, they are the most typical eutrophic black alder swamps, but are concentrated in southernmost Finland (Appendix 1).

For the classification of black alder sites in this study, I apply the new classification system of Finnish mire types, which classifies the black alder swamps into the so-called wooded or forested swamps (Eurola 1969, Eurola & Kaakinen 1977 and 1978, Eurola et al. 1984 and Kaakinen et al. 2008, Eurola et al. 2015). Typical for these swamps is a specific mire vegetation favouring a thin peat layer and limnogene watering (Eurola & Kaakinen 1977). According to Tuomikoski (1955) there is a lot of species typical to shore belt vegetation. Also the black alder itself belongs to this group.

Black alder swamps occur mainly in southern and central Europe, especially in Belarus and in the Baltic countries (Fig. 1 and Bodeux 1955, Matustzkievitch et al. 1958, Jurkevitch et al. 1968, Berta 1970, Glavač 1972, Prieditis 1993a, b and c, Prieditis 1997b). In Finland, black alder swamps are concentrated in the southernmost part of the country. Eutrophic vegetation communities such as the *Iris*- and *Thelypteris*-types occur mainly in the hemiboreal zone. However, mesotrophic swamps such as the *Athyrium–Calla*-type are found in the southern boreal zone and sproradically even in the middle boreal zone (Dierssen 1982 and 1996) (Fig. 3 and Appendix 1). Most of the black alder swamps in Åland are found in the lakeshores (Jaatinen 1950). Although this archipelago has been exposed to human influence for a long time under, the black alder swamps in Åland have tolerated ditching and grazing better than in mainland sites. Because the soil contains a lot of calcium there, the alder swamps have large plant diversity. Also Jaatinen (1950) regards alder swamps as the most interesting ecosystems of the shore vegetation in Åland, but recognizes that their classification is challenging due to their heterogeneity. He follows the syntaxonomy of Almquist (1929) and classifies these mires into five groups according to the occurrence of trees and undergrowth. In four groups of them, black alder is dominating species and the fifth group is birch-dominated swamps.

According to the species composition all of those communities above have a corresponding type in my classification. Most of them are included in the most eutrophic *Thelypteris* and *Iris* types as well as to *Phragmites* and paludified

Carex types, whereas the swamps of the *Athyrium* group, more commonly found in mainland sites, do not have a clear counterpart in the descriptions of Jaatinen (1950).

6.2.2. (B1) Phragmites–Alnus glutinosa community

There are only a few earlier observations concerning the *Phragmites australis–Alnus glutinosa* community type, which is propably mainly because it is a mixture of both aquatic and terrestrial (telmatic) vegetation (see Kujala 1924a). In aquatic vegetation reed is a very common helophyte on most lakes and seashores of Finland (e.g. Vaheri 1932, Aario 1933b, Pantsar 1933, Pohjola 1933, Maristo 1935 and 1941, Vaarama 1938, Jaatinen 1950, Luther 1951a, b and Uotila 1971). On the sheltered bays, *Phragmites australis* has a significant role in the beginning of paludification (Jalas 1958c).

The *Phragmites australis–Alnus glutinosa* community has formerly been described in Finland, i.e. in Åland (Kujala 1924a and Jaatinen 1950). Most descriptions are from the seashores, where these young successional communities are common (Kujala 1924a and Kalliola 1973). Jaatinen (1950) describes 13 *Phragmites* communities on the shores of Åland. They correspond to the communities described by Almquist (1929) and Du Rietz (1932). Black alder forms the *Alnus glutinosa–(Salix cinerea)–Phragmites australis* community on the lakeshores of Åland. When the canopy of trees increases, *Phragmites* turns sterile and gradually disappears, but may remain as a relict in the mire margins. In my study material, the *Phragmites australis–Alnus glutinosa* belts occur in ten sites, most of them located on the seashores.

Phragmites australis is a common helophyte also on the inland lakeshores and forms open reed swamps (Jalas 1958c, Kaakinen et al. 2008). Most reed–black alder communities can be found on the shores of the southern eutrophic lakes of *Typha–Alisma* type as well as on the lakeshores of the *Potamogeton* type in Åland (Maristo 1941, Jaatinen 1950, Vaarama 1961). In this material, such inland examples are Sites no. 56 and 86 (Appendix 1 and Ruuhijärvi et al. 2006b). Both of them are paludified infilled lakes. *Phragmites* grows there well but is sterile. It is bordered by the *Equisetum fliviatile* and *Athyrium–Calla* communities.

Dense *Phragmites* vegetation produces a lot of litter and if the water table level prevails high, paludification can begin (Jalas 1958c). This kind of reed-rich swamp vegetation has been described formerly in Finland by Cajander (1913), Aario (1932), Paasio (1936), Brandt (1949) and Lukkala & Kotilainen (1951). Since the establishment of black alder seedlings on open reed swamp, the site can be classified as the *Phragmites–Alnus glutinosa* type.

In later successional stages after the beginning of paludification, the coverage of *Phragmites* decreases and finally after hundreds of years, only relicts of the plants remain. (Cajander 1913, Aario 1932, Jaatinen 1950, Pakarinen & Uotila 1971). Elsewhere in Europe reed and black alder communities are often described apart from each other. In Central Europe the “pure” black alder swamps belong to the type *Alnetalia glutinosae* (Tüxen 1937, Ellenberg 1963), and the dryer black alder -rich mixed decidous forests to the type *Fagetalia* (Scamoni 1954, Passarge 1956, Krausch 1960, Ellenberg 1963). Usually, together with sedges, the reed communities belong to aquatic vegetation (Ellenberg 1963). However *Phragmites* grows on wet swamps (in Erlensumpfmoor), but is not described as a type-species in the *Cariceto elongatae–Alnetum medioeuropaeum* community (Bodeux 1955, Matuszkiewicz et al. 1958). However, in Belarus, the coverage of *Phragmites* in eutrophic black alder swamps is considerable. These swamps have been classified into four community types: *Phragmites–Iris, Phragmites–Filipendula, Phragmites–Thelypteris* and *Betula–Phragmites–Salix* (Jurkevitch et al. 1968). The *Sphagnum*-rich type is not included in these communities.

6.2.3. (B2) Paludified Carex–Alnus glutinosa community

The *Carex–Alnus glutinosa* swamps differ from the *Carex–Alnus glutinosa* forests in the characteristics of the substrate and the plant species composition. The former sites are paludified and characterized by typical mire plants, whereas the latter sites occur on mineral soils and have more wetland and shore plant species. Only some descriptions concerning pure sedge–black alder swamps in Finland are found in the earlier literature. In most cases, these communities have been classified together with wooded or semi-open tall sedge fens, where black alder grows sporadically (e. g. Pakarinen & Uotila 1971, Heikkilä 2006).

Carex–Alnus glutinosa swamps are included in the late successional phases of the *Carex*-dominated black alder communities. Their origin is often open tall sedge fens or swamps on lake- and seashores or in mire margin areas. The initial stage is sedge and black alder -dominated community on mineral soil sites or in paludified fen, or *Macrocaricetum*, occupied by black alder (Cajander 1913, Aario 1932, Paasio 1936 and 1941, Brandt 1949, Lukkala & Kotilainen 1951, Ruuhijärvi 1960, Eurola 1962, Eurola & Kaakinen 1978, Eurola et al. 1984 and 1995, Kaakinen et al. 2008). In the brook valleys, this type of black alder swamp is less common. In contrast to the *Carex–Alnus glutinosa* community on mineral soils, on these sites, the peat formation starts before the black alder has been able to occupy the entire area.

In an open *Carex* swamp, several *Carex* species may occur mixed or alone in small colonies. Jaatinen (1950) presents 10 different *Carex* swamps or swampy meadows on the lake shores of Åland. As well Brandt (1948) presents in Ostrobothnia many open swamps, such as *Carex rostrata, C. canescens, C. elata* and *C. aquatilis* swamps. In this study material, all tall sedges belonging to a collective so called *Macrocaricetum* group, because the material is not sufficient to describe each species to community or variant of their own.

In European studies, the treeless tall sedge communities are included as a rule to the *Macrocaricetum* community (e.g. Tüxen 1937 and 1955, Ellenberg 1963). The spreading of *Alnus glutinosa* into that community will take place similarly as in Finland. For example in Great Britain, the speed of *Alnus glutinosa* spreading into an open sedge swamp can be 0.6–1.0 m/year on average (Pigott & Wilson 1978).

One kind of counterpart for paludified sedge–black alder community is the typical eutrophic black alder swamp described by Jurkevitch et al. (1968) in Belarus. Many similarities are also found with the swampy *Sphagnum* tall sedge fens (association *Sphagnum–Alnetum glutinosae*) (Passarge & Hofman 1968, Bodeux 1955) and with the *Carici elongatae–Alnetum* typicum var. *Macrocaricetum* and *Carici elongatae–Alnetum Sphagnetosum* described by Berta (1970) in East Slovakia in the valley of river Tisza. The black alder community *Carici elongatae–alnetum boreale* subassociation *Sphagnum acutifolium* described by Bodeux (1955) approaches the *Carex–Alnus glutinosa* swamp described in my study, but the species composition is different. Only one common species, *Sphagnum girgensohnii,* could be found. The peat layer is thinner in Finland compared to many Central European black alder peatlands. For example, Radomski (1962) described the depth of peat layer of 6.5 m in black alder swamps in the lower valley of river Oder. Nearly similar peat depths have bee reported by Jurkevitch et al. (1968) in Belarus.

Also those *Alnus glutinosa–Carex vesicaria* swampy forests described by Almquist (1929) in Sweden resemble both my *Carex–Alnus glutinosa* swamps as well as Cajander's *Carex rostrata* mires covered by black alder stands (Cajander 1913). All swamps mentioned above have several common species especially in the hollows such as *Carex canescens, C. aquatilis, Peucedanum palustre, Lysimachia thyrsiflora, Cicuta virosa* and *Calla palustris*. However, the hummock vegetation is largely different. For example, in the swamps described by Alquist (1929), *Vaccinium uliginosum, Vaccinium vitis-idea, Equisetum palustre* and *Juniperus communis* typically grow on hummocks, but they are absent in the *Carex–Alnus* glutinosa swamps described in this study (Dierssen 1982 and 1996).

As well in the lowlands of northern Germany, a black alder swamp type *Carici–Alnetum caricetosum* described by Glavač (1972) resembles my *Carex–Alnus glutinosa* swamps, but the vegetation is more lush and diverse.

6.2.4. (B3) Equisetum fluviatile–Alnus glutinosa community

Most *Equisetum fluviatile–Alnus glutinosa* swamps are located on shallow and sheltered lakeshores and developed from open *Equisetum* swamps (Vaarama 1938, Uotila 1971). However, this community is rare, because horsetail favours gyttja or muddy soils mostly unfavourable for establishment of black alder (Jaatinen 1950, Tuomikoski 1958a), and the horsetail stands may be very dense; 700–1000 shoots/m² (Vaheri 1932, Pohjola 1933 and Aario 1933a).

The favourable water table level for *Equisetum fluviatile* varies from 100 cm above to 30 cm below soil surface (Lumiala 1944). Because of large living total biomass, a dense *Equisetum* stand produces a lot of litter annually (Kansanen et al. 1974). It accelerates the paludification process. An open *Equisetum* swamp will develop into a black alder swamp, and in many sites into an *Athyrium–Calla* or *Phragmites–Alnus glutinosa* community. Sometimes *Equisetum fluviatile* forms mixed stands with *Menyanthes trifoliata*. This kind of community can be regarded as a variant, or when *Menyanthes* is the dominant species, as an independent *Menyanthes–Alnus glutinosa* type. Unfortunately I did not have enough sample sites to describe this type in this material.

On lakeshores the succession results in dryer black alder communities and *Equisetum fluviatile* gradually disappears. In mire margins, it may remain longer by means of its rooting system reaching mineral soil beneath the peat layer (c.f. Kansanen et al 1974). In sites with thick peat layer, I have not observed many pure *Equisetum fluviatile–Alnus glutinosa* communities. In some earlier studies, the residues of *Equisetum fluviatile* have been found in the bottom of mires together with black alder and *Carex* species (Auer 1924, Kujala 1924a, Aario 1932 and Heikurainen 1960). This indicates that black alder swamps of the *Equisetum* type have been the common type in lakeshores and probably more frequent than in present.

According to the Finnish classification system, the *Equisetum fluviatile – Alnus glutinosa* community can be classified into swampy herb-rich spruce mires (germ. Kraut und Grassbrücher, Cajander 1913, Eurola & Kaakinen 1978, Kaakinen et al. 2008). The prephase is a swampy rich fen, which is later occupied by the black alder. They are extremely wet and flourishing mires. The dominant tree species may be spruce or birch and black alder. The field layer species are nearly identical to my *Equisetum fluviatile–Alnus glutinosa* community presented in this study. According to Cajander (1913), these kinds of mires have previously been more frequent in southwestern-Finland, as the *Equisetum* type described in this study (Chapter 5.5.4. and Appendix 1).

6.2.5. (B4) Thelypteris palustris–Alnus glutinosa community

Black alder swamps of the *Thelypteris* and *Iris* -dominated types are the most species- and nutrient-rich wooded swamps in Finland. Their main area is limited to the hemiboreal zone in southwestern Finland (Tuomikoski 1958b, Ahti et al. 1968, Fig. 3 and Appendix 1). They originate as open swamps in the shores of eutrophic lakes and ponds (Eurola 1969, Eurola & Kaakinen 1978). Most typical swamp is a floating “raft of vegetation” (Fig. 12 a). *Thelypteris palustris* is the most common vascular plant on the raft (Tuomikoski 1958b).

This kind of black alder swamp is nowadays very rare in Finland. I know of only three sites. However, during the warm Atlantic period these swamps were more common in Finland. Auer (1924) describes very similar black alder swamp from Sääksmäki, 120 km north from Helsinki. It is located in the shore of Lake Vanajavesi. Its vegetation consists of *Phragmites autralis, Equisetum fluviatile, Iris pseudacorus* and *Carex species* together with some water plants, such as *Trapa natans, Myriophyllum* and *Sparganium* species (Auer 1924, look also chapter 3).

The northern limit of *Thelypteris palustris* in Finland reaches up to southern Lapland, but its main area is in southwestern Finland (Erkamo 1956, Tuomikoski 1958b, Hämet-Ahti et al. 1998). As a rule it forms open swamps on the shores of eutrophic lakes and ponds (Eurola & Kaakinen 1978). Jaatinen (1950) describes many *Thelypteris palustris* communities on floating rafts close to open water on the shores of eutrophic paludified brown-moss lakes in Åland (Fig. 12 a). Similar vegetation occurs elsewhere on the Baltic isles, but more sporadically (Uotila & Ahti 2009).

Besides *Thelypteris palustris* and *Alnus glutinosa*, the third characteristic species of that community group is *Salix cinerea*. Sometimes also *Calla palustris* and tall sedges grow together with *Thelypteris palustris* (Jaatinen 1950).

In the successional development, *Thelypteris palustris* can be substituted by *Potentilla palustris*, *Calla palustris* or *Menyanthes trifoliata*, but seldom all together. In the nutrient-poorer sites, *Calla palustris, Iris pseudacorus, Typha latifolia* and tall sedges grow together with *Thelypteris palustris* (Jaatinen 1950, Mäkinen 1978a). Floating peat rafts are common in the southern boreal zone on the shores of small acidic and paludifying lakes, but the black alder is absent, and the raft is occupied by *Sphagnum* species and *Menyanthes trifoliata* (Kivinen 1948).

Elsewhere in Europe, *Thelypteris palustris–Alnus glutinosa* swamps are more abundant. For example, Almquist (1929) describes a very typical *Thelypteris palustris–Alnus glutinosa* swamp in Uppland, Central Sweden. The accompanying species are the same ones as in Finland: *Calla palustris, Potentilla palustris, Iris pseudacorus, Menyanthes trifoliata* and *Lysimachia thyrsiflora.* The pre-phase is an open swamp on lakeshore, where *Potentilla palustris* and *Thelypteris palustris* are dominant.

Also Vallin (1925) describes a typical open swamp in South Sweden in Hallands Väderö, where *Thelypteris palustris* and *Carex vesicaria* are dominant. In hollows, also *Iris pseudacorus* and *Hottonia palustris* grow.

Corresponding communities have been found in Switzerland (Koch 1926). There are many common species with the Finnish *Thelypteris* type. According to Koch, this black alder community belongs to the *Cariceta elongatae–Alnetum* community, as well as to the *Thelypteris* variant described by Berta (1970) in East Slovakia in the valley of river Tisza. One important characteristic species is *Carex elongata*. However, in my material this sedge species is absent in the *Thelypteris* type.

In England Pigott & Wilson (1978) describe a *Carex rostrata* community that makes a floating raft on water courses. In that community, *C. rostrata, C. vesicaria, Potentilla palustris* and *Menyanthes trifoliata* are dominant species. All these herbs are present in the Finnish *Thelypteris* type. This kind of open swamp makes a good growing site for black alder seedlings and later on for a black alder swamp.

The subcommunity *Carici elongatae–Alnetum thelypteridetosum* described by Prieditis (1993a) in Latvia also has many similarities with the Finnish *Thelypteris* type. Both of them can be found in extremely mesic substrate on woody-herbaceous peat. They also have many identical diagnostic species such as *Alnus glutinosa, Thelypteris palustris, Solanum dulcamara* and *Pseudobryum cinclidioides.*

More extensive *Thelypteris palustris–Alnus glutinosa* communities occur in Belarus (Jurkevitch et al. 1968). The type has been devided into six communities. Dominating characteristic species together with *Thelypteris palustris* are: *Filipendula ulmaria, Carex vesicaria* and *C. pseudocyperus, Scirpus silvaticus, Hottonia palustris, Menyanthes trifoliata* and *Phragmites australis*. These species show that the distribution range of *Thelypteris palustris* is more extensive in Belarus than in Finland.

6.2.6. (B5) Iris pseudacorus– Alnus glutinosa community

Iris pseudacorus is known as a shore plant in eutrophic lakes. My best sampling sites are located in Åland (study site 30, Lake Dalkarbyträsket) and in Kirkkonummi (Site no. 76, Lake Gillobackaträsket). Iris grows more often together with other swamp herbs than alone. E. g. Cajander (1913) mentioned *Iris* occurring on *Equisetum fluviatile* swamps. Eurola & Kaakinen (1978) classified the *Iris* swamps into tall sedge herb-rich swamps.

Forested *Iris pseudacorus–Alnus glutinosa* sites have not been described previously in Finland, but the same characteristic species as mentioned in this study, have been described by Pertula (1958a) occurring on wet black alder swamps on the lakeshores in southernmost Finland. His list can be considered as the first description of the *Iris* type black alder swamps. Kujala (1924a) also presents some *Iris pseudacorus* -dominated black alder sites and Jaatinen (1950) presents herb-rich swamps and swampy forests. Jaatinen describes the *Iris pseudacorus–Carex rostrata* community in a lakeshore forest in Godby, Åland, where in most cases *Iris pseudacorus* makes small, 5–10 m² wide clones on open swamps and in the stand gaps. In shady conditions *Iris* is sterile and regenerates only vegetatively. In southern Finland, pure and mixed *Iris pseudacorus* vegetation coverage is the largest on muddy lakeshores (Perttula 1958a). Smaller flecks and single communities can be found in other swamps and on mineral soil sites (Cajander 1913, Perttula 1958a, Eurola & Kaakinen 1978).

Elsewhere in Europe, the iris – black alder community is more commonly found (see, e. g. Vallin 1925, Jurkevitch et al. 1968, Passarge & Hoffman 1968, Berta 1970 and Glavač 1972). Most typically, the alders grow on the hummock sites and irises occur on wet hollows (Appendix 1, Site no. 30 and Figure 13b). Vallin (1925) describes a very similar *Iris pseudacorus – Alnus glutinosa* community to my study sites in Halland's Väderö in southern Sweden.

6.2.7. (B6) Athyrium filix-femina–Calla palustris community

Most of the *Athyrium–Calla* type sites are originated from open swamps or fens. Kujala (1924a) describes a site of this type located in Pälkäne, southern Finland: "In some places of the forest there are still open wet meadows, which are not occupied by black alder. In these sites, tall sedges (*Carex rostrata*) are dominating together with mire mosses and herbs such as *Aulacomnium palustre, Drepanocladus intermedius* and *D. exannulatus*. On the *Sphagnum* carpet, there are occurring *Vaccinium oxycoccos, Drosera longifolia* and plenty of black alder seedlings". Nowadays, there is a tall homogeneous black alder swamp of *Athyrium–Calla* type on this same site, and only one plant species presented by Kujala (1924a) exists (Fig. 14a, Mäkinen 1979b). The paludification process has proceeded from wet sparsely forested mineral soil to mesotrophic swamp covered by stocked alder stand with closed canopy.

The name species of the *Athyrium–Calla* type are also characteristic in many other site types. Depending on the hydrology and the age of the community, the balance between these species varies. In wet sites, *Calla palustris* is usually dominant and *Athyrium filix-femina* is rare or even absent (Heikkilä 2006). Such communities can be considered either as a variant or a new type: the *Calla palustris–Alnus glutinosa* swamp (Chapter 5.5.8.). In dryer sites, *Athyrium filix-femina* may be dominant and forms lush hummock-type vegetation. If the flark levels are wet and the field layer is mosaic-like, a variant of the *Athyrium–Calla* type may occur. If the flarks dry out, the site develops gradually into the *Athyrium–Alnus glutinosa* forest (Chapter 5.6.3. C2).

Black alder swamps of the *Athyrium–Calla* type are most typical in inland lakeshores on formerly water-covered soils. Cajander (1913) has previously described sites largely resembling the *Athyrium–Calla* type in the shores of Lake Ladoga. Only the peatlayer is deeper and the number of vascular mire plant species larger than those described in this study. In the tree layer, the spruce and the birch dominate, but the black alder may sometimes be abundant in southern Finland (Cajander 1913).

This type of black alder community is also known elsewhere in Europe, but with different names (e.g. Preising 1943, Bodeux 1955, Almquist 1965, Laasimer 1965, Jurkevitch et al.1968, Dierschke et al. 1973 and Prieditis 1993a and 1997a, b). Jurkevitch et al. (1968) describe in Belarus three communities: *Urtica–Athyrium, Filipendula–Athyrium* and *Carex–Athyrium*. In all of them, *Athyrium filix-femina* is a characteristic species. Also *Calla palustris* is rather common (frequency 71 %). In Latvia, Prieditis (1997a) presents three communities, where *Athyrium filix-femina* and *Calla palustris* are most frequent. The highest frequency of *Athyrium filix-femina* is found in the *Carici elongatum–Alnetum cardaminetosum* community and that of *Calla palustris* in the *Sphagnum squarrosum–Alnetum* community. However, most diagnostic species are the same as in the *Carici elongatum–Alnetum* typicum community and also in the Finnish *Athyrium–Calla* type. The relatively high frequency of *Carex elongata* (23 %) indicates a distinct correspondence between the Finnish *Athyrium–Calla* type and the Central European *Carici elongatae–Alnetum glutinosae* type sites (Bodeux 1955).

6.2.8. (B7) Scirpus sylvaticus– Alnus glutinosa community

In this community, *Scirpus sylvaticus* is a characteristic species. Its common growing sites are primarily brook sides in forested swamps and spring brooks, because it benefits from flowing, nutrient-rich waters (Jalas 1958a). It grows well in the intermediate and flark levels of nutrient-rich swamps (Eurola & Kaakinen 1978). Large pure stands of *Scirpus sylvaticus* are found on low-lying lakeshores with regular spring flooding. In this study, one typical example of this small-sized site type is found close to Lake Lohjanjärvi (Site no. 53 Appendix 1). There, the soil of the site is highly calcareous. *Scirpus* grows as fertile in the small openings, but it is sterile below the alder canopy.

The *Scirpus sylvaticus–Alnus glutinosa* community has not been described earlier in Finland, but for instance Kujala (1924a) considers *Scirpus sylvaticus* as an important and characteristic species in black alder swamps. Ruuhijärvi (1960) mentioned that both *Scirpus sylvaticus* and *Alnus glutinosa* grow together in swamps in the Osthrobothnia and Kainuu regions.

Athyrium filix-femina makes hummocks together with the black alder. Sometimes the root hummocks of alders may be >1 m. In wet flarks, *Scirpus sylvaticus* is dominant, while in dryer sites *Calamagrostis canescens* dominates. The structure of these swamps is mosaic-like and resembles the *Athyrium–Calla* type.

Elsewhere in Europe *Scirpus sylvaticus* is also often described in black alder swamps among other swamp plants (e.g. Almquist 1929, Runge 1964, Laasimer 1965, Jurkevitch et al. 1968 and Prieditis 1993a). In central Sweden, Almquist (1929) describes the *Alnus glutinosa–Scirpus sylvaticus* community in mesic mineral soils in brook valleys. The species composition varies, but *Scirpus sylvaticus* dominates together with many herb-rich forest plants. In Latvia, Prieditis (1993a) describes *Scirpus sylvaticus* as a characteristic species in the subcommunity *Carici elongatae–Alnetum caricetosum elatae*. Other characteristic species, *Carex acutiformis*, *Carex elata, Carex vesicaria* and *Equisetum fluviatile* are absent in my material, but *Carex elongata* has its highest frequency (23 %) (Appendix 2). Jurkevitch et al. (1968) include *Scirpus* and *Thelypteris* communities to the *Thelypteris* type sites.

6.3. (C) Herb-rich black alder forests

6.3.1. About the occurrence and classification of the sites

As a result of bedrock elevation in Finland, the black alder communities in the shores of sea and lakes gradually become dryer if springs and brooks do not water the site. As the soil moisture decreases, the amount of swamp and shore plants decrease, as well. They are compensated by grove herbs, which favour mesic conditions. In these deciduous herb-rich forests, the soil is granular in surface and rich in nutrients. The organic matter is mixed with mineral soil making a loose humus layer. These herb-rich forests deviate distinctly from the dominating coniferous forests (Kujala 1961). They have high species diversity and many vegetation layers. In this study, the diversity, including that of vascular plants and mosses, varies from 104 to 214 taxa according to the vegetation type. In conifer-dominated forests there is a uniform moss carpet and podsolic soil. However, in herb-rich black alder forests, the moss carpet is usually scattered and and gley soil is common.

Because of the characteristic species, the herb-rich forests in Finland, especially in Åland and in the southern hemiboreal vegetation zone, resemble the vegetation in central European temperate zone (Kujala 1924a, Kujala & Ulvinen 1964, Jaatinen 1950, Ahti et al. 1968, Lehtojensuojelutyöryhmä 1988, Alanen et al. 1995, Prieditis 1997b and Pääkkönen & Alanen 2000). Most of the herb-rich black alder forests are found in the so-called *Anemone* zone, in southwestern part of Lake-Finland (Jalas & Perttula 1965, Lehtojensuojelutyöryhmä 1988). The growth rate of black alder stand volume usually exceeds that of birch species (Kalela 1961 and Ilvessalo 1965).

Herb-rich forests are classified in Finland according to soil moisture into three groups: dry, mesic and moist groves (Kujala 1961, Lehtojensuojelutyöryhmä 1988, Valta & Routio 1990, Tonteri et al. 2008). Formerly, they were classified either according to the growing site (Lehtojensuojelutyöryhmä 1988, Valta & Routio 1990 and Toivonen & Leivo 1993) or dominating species (14 types, Valle 1919, Mäkelä 1936, Mikkola 1937, Tapio 1953 and Koponen 1961). Black alder dominated forests were not included in that classification, but were classified as "other herb-rich vegetation" (Lehtojensuojelutyöryhmä 1988, Valta & Routio 1990, Pääkkönen & Alanen 2000).

The black alder forest site types presented in this study (*Athyrium, Athyrium–Filipendula, Filipendula, Urtica* and *Rubus* types) are included, in my opinion, in the mesic and dry mesotrophic herb-rich forests (Tonteri et al. 2008 and Kekäläinen et al. 2008). They are classified into fern dominated herb-rich forests and tall herb -dominated forests (Lehtojensuojelutyöryhmä 1988 and Tonteri et al. 2008). The *Athyrium*–black alder community belongs to that group and to the collective *Filices* type (FT) (Cajander 1916, Cajander & Ilvessalo 1921, Kujala 1961). The *Athyrium–Filipendula–Alnus glutinosa* community is a mesotrophic intermediate type between the fern-dominated herb-rich forests and the tall herb dominated forests. All the other black alder forests, *Filipendula, Urtica* and *Rubus* communities are tall herb dominated forests (Tonteri et al. 2008 p. 280). The *Rubus idaeus–Alnus glutinosa* community is similar to the mesic or dry herb-rich forests according to the field and ground layer species as well as the soil, which never is covered by flooding.

In the shores of the Baltic Sea, many of these black alder dominated herb-rich forests were formerly included into a collective *Lychnis diurna* type (LT) (Cajander 1902, Kujala 1924a Perttula 1941 and Skult 1956). This is characterized by *Silene dioica* (formerly *Lychnis diurna* or *Melandrium dioicum* or *M. rubrum*). Because the corresponding *Athyrium filix-femina, Filipendula ulmaria* and *Rubus idaeus*-rich black alder communities are found inland and in lake shores, I divide the LT-type black alder forests into four herb-rich communities.

Hinneri (1972) has also divided the collective *Lychnis diurna* type in southwestern archipelago of Finland, describing in calcium-rich till soils a new ash–black alder community and a *Geranium sanquineum–Melandrium rubrum* -type community. Characteristic species in the field layer are *Silene dioica, Heracleum sphondylium* and *Geum urbanum* together with many typical grove plants. This site type is similar to the *Lychnis diurna* site type (LT) occurring in the coastal areas of Finland and to the *Alno–Ulmion* type in the lowlands of the northeastern Germany (Hinneri 1972, Kujala 1924a, Passarge & Hoffman 1968).

In the outer archipelago of southwestern Finland, the succession of the black alder communities is in the early stage. Skult (1956) classified the seashore black alder groves into three collective groups: herb-rich sites, grassy black alder stands with juniper, and *Filipendula ulmaria* -rich sites. The latter corresponds to the *Filipendula*-type presented in this study. Farther away from the sea, species composition in the field layer approaches that of the *Rubus* type sites with tall old alders. *Silene dioica* is also very common, indicating a correspondence to the *Lychnis diurna* group.

The *Urtica* and *Rubus* type groups are strongly influenced by grazing and cutting of twigs from the trees for sheep (Haeggström 1983 and chapter 2.7). Both of them are the last stages in the succession development of black alder belts on the shores of the inner archipelago and approach my *Rubus* type. They resemble the forested meadows in Åland described by Palmgren (1915–1917 and 1961).

In Åland, the coverage of black alder is remarkable. Grazing and other agricultural activities have had a great influence on the shore forests until the 1950´s (Jaatinen 1950). Jaatinen (1950) describes in mineral soil sites in Åland lakeshores several black alder communities following the classification by Almquist (1929). From these communities at least the *Alnus glutinosa–Filipendula ulmaria* community in nutrient rich sediment soils, and on poorer soils, the *Alnus glutinosa–Agrostis canina–Juncus filiformis* community are similar to my classification. As well Palmgren (1912) described in Åland a *Filipendula ulmaria–Alnus glutinosa* community bordering the *Hippophaë* belt. Along the succession, the canopy coverage of alders and *Filipendula* increase and occupy the site from *Hippophaë rhamnoides*.

Some herb-rich forests in Åland are classified to a *Sanicula* forest type according to *Sanicula europea* (Cajander & Ilvessalo 1921). It can be found in calcium-rich soil sites. In these sites, black alder is present, but not a dominant tree species. Because of that, these sites were not described in this study.

6.3.2. (C1) Athyrium filix-femina–Filipendula ulmaria–Alnus glutinosa community

The name species of this site type, *Filipendula ulmaria*, has a wide range from littoral to fresh meadows (Jalas 1965). It grows also on nutrient-rich swamp hummocks together with *Athyrium filix-femina*. During succession development and drainage, the proportion of swamp species decreases, resulting finally in the community described here.

The total number of species is relative large (184 species), because there are both true herb-rich forest species and some swamp species (Appendix 2). Because the former species dominate, this type does not belong to the black alder swamps. Another reason may be that the soil texture is usually fine-grained sediment. In the soil surface, there is up to 20 cm thick mesic humus-rich layer, similar to the peat layer in the black alder swamps (Laine & Vasander 1990 and 1996). Because of that the mesic black alder forests of *Athyrium–Filipendula* type probably have corresponded to thin-peated herb-rich hardwood forests (Cajander 1913, Ruuhijärvi 1960, Eurola & Kaakinen 1978, Eurola et al. 1984, Vasander 1996). The dryer communities characterized by *Athyrium filix-femina* and *Filipendula ulmaria* were classified as tall herb dominated forests (Valle 1919, Koponen 1967, Lehtojensuojelutyöryhmä 1988, Pääkkönen & Alanen 2000, Tonteri et al. 2008 p. 280). Many typical mire and herb-rich forest plants are, however, absent or sparse. E.g. *Sphagnum* species are absent in many sites (Appendix 2). In many sites, *Oxalis acetosella* is common in the lower field layer, because it is shade tolerant. Such communities have been earlier called *Oxalis–Filipendula* type (OFiT). They are common in hemiboreal and southern boreal vegetation zones of Finland (Eurola 1999).

Black alder forests of the *Athyrium–Filipendula* type also occur in Central Europe (e. g. Jurkevitch et al. 1968, Radomski 1968, Berta 1970, Dierschke et al. 1973). They are intermediate communities between wet black alder swamps and dryer black alder forests (Radomski 1968). The *Athyrium–Filipendula* type resembles the *Carici elongatum–Alnetum urticetosum* community described by Berta (1970) in the lowlands of East-Slovakia. In Belarus, Jurkevitch et al. (1968) classify the *Athyrium–Filipendula* community with a collective *Filipendula–Alnus glutinosa* type, which includes five communities. The characteristic species of the *Athyrium–Filipendula* community are very similar to the *Athyrium–Filipendula* type described in this study. However, some southern species are rare or absent in Finland.

According to species composition, the Finnish *Athyrium–Filipendula* type resembles some Latvian wetland forests described by Prieditis (1997a). For example, the *Carici elongatae–Alnetum cardaminetosum* community has many common characteristic species (e.g. the name species) with the *Athyrium–Filipendula* type.

6.3.3. (C2) Athyrium filix-femina–Alnus glutinosa community

The *Athyrium*-rich black alder forests belong to the collective *Filices* type (FT) described previously in Finland (e.g. by Cajander 1909, Cajander & Ilvessalo 1921, Kujala 1961 and Kalela, A. 1961, Lehto & Leikola 1987). This conclusion may be done on the basis of 17 common plant species, according to Kujala's description (1961). Furthermore, he states that "also the black alder may be a dominant tree in *Filices* type". Similar vegetation descriptions with dominating *Alnus glutinosa* and *Athyrium filix-femina* were made by Perttula (1941) in the coastal southwestern Finland. In the forest classification, this *Filices* type belongs to the group of eutrophic herb-rich forests (Tonteri et al. 2008).

It is often difficult to draw the line between fern-rich forests in wet mineral soil and young fern swamps, as many plant ecologists have confessed. Most peatland scientists include fern-rich black alder communities in thin-peated mires to eutrophic paludified hardwood-spruce forests or herb-rich hardwood-spruce swamps on deeper peat layer (e.g. Lukkala & Kotilainen 1951, Laine & Vasander 1996). In mineral soil sites, they belong to the collective *Filices* type mentioned above. This type described here deviates, however, a little from the last- mentioned type, where many characteristic species such as *Daphne mezereum, Rosa acicularis, Matteuccia struthiopteris, Trollius europaeus, Actaea spicata, Convallaria majalis* etc. are absent. Thus, I classify this black alder community to mesic mesotrophic herb-rich forests.

The differences between the *Athyrium filix-femina–Alnus glutinosa* communities in peatlands and in mineral soil sites are often hard to describe. If the soil moisture increases, the herb-rich *Athyrium*–black alder forest may develop into a thin-peated nutrient-rich fern-spruce mire (LhK) or in my classification into the *Athyrium–Filipendula* forest (Kaakinen et al. 2008). If the moisture still increases, it may lead to the *Athyrium–Calla* swamp, which in Cajander's classification (1913) belongs to the herb-rich hardwood-spruce swamps (RhK). If soil moisture decreases e.g. during land elevation, the dominant black alder trees start gradually suffer from competition by spruces, and the species composition in the field layer will change along with the increasing shade (Fig. 18). In this case, the *Athyrium filix-femina–Alnus glutinosa* community is the last stage in the succession of the black alder forest. According to the 8th forest inventory (1989-94), the area of *Athyrium*-dominated herb-rich forests was increasing in southern Finland (Nousiainen 2001).

The collective *Filices* type is divided into subtypes on the basis of the species composition, e.g. the tall ferns, but the proportion of black alder is small, or it is absent. (e.g. Mäkelä 1936, Perttula 1950, Koponen 1961, Mäkirinta 1968 and 1982, Valta & Routio 1990, Pääkkönen & Alanen 2000). Similar phenomenon may take place in the *Athyrium–Oxalis* communities (see Linkola 1929, Mäkelä 1936, Tapio 1953 and Koponen 1961).

In other countries of Europe, black alder stands characterized by ferns have also been described (e.g. Vallin 1925, Almquist 1929, Malmström 1956, Passarge & Hofmann 1968, Jurkevitch et al. 1968, Dickmann 1994 and Påhlsson 1994). In these descriptions, there are many common plant species with my *Athyrium* type. Almquist (1929) mentions that these kinds of forests characterized by ferns are rare in Uppland inland valleys but cover large areas in the shore forests. As well in the Baltic States, corresponding vegetation is known in black alder forests (e. g. Laasimer 1965 and Prieditis 1997a, b). For example, the vernal aspect in the *Carici remotae–Fraxinetum* community in Latvia is very similar to the Finnish *Anemone* variant (Prieditis 1997a). However, some southern grove species are absent in our *Athyrium filix-femina–Alnus glutinosa* communities.

6.3.4. (C3) Filipendula ulmaria–Alnus glutinosa community

Filipendula ulmaria is a common species in Finland (Hämet-Ahti et al. 1998) and nearly in all of Europe (Jalas 1965). It favours mesic and light meadows and herb-rich forests in nutrient-rich mineral soil or in thin-peated peatlands (Valle 1919, Mikkola 1937, Jaatinen 1950, Tapio 1953, Koponen 1961 and Jalas 1965). Its demands concerning the conditions and properties of the growing sites are very similar with the ones of the black alder and therefore they make together large communities especially in shore forests but also at brooks. This community type is the most common black alder forest type in Finland.

The *Filipendula* type is equal to the *Filipendula* sites described earlier (Palmgren 1912, Vallin 1925, Almquist 1929, Brandt 1933, Pankakoski 1939, Perttula 1941 and 1950, Jaatinen 1950, Skult 1956, Havas 1967, Jurkevitch et al. 1968 and Tyler 1969). However, the black alder is not necessarily the dominant species in the tree layer. For example, on the shores of the Gulf of Bothnia, the grey alder may replace the black alder (Havas 1967, Keränen 1973 and Kekäläinen et al. 2008). In earlier descriptions, the *Filipendula*-dominated black alder forests are often classified into the herb-rich *Oxalis–Filipendula* type (OFiT) in the group of mesic eutrophic herb-rich forests (Lehtojensuojelutyöryhmä 1988, Eurola 1999, Pääkkönen & Alanen 2000 and Tonteri et al. 2008).

Especially the *Filipendula* -rich black alder forests described by Skult (1956) in the Korppoo archipelago in southwestern Finland correspond to my *Filipendula* type. The black alder is a dominant tree species and tall *Filipendula* vegetation grows in the field layer. According to Skult (1956), the *Filipendula*-rich black alder forests in Korppoo have similarities with the "*Hippophaëta Ulmariosa*" black alder groves described by Palmgren (1912) in Åland. Also on the shores of the Bothnian Bay, very similar *Filipendula* type (FiT) sites occur in mesic black alder forest described by Keränen (1973) and Kekäläinen et al. (2008).

Filipendula -rich black alder forests occur widely in Northern Europe. They seem to be very similar in the Karelian Isthmus, in the shores of Loch Lomond in Scotland, as well as in the Baltic shores south of Stockholm, where I have explored them (e.g. Vallin 1925, Almquist 1929, Sjörs 1948, Lohmeyer 1951, Bodeux 1955, Krausch 1960, Gillner 1960, Laasimer 1965, Jurkevitch et al. 1968, Passarge & Hofmann 1968, Tyler 1969 and Möller 1970). In Belarus, the *Filipendula* type includes also some moist communities similar to the *Athyrium–Filipendula* type (chapter 5.6.2 C1 and Jurkevitch et al. 1968).

In Central Sweden, similar *Filipendula ulmaria–Alnus glutinosa* communities are common, especially on the shores of the Baltic Sea (Almquist 1929, Malmström 1956, Tyler 1969 and Påhlsson 1994). They are nearly uniform with my *Filipendula*-type sites. They belong to the primary succession series from seashore meadows to herb-rich black alder forests (Tyler 1969). Along with land elevation, the alder forest develops into conifer-dominated forests or to oak forests (Skult 1956). In many coastal areas, the *Filipendula ulmaria–Alnus glutinosa* community borders the *Phragmites* type and changes to the *Urtica* type during land elevation.

When the soil moisture increases, hygrophile species, such as *Iris pseudacorus, Caltha palustris, Viola palustris* and *Solanum dulcamara,* may appear in the field layer. On hummocks, *Anemone nemorosa, Oxalis acetosella, Viola riviniana* and *Maianthemum bifolium* may occur (Tyler 1969). However, if the soil moisture decreases, the proportion of *Rubus idaeus* increases and the site approaches the *Rubus ideus* variant in the *Filipendula* type or the dryer *Rubus idaeus–Alnus glutinosa* type. According to Almquist (1929) most coastal forests in Central Sweden belong to the collective herb-rich *Alnus glutinosa–Ulmaria* group. In these sites, *Anemone nemorosa* is a character species. That is similar to my *Anemone* variant in the *Filipendula* type and resembles some Latvian wetland forest types (Prieditis 1997a). The vernal aspect of the *Carici remotae–Fraxinetum* type resembles the Finnish *Anemone* variant of the *Filipendula* type, but both name species are absent in my variant, as well as many southern herb-rich forest species such as *Mercurialis perennis, Ranunculus cassubicus* and *Galeobdolon luteum.*

In Central Europe, *Quercus robur* and *Carpinus betulus* often form mixed stands together with *Alnus glutinosa* and *Filipendula ulmaria*. These sites are called *Querceto–Carpinetum filipenduletosum* (Tüxen 1955, Bodeux 1955). The *Filipendula* type in Finland is poorer in species richness than those in Central Europe (Passarge & Hofmann 1968). For instance in Finland, the species *Carex remota, Circaea lutetiana* and *Lysimachia nummularia* are absent. Many hygrophytes are replaced by mesophyte species, because the water table level is close to soil surface for only a short period in springtime.

6.3.5. (C4) *Urtica dioica–Alnus glutinosa* community

Urtica dioica favours moderately shady places and thrives under the canopy of the black alder close to lakeshores and coastal areas. It has been suggested that these shore forests are the original growing sites of the nettle in Finland (Pettersson 1965a, Suominen & Hämet-Ahti 1993). Many of these sites have been grazed until the 1950's, but have no more a clear cultural influence. According to Linkola (1916) and Hämet-Ahti et al. (1998), *Urtica dioica* belongs, especially in inland areas, to the group of anthropochores. These species are mostly sterile in sites with moderate human influence. Tall herb meadows and deciduous forests differ from the *Urtica dioica–Alnus glutinosa* communities described here (Lehtojensuojelutyöryhmä 1988). Black alder makes the soil suitable for the nitrophile nettle by means of the *Francia* actinomycetes in their root nodules (Weber 1986, Smolander & Sundman 1987, Smolander et al. 1988). Elevated nitrogen concentrations and tall *Urtica* vegetation have been found especially near decaying alder stumps.

Regional distribution of this type of black alder forests is concentrated in the southwestern part of Finland, where most black alder forests are located (Appendix 1). *Urtica dioica* has not been used formerly as a type species in the classification system of Finnish forest vegetation, but when forming large areas with several hectares pure communities, it is part of the succession of herb-rich forests, between the *Filipendula ulmaria* and the *Rubus idaeus* communities (Pettersson 1965). In the classification of forest site types, the *Urtica* type is connected to mesic tall herb dominated forests such as the *Filipendula*-rich black alder community (Tonteri et al. 2008).

Elsewhere in Europe, *Urtica dioica* has been accepted as a characteristic species of the black alder community (e.g. McVean 1953). Also Jurkevitch et al. (1968) in Belarus divide *Urtica*-rich black alder stands into 11 community types, which differ a little from each other in their vegetation and ecology. In the field layer, there are many common species with my study material. For the Belarussian *Filipendula–Urtica* and *Athyrium–Urtica* communities, there are counterparts to the sites in Finland, but my scanty material is not sufficient to describe corresponding communities or variants within the *Urtica* type. In Finland, *Urtica* has a notable role (frequency 41 %) also in the raspberry–black alder community (Appendix 2).

Berta (1970) mentions nettle as a dominating herb in many communities in Eastern Slovakia and according to the species composition and edaphic-ecological factors he distinguishes a new subcommunity, the *Urticetosum*, from the *Carici elongatae–Alnetum* community. Also Möller (1970) describes an *Urtica* subcommunity in Northern Germany.

6.3.6. (C5) Rubus idaeus–Alnus glutinosa community

The range of growing conditions of *Rubus idaeus* is large. Its natural growing sites are light forest margins and clear-cut areas in fertile coniferous forest sites (Vaarama 1965). One notable growing site of black alder forests is the *Rubus idaeus–Alnus glutinosa* community. Along with succession, the stand canopy becomes sparser and the soil becomes dryer especially on seashores because of land elevation. All these changes favour nitrophile light-favouring plants like the raspberry.

Separate black alder communities with dominating *Rubus idaeus* are described previously in Finland only on the shores of the Bothnian Bay by Keränen (1973). He uses the type name IT (*Idaeus* type). He has classified these raspberry–black alder communities to costal alder-dominated dry herb-rich forests (c.f. Kekäläinen et al. 2008). Some vegetation descriptions of certain sites made by Kujala (1924a) fit very well in the material of this study. However, Kujala includes these communities to the group of herb-rich seashore forests, which are similar to the *Lychnis diurna* (= *Silene dioica*) type described by Cajander (1902).

Also Skult (1956) describes in the outer archipelago of southwestern Finland a herb-rich black alder forest, which equals my *Rubus* type based on its location and species composition. The type species is *Rubus idaeus*, but the coverage of other herbs, such as *Silene dioica*, is large. According to Skult (1956), this type equals Cajander's (1902) *Lychnis diurna* type. Also grassy and *Juniperus*-rich black alder forests described by Skult (1956) may be included to my *Rubus* type, but their species composition is considerably different due to intensive grazing. The black alder belt at the Bromarv seashore described by Perttula (1941) resembles my *Rubus* type by its species composition, including the characteristic species.

The systematic position of the *Rubus idaeus–Alnus glutinosa* community in Finland is very clear. Along succession, black alder stands of the *Rubus* type approach the other herb-rich deciduous forest types in Finland (Cajander 1902, Kalela 1949 and 1961, Tapio 1953 and Kujala 1961). Especially the species of the *Oxalis–Maianthemun* type (OmaT) (e.g. the name species) become more frequent, which indicates a close relationship between the *Rubus* and the OmaT -types. On low-lying shores, this community often borders with *Athyrium*-rich black alder forests (see chapter 5.6.3 C2).

Rubus idaeus is frequent also elsewhere in the shore forests of the Baltic Sea (Vallin 1925, Almquist 1929, Laasimer 1965), but does not appear as a characteristic species in vegetation descriptions probably because of its wide ecological amplitude. It seldom forms pure communities except in nutrient-poor sandy soils. However Tyler (1969) mentioned that *Rubus idaeus* often grows in the innermost dryer parts of the *Alnus glutinosa–Filipendula ulmaria* communities in Sweden. Thus the succession order of the belts is the same as in my descriptions in Finland.

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Tiivistelmä: Tervaleppäyhdyskuntien ekologia ja kasvillisuus Suomessa

Tervaleppä on levinnyt Suomessa yksittäisinä puina Rovaniemen korkeudelle saakka, mutta yhtenäisten metsiköiden esiintyminen keskittyy Etelä-Suomeen ja järvialueelle. Muualla Euroopassa tervaleppä on yleisempi kuin meillä. Laajimmat metsät, kooltaan jopa 10 km^2, löytyvät Keski-Euroopasta Venäjältä, Valkovenäjältä, Puolasta ja Baltian maista.

Tervalepän kasvupaikat määräytyvät maaperän kosteuden ja ravinteiden mukaan. Kosteusrajat ulottuvat avoimilta rantaniityiltä vesirajasta havumetsän reunaan. Purolaaksoissa ja kohosoiden reunassa tervalepikot ovat kapeampia, purolaaksoissa usein havumetsän puristuksessa. Ravinteet ja pohjaveden

korkeus määräävät tervalepikon aluskasvillisuuden – kehittyykö lepikosta rehevä metsäluhta vai kuivempi lehto. Lehtojen osuus Suomen tervalepikoista on suurempi kuin luhtien, mutta luhdat ovat meillä uhanalainen suotyyppiryhmä ja sen vuoksi tärkeä tutkimuskohde. Keski-Euroopassa ne ovat yleisempiä maaperän runsaampien ravinteiden ja suotuisan ilmaston vuoksi.

Tässä tutkimuksessa käsitellään Suomen tervalepikoiden kasvillisuutta ja siihen vaikuttavia ekologisia tekijöitä; kasvualustan, maankohoamisen, kosteuden, ilmaston ja ihmistoiminnan vaikutusta. Tutkimusaineisto perustuu 200 tutkittuun tervalepikkoon eri puolilta Suomea ja niistä kuvattuihin 650 näytealaan. Kultakin näytealalta on tutkittu puusto, aluskasvillisuus ja kasvualusta. Aineisto on ryhmitelty 14 erilaiseen yhdyskuntaan maastohavaintojen ja tilastollisen käsittelyn perustella soveltaen Cajanderin metsä- ja suotyyppiluokittelua. Tuloksia on verrattu Pohjoismaissa, Baltiassa ja Keski-Euroopassa tehtyihin kasvisosiologisiin tutkimuksiin. Näytealat on kuvattu luonnontilaisista tervaleppämetsiköistä, joissa tervaleppä on valtapuuna.

Aloitin tutkimuksen opinnäytetyönä Kujalan 1924 kuvaamista laajoista tervaleppäluhdista Hämeessä jo vuonna 1959. Laajensin tutkimusta myöhemmin koko maan kattavaksi ja otin mukaan myös tervaleppävaltaiset lehdot ja litoraalimetsät. Tutkimuksen painopiste on ollut Hämeessä, Lounais-Suomessa ja Ahvenanmaalla, missä on säilynyt eniten luonnontilaisia tervalepikoita. Suuri osa näytealoista on merenrantalepikoista, joita syntyy edelleen maankohoamisen seurauksena.

Monet tervaleppämetsiköt sijaitsevat rannoilla. Tämä johtuu siitä, että vesi on paras siementen levittäjä. Keväällä karisevat siemenet kelluvat vedessä, kulkeutuvat aaltojen mukana rannalle ja itävät vesirajassa. Tästä alkaa tervalepikoiden sukkessiokehitys. Metsän varttuessa ja kasvualustan kuivuessa maankohoamisen seurauksena aluskasvillisuus muuttuu. Kivennäismaalla valtalajeina ovat usein sarat tai korpikastikka ja ranta-alpi. Tulvarantojen tervalepikot onkin nimetty näiden lajien mukaan. Paikallisesti isosorsimo voi syrjäyttää sarat.

Jos kasvualusta pysyy kosteana, lepikko voi soistua. Sen vuoksi olenkin erottanut saravaltaiset soistuneet lepikot kivennäismaan yhdyskunnista. Soistumisen seurauksena tervalepikon aluskasvillisuus muuttuu täysin. Usein soistuminen johtuu tervalepikkoon virtaavasta pinta- tai pohjavedestä, joka tuo jatkuvasti uusi ravinteita. Turvekerros on aluksi ohut, 20–30 cm, mutta vahvistuu metsikön vanhetessa. Jos tervalepikkoon tulee lähdepurojen myötä runsaasti ravinteita tai kasvualusta on alun perin rehevä, syntyy erittäin komeita tervaleppäluhtia, jotka poikkeavat sekä ulkonäöltään että lajistoltaan kaikista Suomen suotyypeistä. Kukkivat kurjenmiekat, vehka, nevaimarre tai suuret saniaiset tuovat eteläisen leiman yhdyskuntaan. Tällaiset luhdat ovatkin levinneisyydeltään eteläisiä, lähinnä hemiboreaalisessa vyöhykkeessä.

Olen jakanut tutkimani tervaleppäluhdat vallitsevan aluskasvillisuuden mukaan seitsemään tyyppiin: järviruoko-, suursara-, järvikorte-, nevaimarre-, kurjenmiekka-, hiirenporras-vehka- ja korpikaisla valtaisiin tervalepikoihin. Poikkeavan kasvillisuutensa ja harvinaisuutensa vuoksi kaikki mainitut tervaleppäyhdyskunnat ovat meillä erittäin uhanalaisia ja pyritään säilyttämään soidensuojeluohjelman puitteissa.

Kolmas ryhmä tervaleppäyhdyskuntia eli lehtomaiset metsät ovat yleisempiä kuin luhdat mutta silti suojelun arvoisia. Olen jakanut ne vallitsevan aluskasvillisuuden mukaan viiteen tyyppiin: hiirenporras-, mesiangervo-, nokkos- ja vadelmavaltaisiin tervalepikoihin. Viides yhdyskunta on mesiangervon ja hiirenportaan muodostama sekakasvusto. Se on välittävä tyyppi tervaleppäluhtiin. Näiden lehtomaisten tervaleppäyhdyskuntien levinneisyyden painopiste on Suomenlahden rannikolla ja Järvi-Suomessa. Ne rajoittuvat yleensä edellä mainittuihin tervaleppäluhtiin tai sukkession loppuvaiheessa (vadelmatyyppi) havumetsiin.

Appendix 1. The black alder (*Alnus glutinosa*) dominated sites inventoried for this study in Finland. The numerical order is following the biogeographical provinces of Finland presented by Hämet-Ahti et al. (1998). The location of the study sites is presented as northern (N) and eastern (E) coordinates with accuracy of 1 km^2. Legend: *Athyrium–Calla* = Abbreviation of the type name. Look at chapter 5.1 and Appendix 2, Types = Dominating black alder communities on the site, RhK = Herb-rich hardwood-spruce forest, LhK = Thin-peated, nutrient and herb-rich hardwood-spruce forest, Ob = Ostrobotnia borealis (The biogeographic provinces of Finland according to Hämet-Ahti et al. 1998)

Liitetaulukko 1. Tässä tutkimuksessa inventoidut tervalepikot Suomessa. Kasvupaikkojen järjestys noudattaa luonnonmaantieteellistä maakuntajakoa (Hämet-Ahti ym. 1998). Kasvupaikkojen sijainti ilmoitettu pohjois (N) ja itä (E)-koordinaatein 1 km^2 tarkkuudella.

Nr.	Site	N	E	Site types
	Ob			
1	Hailuoto, Hannuksensuot	7216	387	*Athyrium–Calla*
	Om			
2	Siikajoki, Lumineva	7193	402	*Calamagrostis–Lysimachia thyrsiflora* (RhK)
3	Kannus, Mutkalampi, Lähdeneva	7113	354	*Calamagrostis–Lysimachia thyrsiflora* (RhK)
4	Kokkola, Öja	7086	302	*Rubus*
5	Larsmo, Gertrud	7085	292	*Rubus*
6	Larsmo, Björnvik	7083	291	*Filipendula*
7	Larsmo, Vikarholmen	7074	290	*Rubus*
	Oa			
8	Alahärmä, Voltti, Kojola	7032	292	*Calamagrostis–Lysimachia thyrsiflora*
9	Vörå, Hällnes	7027	261	*Rubus* + *Filipendula*
10	Koivulahti, Kilen	7016	248	*Athyrium–Calla*
11	Vaasa, Hietalahti	7009	229	*Filipendula* + *Rubus*
12	Korsnäs, Bredskäret	6986	207	*Filipendula*
13	Kristiina, Camping	6919	207	*Filipendula*
	St			
14	Merikarvia, Brändöholm	6873	209	*Filipendula* + *Rubus*
15	Ahlainen, Saantee	6856	211	*Filipendula* + *Rubus*
16	Pori, Reposaari, Kappalinsaari	6848	205	*Rubus*
17	Pori, Reposaari, Tukkiviikin lahti	6847	204	*Filipendula* + *Rubus* + *Carex* (min.)
18	Pori, Viasvesi, Rantalankari	6825	211	*Filipendula* + *Rubus*
19	Eurajoki, Verkkokari	6803	210	*Lysimachia–Calamagrostis* + *Rubus*
20	Rauma, Sampaanala	6790	201	*Lysimachia–Calamagrostis* + *Filipendula*
21	Köyliö, Kirkkosaari	6787	249	*Filipendula* + *Rubus*
	Al			
22	Geta, Bolstaholm	6714	106	*Athyrium–Calla*
23	Saltvik, Åsgården, Vilhelmsbo	6709	116	*Filipendula*
24	Saltvik, Rangsby, Kvarnboträsk	6706	116	*Filipendula*
25	Saltvik, Sonnröda 1, NW shore	6704	120	*Filipendula*
26	Saltvik, Sonnröda 2, W shore	6704	120	*Filipendula*
27	Finnström, Godby	6700	112	*Thelypteris*
28	Eckerö, Storby	6702	87	*Filipendula*
29	Hammarland, Marsund, Öra	6701	94	*Filipendula*
30	Jomala, Jättböle, Prästgården	6691	109	*Iris* + *Filipendula*
31	Lemland, Nåtö 1, North shore	6680	109	*Filipendula*
32	Lemland, Nåtö 2, Idvik	6680	109	*Filipendula*
33	Lemland, Nåtö 3, Själskatudden	6680	109	*Filipendula*
34	Lemland Knutsboda, Lindåsen	6681	113	*Filipendula*
35	Lemland, Hellestorp, Storvikträsk	6678	116	*Filipendula*
	Ab			
36	Uusikaupunki (Pyhämaa) Kukainen	6766	188	*Carex* (min.) + *Filipendula*
37	Uusikaupunki (Pyhämaa), Lyökki	6763	184	*Rubus*
38	Uusikaupunki, Uuluoto	6759	189	*Rubus*
39	Lokalahti, Keskikari	6747	196	*Filipendula* + *Rubus*
40	Kustavi, Kevo	6733	188	*Filipendula* + *Rubus*

41	Mietoinen, Aarlahti	6736	217	*Filipendula* + *Urtica*
42	Askainen, Pukkila	6722	218	*Rubus*
43	Piikkiö, Piikkiönlahti	6709	252	*Filipendula*
44	Parainen, Kopparö	6693	235	*Filipendula*
45	Parainen, Tervsund	6692	240	*Athyrium–Calla* + *Filipendula*
46	Bromarv, Pålarv	6661	283	*Filipendula* + *Rubus*
47	Tenhola, Högböle	6661	285	*Filipendula*
48	Tenhola, Lindö	6664	288	*Athyrium–Filipendula* + *Filipendula*
49	Karjaa, Läppträsket, Brynikbacka	6663	313	*Iris* + *Thelypteris* + *Equisetum* + *Athyrium–Filipendula* + *Rubus*
50	Karjaa, Konungsböle, Kvarnträsket	6661	316	*Equisetum*
51	Karjalohja, Lohjansaari	6683	322	*Athyrium–Calla*
52	Lohja, Jalassaari, Ahtiala	6681	329	*Athyrium–Calla*
53	Lohja, Ojamo	6684	335	*Carex* (min.) + *Scirpus*
54	Lohja, Liessaari	6685	334	*Filipendula* + *Rubus*
55	Vihti, Moksi	6710	357	*Athyrium–Calla*
	N			
56	Tenhola, Skogby, Harparskog	6652	294	*Athyrium–Calla* + *Carex* (peat) + *Phragmites* + *Equisetum*
57	Tammisaari, Trollböle, Rödgrundet	6656	299	*Rubus*
58	Tammisaari, Trollböle, Prästkulla	6657	299	*Athyrium* + *Filipendula*
59	Tammisaari, Prästviken	6657	302	*Filipendula* + *Rubus*
60	Tammisaari, Ramsholmen	6655	300	*Athyrium*
61	Tammisaari, Södra viken	6656	301	*Athyrium*
62	Tammisaari, Hagen	6655	301	*Athyrium*
63	Tammisaari, Flyet, Estholmen	6657	303	*Athyrium–Calla*
64	Tammisaari, Norrmark, Gammelbyfjärden	6650	305	*Rubus*
65	Tammisaari, Skärlandet, Baggö road	6648	303	*Filipendula* (pasture)
66	Snappertuna, Bonäs, Österfjärden S	6655	321	*Carex* (peat)
67	Snappertuna, Bonäs, Österfjärden N	6656	322	*Athyrium–Calla* + *Athyrium* + *Urtica*
68	Inkoo, Finnböle, Bonäsudden	6669	323	*Rubus*
69	Inkoo, Finnböle, Kopparviken	6669	324	*Rubus*
70	Inkoo, Joddböle, Oxhagen	6660	329	*Filipendula*
71	Kirkkonummi, Kolsarby, Upinniemi	6668	357	*Lysimachia vulg.–Calamagrostis*
72	Kirkkonummi, Porkkala 1, Lillkanskog N	6658	359	*Athyrium–Calla* + *Iris* + *Carex* (peat) + *Scirpus*
73	Kirkkonummi, Porkkala 2, Lillkanskog N	6658	359	*Athyrium–Calla* + *Carex* (peat)
74	Kirkkonummi, Porkkala 3, Lillkanskog	6657	358	*Filipendula*
75	Kirkkonummi, Porkkala 4, Lillkanskog S	6656	357	*Filipendula*
76	Kirkkonummi, Tolls, Gillobackaträsket	6670	360	*Athyrium–Calla* + *Iris* + *Thelypteris*
77	Espoo, Masala, Ringroad 3	6672	363	*Rubus*
78	Espoo, Kivenlahti 1	6674	367	*Lysimachia vulg.–Calamagrostis*
79	Espoo Kivenlahti 2	6674	368	*Filipendula*
80	Espoo, Suvisaaristo, Ramsösund 1	6669	372	*Filipendula*
81	Espoo, Suvisaaristo, Ramsösund 2	6669	373	*Lysimachia vulg.–Calamagrostis* + *Athyrium*
82	Espoo, Oittaa, Bodomjärvi, Hästberget	6683	371	*Athyrium–Calla*
83	Espoo, Oittaa, Bodomjärvi, Oitviken	6683	370	*Iris*
84	Espoo, Oittaa, Matalajärvi, Högnäs	6683	372	*Lysimachia vulg.–Calamagrostis* + *Ath.–Calla* + *Thelypteris* + *Equisetum*
85	Vantaa, Louhela, Mätäoja	6685	381	*Iris* + *Athyrium–Calla*
86	Vantaa, Syväoja, Lamminsuo	6698	379	*Carex* (peat)+ *Phragmites* + *Athyrium–Filipendula*
87	Helsinki, Lauttasaari, Nackapuisto	6674	381	*Athyrium–Calla* + *Athyrium–Filipendula* + *Filipendula* + *Urtica* + *Rubus*
88	Helsinki, Viikinranta, Refinering plant	6680	389	*Filipendula*
89	Helsinki, Viikinranta, Säynäslahti	6680	389	*Filipendula*
90	Helsinki, Herttoniemi, Ryönälahti	6678	390	*Lysimachia vulg.–Calamagrostis* + *Equisetum* + *Carex* (peat) + *Phragmites* +*Athyrium* + *Filipendula* + *Rubus*
91	Helsinki, Kivinokka, Saunalahti	6677	390	*Filipendula*
92	Helsinki, Kivinokka, Naurissalmi	6677	389	*Filipendula*
93	Helsinki, Östersundom 1, Karhusaari	6683	400	*Athyrium–Calla* + *Iris*+ *Filipendula*
94	Helsinki, Östersundom 2, Karhusaarentie	6683	400	*Phragmites* + *Lysimachia vulg.–Calamagrostis* + *Filipendula* + *Urtica*
95	Helsinki, Östersundom 3, Karlvik	6684	400	*Filipendula*

96	Sipoo, Spjutsund	6682	416	*Filipendula*
97	Porvoo Tolkkinen	6690	422	*Filipendula*
98	Porvoo, Emäsalo, Edesviken	6678	424	*Athyrium–Calla* + Iris + *Filipendula*
99	Mäntsälä, Sulkava	6740	402	*Athyrium* + *Urtica*
100	Perhaja, Strömslandet	6698	454	*Athyrium–Calla* + *Filipendula*
101	Loviisa, Loviisanlahti	6705	458	*Scirpus*
102	Pyhtää, Ahvenkoski	6709	470	*Lysimachia vulg.–Calamagrostis*
103	Pyhtää, Alakylä, Munapirtti	6704	480	*Filipendula*
	Ka			
104	Kotka, Mussalo 1	6706	493	*Filipendula*
105	Kotka, Mussalo 2	6704	494	*Lysimachia* vulg.–*Calamagrostis*
106	Hamina, Jähinniemi, Kilinlahti	6715	512	*Lysimachia* vulg.–*Calamagrostis*
107	Hamina, Vilniemi	6715	512	*Filipendula* + *Rubus*
108	Virolahti, Vilkkilä, Tura	6711	539	*Equisetum* + *Phragmites* + *Scirpus* + *Rubus*
109	Virolahti, Virojoki 1, Huvisaari	6718	540	*Rubus*
110	Virolahti, Virojoki 2, Kiukkusenpohja	6719	540	*Filipendula*
	Ta			
111	Kuru, Aurejärvi	6881	309	*Lysimachia vulg.–Calamagrostis*
112	Ruovesi, Helvetinkolu	6887	334	*Lysimachia vulg.–Calamagrostis*
113	Tottijärvi, Kirkonkylä	6814	303	*Carex* (peat)
114	Eräjärvi, Rantalankulma	6826	373	*Lysimachia vulg.–Calamagrostis*
115	Sahalahti, Saarioinen, Karhusaari	6823	357	*Lysimachia vulg.–Calamagrostis*
116	Kangasala, Peliniemi	6820	351	*Lysimachia vulg.–Calamagrostis*
117	Kangasala, Pelisalmi 1, Pullosaari	6820	351	*Lysimachia vulg.–Calamagrostis*
118	Kangasala, Pelisalmi 2, Isosaari	6820	350	*Carex* (min.)
119	Kangasala, Pelisalmi 3, Matinsaari	6820	350	*Rubus*
120	Kangasala, Kirkonkylä, Sorola	6821	344	*Athyrium –Filipendula* + *Filipendula*
121	Kangasala, Liuksiala	6818	342	*Urtica*
122	Kangasala, Tiihala 1, Depression	6816	343	*Athyrium–Calla*
123	Kangasala, Tiihala 2, Talviahde	6816	345	*Athyrium–Calla*
124	Pälkäne, Saarikylät 1, Tiitola	6808	346	*Rubus*
125	Pälkäne, Saarikylät 2, Selkäsaaret	6809	348	*Lysimachia vulg.–Calamagrostis*
126	Pälkäne, Uusi-Mälkilä, Kinnasaari	6810	349	*Athyrium–Calla*
127	Pälkäne, Mälkilä, Sipilä	6808	348	*Rubus*
128	Pälkäne Myttäälä N 1, Lautaanranta	6807	348	*Athyrium–Calla* + *Athyrium*
129	Pälkäne, Myttäälä N 2, Lautaanvuoret	6807	349	*Athyrium–Calla*
130	Pälkäne, Seittye 1, Jussila	6807	348	*Rubus*
131	Pälkäne, Seittye 2, Pirttisaaret	6806	347	*Carex* (min.)
132	Pälkäne, Seittye 3, Kivistö	6805	347	*Carex* (min.)
133	Pälkäne, Seittye 4, Tinasalmi	6806	346	*Carex* (min.)
134	Pälkäne, Hausalo, Selkäsaari	6806	344	*Rubus*
135	Pälkäne, Huhti 1, Ämmö	6804	349	*Lysimachia vulg.–Calamagrostis*
136	Pälkäne, Huhti 2, Siiponiemi	6805	350	*Carex* (min.)
137	Pälkäne, Myttäälä S 1, Pispa	6805	350	*Iris* + *Athyrium–Filipendula* + *Filipendula*
138	Pälkäne, Myttäälä S 2 ,	6805	350	*Carex* (min.) + *Lysimachia vulg.–Calamagrostis*
139	Pälkäne, Myttäälä S 3, Oravalinna	6806	350	*Athyrium–Calla* + *Athyrium–Filipendula* + *Filipendula*
140	Pälkäne, Myttäälä S 4, Kaupilahti	6806	351	*Athyrium–Calla* + *Equisetum* + *Scirpus* + *Athyrium–Filipendula* + *Filipendula*
141	Pälkäne, Mälkilä, Koivulahti	6806	351	*Athyrium–Calla*
142	Pälkäne, Mälkilä, Mäljänranta	6806	352	*Athyrium–Calla* + *Athyrium–Filipendula*
143	Pälkäne, Onkkaala, Keiniänranta	6806	353	*Athyrium–Calla* + *Athyrium–Filipendula* + *Athyrium* + *Filipendula* + *Rubus*
144	Pälkäne, Pappila, Pappilanranta	6806	345	*Carex* (min.) + *Athyrium–Filipendula* + *Athyrium* + *Rubus*
145	Pälkäne, Kirpu	6811	354	*Carex* (min.) + *Calla*
146	Pälkäne, Liessaari	6802	352	*Lysimachia vulg.–Calamagrostis* + *Rubus*
147	Pälkäne, Äimälä 1, Lake shore	6802	351	*Athyrium–Filipendula* + *Filipendula*
148	Pälkäne, Äimälä 2, Myllyoja	6800	351	*Athyrium–Calla* + *Athyrium –Filipendula* + *Rubus*
149	Pälkäne, Harhala, Ylinen	6801	354	*Lysimachia vulg.–Calamagrostis*
150	Pälkäne, Laitikkala, Pintele W	6798	357	*Carex* (min) + *Athyrium–Filipendula* + *Urtica*
151	Luopioinen, Puutikkala	6800	376	*Lysimachia vulg.–Calamagrostis*

152	Hauho, Ilmoila 1, Pärnäniemi	6794	359	*Lysimachia vulg.–Calamagrostis*
153	Hauho, Ilmoila 2,Lentolanlahti	6793	359	*Athyrium–Calla*
154	Hattula, (Tyrväntö) Tykölä 1	6796	350	*Athyrium–Calla + Athyrium*
155	Hattula, (Tyrväntö) Tykölä 2	6796	350	*Athyrium–Filipendula + Filipendula*
156	Hattula, (Tyrväntö) Tykölä 3	6797	350	*Rubus*
157	Hattula, Monaala	6791	353	*Carex* (min.) + *Rubus*
158	Hattula, Retulansaari	6788	356	*Lysimachia vulg.–Calamagrostis + Urtica*
159	Hattula, Tenhola	6780	352	*Lysimachia vulg.–Calamagrostis + Athyrium*
160	Valkeakoski, (Sääksmäki), Suolahti	6791	349	*Carex* (min.) + *Lysimachia vulg.–Clamagrostis + Filipendula + Urtica + Rubus*
161	Valkeakoski, (Sääksmäki), Pappila	6791	342	*Carex* (min) + *Athyrium–Calla + Athyrium–Filipendula + Athyrium*
162	Valkeakoski, (Sääksmäki), Rapola	6791	341	*Carex* (min.) + *Athyrium–Calla + Scirpus + Athyrium–Filipendula + Athyrium + Filipendula + Urtica + Rubus*
163	Valkeakoski, (Sääksmäki), Annila	6792	340	*Carex* (min.) + *Athyrium + Urtica*
164	Valkeakoski, (Sääksmäki), Valto	6795	339	*Carex* (min.) + *Rubus*
165	Valkeakoski, Paino 1	6804	342	*Rubus*
166	Valkeakoski, Paino 2	6804	342	*Rubus*
167	Valkeakoski, Paino 3, Keso	6804	342	*Rubus*
168	Lempäälä, Lippo	6797	329	*Urtica+ Rubus*
169	Lempäälä, Pyhältö	6797	327	*Urtica*
170	Tammela, centrum	6748	322	*Athyrium + Filipendula + Urtica*
171	Tammela, Rauhaniemi	6748	321	*Athyrium–Filipendula + Athyrium + Urtica*
172	Somero, Somerniemi	6723	322	*Athyrium–Filipendula* (LhK)
173	Hämeenlinna, Vanaja	6764	366	*Athyrium–Filipendula*
174	Lammi, Biolog. Station	6773	394	*Scirpus + Athyrium–Filipendula*
175	Lammi, Ylänäinen, Pikku-Pappila	6774	393	*Athyrium–Filipendula + Filipendula*
176	Padasjoki, Vesijako, Apajaiskorpi	6813	393	*Rubus*
177	Padasjoki, Virmaila	6813	415	*Athyrium–Calla*
178	Asikkala, Vääksy	6786	421	*Rubus*
179	Asikkala, Hillilä	6785	416	*Rubus*
180	Kuusankoski, Kuusanlampi	6753	483	*Athyrium–Calla*
	Sa			
181	Hirvensalmi, centrum	6836	488	*Lysimachia vulg.–Calamagrostis + Athyrium–Filipendula + Rubus*
182	Hirvensalmi, Kissakoski 1	6835	488	*Athyrium–Filipendula + Filipendula*
183	Hirvensalmi, Kissakoski 2	6836	487	*Athyrium–Calla* (*Lysimachia thyrsiflora*)
184	Juva, Taipale	6863	547	*Rubus*
185	Anttola	6830	534	*Lysimachia vulg.–Calamagrostis*
186	Puumala	6817	571	*Lysimachia vulg.–Calamagrostis*
187	Ruokolahti, Rasila	6800	597	*Lysimachia vulg.– Calamagrostis + Athyrium–Calla + Athyrium–Filipendula*
	Kl			
188	Parikkala, Siikalahti	6830	636	*Carex* (peat) + *Scirpus*
	Sb			
189	Tuusniemi, Juojärvi, Pajulahti	6970	574	*Athyrium–Filipendula*
190	Lapinlahti	7022	515	*Lysimachia vulg.–Calamagrostis*
	Kb			
191	Kesälahti, Villala	6885	634	*Lysimachia vulg.–Calamagrostis*
192	Lieksa, Siikavaara, Siikasaari	7017	648	*Lysimachia vulg.–Calamagrostis*
193	Pyhäselkä, Reijola, Löttölahti	6941	644	*Lysimachia vulg.–Calamagrostis + Rubus*
194	Joensuu, Kuhasalo, Tikanniemi	6944	640	*Lysimachia vulg.–Calamagrostis*
195	Liperi, Kuorinka	6949	623	*Lysimachia vulg.–Calamagrostis*
196	Outokumpu, Viinijärvi	6956	613	*Lysimachia vulg.–Calamagrostis*
197	Outokumpu, Sysmäjärvi	6957	605	*Carex* (min.)
	Ok			
198	Paltamo, Petäjälahti, Luodelahdensuo	7156	514	*Equisetum–Calamagrostis* (RhK)
199	Vaala, Jaalanka	7159	510	*Menyanthes–Equisetum–Calamagrostis* (RhK)
200	Vaala, Niskankylä, Siirasoja	7163	480	*Athyrium–Filipendula* (LhK)

Appendix 2. Mean frequency % (interpolated) of species found in the studied black alder (*Alnus glutinosa*) communities. The character species of all black alder stands and site types are marked with bold. See the description of the abbreviations of the site types in the end of the table.

Liite 2. Keskimääräinen lajin esiintyvyys tutkituissa tervaleppäyhteisöissä. Metsikkö- ja kasvupaikkakohtainen tyyppilaji lihavoitu. Kasvupaikkatyyppien lyhenteiden selitykset taulukon lopussa.

Site type code	A1	A2	B1	B2	B3	B4	B5	B6	B7	C1	C2	C3	C4	C5
Site type	Cx.m.	Lys.	Phr.	Cx.p.	Eq.	Thel.	Iris	AtCa.	Sci.	At.Fil.	At.for.	Fil.	Urt.	Rub.
Number of Stands	16	28	5	8	5	3	8	40	8	27	17	64	15	49
Number of Sites	25	52	15	25	14	9	23	145	12	60	31	122	41	78
Number of Species	137	230	69	88	69	90	115	189	88	184	105	165	104	214
Species														
Acer platanoides	0	2	0	0	0	0	0	3	0	8	19	12	0	11
Alnus glutinosa	**100**	**100**	**100**	**100**	**100**	**100**	**100**	**100**	**100**	**100**	**100**	**100**	**100**	**100**
Alnus incana	24	35	7	4	7	0	0	38	17	**45**	26	18	32	27
Betula pendula	0	4	0	0	0	0	4	1	8	7	0	0	0	6
Betula pubescens	20	56	13	28	29	67	48	62	67	42	29	32	10	33
Cornus alba	0	0	0	0	0	0	0	2	0	7	6	1	12	1
Fraxinus excelsior	0	0	0	0	0	0	0	0	0	3	6	6	0	5
Juniperus communis	0	10	0	0	0	0	4	3	0	2	0	13	2	21
Lonicera xylosteum	0	2	0	0	0	0	0	0	0	0	0	1	2	1
Myrica gale	0	0	33	32	0	0	0	1	0	0	0	0	0	0
Picea abies	16	27	13	12	14	0	22	23	8	32	19	31	2	33
Pinus sylvestris	0	10	0	0	0	0	0	3	0	3	0	1	2	6
Prunus padus	8	29	0	0	7	0	4	52	33	**73**	61	61	54	58
Rhamnus frangula	24	38	13	12	53	22	17	48	**83**	25	23	11	17	31
Ribes alpinum	0	2	0	0	0	0	0	2	0	2	6	7	0	8
Ribes nigrum	4	2	0	0	0	0	4	8	17	15	3	3	7	6
Ribes spicatum	20	21	0	4	0	0	9	52	25	**62**	58	55	**68**	**65**
Salix aurita	0	2	0	12	0	33	9	0	25	0	0	0	0	0
Salix caprea	4	12	0	0	0	11	13	3	25	13	3	2	2	4
Salix cinerea	8	6	7	0	7	**56**	**43**	3	0	0	0	2	0	1
Salix myrsinifolia	0	33	0	4	27	0	13	14	8	18	6	9	5	3
Salix pentandra	0	13	0	0	7	33	17	3	0	5	6	1	0	1
Salix phylicifolia	4	10	20	12	14	**44**	**48**	5	17	2	0	3	0	1
Sambucus racemosa	12	6	0	0	0	0	0	6	0	10	**26**	7	20	18
Sorbus aucuparia	24	48	0	4	21	11	35	55	50	58	65	48	37	**85**
Viburnum opulus	0	0	0	0	0	0	0	2	8	0	0	8	0	4
Adoxa moshatellina	0	0	0	0	0	0	0	1	8	0	0	2	0	0
*Aegopodium podagrari*a	0	2	0	0	0	0	0	1	17	17	0	5	2	6
Agrostis canina	0	4	**27**	0	0	0	0	7	0	2	0	0	0	0
Agrostis capillaris	**44**	25	0	16	0	0	0	0	0	3	6	8	5	23
Agrostis gigantea	0	0	0	0	0	0	0	0	0	0	0	0	0	6
Alcemilla vulgaris	0	2	0	0	0	0	0	0	0	0	0	2	0	3
*Alisma plantago-aquati*ca	**24**	8	0	8	0	0	0	1	0	0	0	0	0	0
Alopecurus aequalis	0	0	0	0	0	0	0	2	0	2	0	0	0	0
Anemone nemorosa	0	0	0	0	0	0	0	1	8	13	26	**27**	2	12
Angelica sylvestris	0	13	0	0	0	0	0	1	8	17	0	**29**	5	17
Anthriscus sylvestris	0	6	0	0	0	0	0	0	0	10	6	16	15	9
Athyrium filix-femina	0	29	0	0	14	11	0	**94**	**50**	**98**	**100**	24	32	28
Bidens tripartita	**16**	6	0	0	0	0	9	1	0	0	0	1	0	1
*Calamagrostis arundina*cea	0	2	0	0	0	0	0	0	0	0	0	0	0	8
*Calamagrostis canesce*ns	0	13	0	4	14	11	9	3	**33**	2	0	2	2	3
*Calamagrostis purpure*a	20	**60**	13	20	14	44	**83**	17	25	30	10	9	5	18
Calla palustris	36	12	7	36	7	**89**	**70**	**66**	8	3	0	1	0	0
Caltha palustris	40	27	0	16	21	44	17	**46**	33	**53**	19	34	15	5
Calystegia sepium	0	2	0	0	0	0	0	0	0	3	3	0	0	3
Cardamine amara	0	2	0	0	0	0	13	7	0	7	0	2	0	0
Cardamine pratensis	**28**	8	0	4	0	11	4	1	**25**	0	6	2	0	1

Carex acuta	4	12	**40**	8	14	33	30	0	0	0	0	0	0	0
Carex aquatilis	0	0	0	**20**	0	0	4	1	0	0	0	0	0	0
Carex brunnescens	0	2	0	0	0	0	0	2	0	2	0	1	0	0
Carex canescens	12	13	0	20	**47**	11	17	**37**	0	13	16	10	2	9
Carex echinata	0	0	0	0	0	0	0	5	0	2	3	0	0	0
Carex elata	0	4	0	0	0	0	9	0	0	0	0	0	0	0
Carex elongata	4	4	0	4	0	0	9	**23**	**33**	12	13	2	12	0
Carex flava	4	0	13	0	0	0	0	0	0	0	0	0	0	0
Carex lasiocarpa	0	0	**20**	**24**	0	0	0	1	0	0	0	0	0	0
Carex nigra	**20**	6	**27**	12	**29**	**33**	9	5	8	0	0	1	0	1
Carex pallescens	0	2	0	0	0	0	0	0	0	5	0	1	0	3
Carex pseudocyperus	0	0	0	0	7	11	13	0	0	0	0	0	0	0
Carex rostrata	12	17	20	**56**	7	22	**61**	7	8	0	0	0	0	0
Carex vesicaria	**72**	31	0	**20**	0	11	**30**	2	0	0	3	0	0	0
*Chrysosplenium alterni*folium	0	2	0	0	0	0	0	3	**25**	17	0	0	5	1
Cicuta virosa	20	10	7	12	27	11	**52**	20	0	0	0	0	0	0
Circaea alpina	4	2	0	0	0	0	0	12	0	5	10	2	0	8
Cirsium helenioides	0	0	0	0	0	0	0	1	0	12	0	1	0	3
Cirsium palustre	4	6	0	4	0	0	0	5	8	7	0	4	10	5
Cirsium vulgare	0	2	0	0	0	0	0	0	0	0	0	2	2	4
Crepis paludosa	0	0	0	0	0	0	0	0	**17**	12	0	4	0	1
Deschampsia cespitosa	32	**65**	13	28	36	11	4	35	**50**	38	42	40	39	**67**
Deschampsia flexuosa	4	0	0	0	0	0	0	2	0	5	0	1	0	1
Dryopteris cristata	0	0	7	0	0	0	4	0	0	0	0	0	0	0
Dryopteris carthusiana	40	40	0	8	7	22	**43**	**50**	33	**43**	**45**	23	**54**	**73**
Dryopteris expansa	0	0	0	0	0	0	0	1	0	2	13	1	0	1
Dryopteri filix-mas	0	0	0	0	0	0	0	0	0	3	0	2	0	0
Elytrigia repens	0	0	0	0	0	0	0	1	0	2	0	1	0	4
*Epilobium angustifoliu*m	4	2	0	0	0	0	0	1	0	5	3	4	5	21
Epilobium montanum	4	2	0	0	0	0	0	2	0	2	3	0	7	1
Epilobium palustre	12	4	7	8	0	0	4	8	25	3	0	1	0	3
Equisetum arvense	24	31	0	0	7	0	4	**50**	25	**47**	39	29	29	5
Equisetum fluviatile	17	12	27	40	**100**	44	**70**	22	0	7	0	5	0	0
Equisetum sylvaticum	0	10	0	0	0	0	0	10	17	22	6	11	0	13
Filipendula ulmaria	12	27	60	20	53	67	70	35	50	**100**	23	**100**	49	42
Fragaria vesca	0	6	0	0	0	0	0	3	0	5	6	4	5	15
Galium trifidum	12	17	0	0	0	0	0	3	8	8	13	12	2	18
Galium palustre	**88**	**63**	27	52	**73**	22	**70**	50	42	38	26	13	15	17
Galium uliginosum	0	8	0	0	0	0	0	0	0	3	0	2	0	0
Geranium sylvaticum	0	0	0	0	0	0	0	0	0	3	0	7	0	3
Geum rivale	4	8	0	0	0	0	4	6	25	**52**	26	29	10	6
Glechoma hederacea	8	4	0	0	0	0	0	0	0	0	0	0	5	3
Glyceria fluitans	12	6	0	0	0	0	0	2	0	0	0	0	0	0
Glyceria maxima	**32**	6	0	0	0	0	0	3	0	0	3	0	15	0
*Gymnocarpium dryopte*ris	0	2	0	0	0	0	17	10	0	18	16	4	0	13
Humulus lupulus	0	0	0	0	0	0	0	0	0	2	0	0	0	4
Huperzia selago	0	0	0	0	0	0	0	3	0	0	3	0	0	1
Impatins noli-tangere	0	6	0	0	7	0	0	**44**	17	**32**	23	8	12	5
Iris pseudocarus	0	10	13	12	**80**	**78**	**100**	1	17	0	0	1	0	0
Juncus filiformis	24	**40**	7	4	0	0	4	3	0	0	0	1	0	0
Lactuca sibirica	0	10	0	0	0	0	0	0	0	0	0	0	0	0
Lemna minor	0	0	0	8	0	**33**	**39**	6	0	0	0	0	0	0
Leontodon autumnalis	0	4	0	0	0	0	0	0	0	0	0	2	0	1
Luzula multiflora	0	2	0	0	0	0	0	0	0	0	0	1	0	4
Luzula pilosa	0	6	0	0	0	0	0	1	0	2	0	2	0	8
Lycopodium annotinum	0	2	0	0	0	0	0	1	0	5	0	0	0	0
Lycopus europaeus	**40**	21	20	4	21	33	17	13	17	3	0	2	0	3
Lysimachia thyrsiflora	36	35	60	52	57	44	43	**82**	50	30	42	11	0	14
Lysimachia vulgaris	44	**100**	**67**	40	**67**	33	48	27	17	22	16	33	20	24
Lythrum salicaria	**64**	44	27	36	40	11	52	12	0	3	3	8	2	5

Maianthemum bifolium	0	6	0	0	0	0	17	8	8	28	19	9	0	**40**
Matteuccia struthiopteris	0	0	0	0	0	0	0	3	0	3	0	0	0	0
Melampyrum pratense	0	10	0	0	0	0	0	0	0	0	0	0	0	1
Melampyrum sylvaticum	0	10	0	0	0	0	0	0	0	2	0	2	0	3
Melica nutans	0	4	0	0	0	0	0	0	8	5	0	2	0	8
Mentha arvensis	28	21	0	0	0	0	0	0	0	3	3	2	0	1
Menyanthes trifoliata	0	0	7	16	**47**	22	26	8	0	2	0	1	0	0
Milium effusum	0	0	0	0	0	0	0	0	0	2	0	0	0	8
Moehringia trinervia	0	4	0	0	0	0	0	1	0	2	3	2	2	6
Myosotis scorpioides	**56**	21	0	0	0	0	4	16	8	13	13	5	27	4
Oxalis acetosella	0	19	0	0	0	0	4	31	25	**53**	**48**	23	5	**67**
Paris quadrifolia	0	2	0	0	0	0	4	10	8	**27**	3	**24**	2	14
Persicaria amphibia	**24**	10	0	0	0	0	0	0	0	0	0	0	0	0
Persicaria lapathifolia	8	0	0	0	0	0	0	0	0	0	0	0	0	3
Peucedanum palustre	52	58	**93**	**84**	60	**89**	**78**	43	25	15	6	19	2	21
Phalaris arundinacea	4	23	0	0	0	0	0	0	0	0	3	2	2	1
Phegopteris connectilis	0	0	0	0	0	0	0	6	17	23	16	3	0	6
Phragmites australis	0	2	**100**	4	0	0	4	0	0	0	0	0	0	0
Plantago major	0	0	0	0	0	0	0	0	0	0	0	0	0	5
Poa nemoralis	0	10	0	0	0	0	0	1	0	2	0	1	0	5
Poa pratensis	4	8	0	0	0	0	0	1	0	0	0	0	2	0
Poa trivialis	12	2	0	0	0	0	0	1	0	5	6	1	0	4
Potentilla erecta	4	6	0	0	0	0	0	0	0	7	0	2	0	8
Potentilla palustris	44	48	**80**	52	60	22	65	50	25	0	0	7	2	0
Prunella vulgaris	4	6	0	0	0	0	0	1	0	3	3	2	0	3
Ranunculus acris	0	13	0	0	0	0	0	0	0	3	3	6	7	9
Ranunculus auricomus	4	0	0	0	0	0	0	0	8	17	0	13	0	1
Ranunculus repens	44	38	0	0	0	11	22	18	17	27	19	9	**34**	15
Ranunculus reptans	8	6	0	0	0	0	0	0	0	0	0	0	0	0
Rubus idaeus	8	38	0	0	0	11	17	36	25	57	65	34	34	**100**
Rubus saxatilis	0	4	0	0	0	0	4	1	17	7	3	6	0	8
Rumex acetosa	4	2	0	0	0	0	4	1	0	3	3	6	0	15
Rumex hydrolapathum	0	0	0	0	0	**33**	0	0	0	0	0	0	0	0
Scirpus sylvaticus	0	2	0	0	7	0	9	4	**100**	3	0	5	7	0
Scutellaria galericulata	**40**	**35**	0	0	21	11	9	9	8	0	3	3	5	5
Silene dioica	0	2	0	0	0	0	0	0	0	5	13	11	0	27
Solanum dulcamara	44	15	7	0	40	**100**	57	**50**	25	23	23	12	7	6
Solidago virgaurea	0	0	0	0	0	0	0	0	0	5	0	0	0	3
Stachys palustris	**28**	4	0	0	0	0	0	3	0	3	0	2	0	1
Stellaria media	8	10	0	0	0	0	0	1	0	5	6	4	0	15
Stellaria nemorum	0	0	0	0	0	0	0	0	0	7	6	2	0	6
Stellaria palustris	12	2	0	0	0	0	0	5	0	0	0	0	0	1
Taraxacum officinale	**24**	17	0	0	0	0	0	1	0	2	3	3	12	9
Thalictrum flavum	8	0	0	0	0	0	0	0	0	2	0	4	2	1
Thalictrum simplex	8	8	0	0	0	0	0	0	0	0	0	0	2	0
Thelypteris palustris	0	0	0	0	0	**100**	35	0	0	0	0	0	0	0
Trientalis europaea	0	15	0	0	0	0	0	32	25	**42**	**39**	18	2	**53**
Tussilago farfara	8	6	0	0	0	0	0	2	0	0	0	0	0	1
Typha latifolia	0	0	0	16	0	**44**	17	0	0	0	0	0	0	0
Urtica dioica	16	13	0	0	0	11	4	19	25	58	42	50	**100**	41
Vaccinium oxycoccos	0	0	13	**20**	7	0	0	0	0	0	0	0	0	0
Vaccinium myrtillus	0	4	0	4	0	0	9	7	0	5	0	3	0	8
Vaccinium vitis-idaea	0	2	0	0	0	0	4	6	0	2	0	1	0	4
Veronica chamaedrys	0	4	0	0	0	0	0	0	0	0	0	0	0	5
Viola epipsila	0	6	0	0	0	0	0	7	8	15	3	3	0	0
Viola palustris	12	**54**	27	36	**73**	**89**	26	**82**	**58**	**58**	**58**	34	12	35
Viola riviniana	4	4	0	0	0	0	0	0	0	0	0	2	0	6
Viola selkirkii	0	4	0	0	0	0	0	0	0	0	0	1	2	3
Amblystegium serpens	20	8	13	8	0	0	0	3	0	3	3	10	**27**	0
Atrichum undulatum	0	8	0	4	7	0	4	5	0	10	6	4	2	5

Barbilophozia barbata	0	4	0	0	0	0	0	0	8	3	0	0	2	5
Brachythecium oedipodium	4	10	33	8	29	0	17	8	0	33	10	19	12	22
Brachythecium populeum	4	6	0	0	0	0	0	1	0	10	0	3	2	5
Brachythecium reflexum	20	**50**	13	12	47	0	13	16	17	43	16	33	32	**53**
Brachythecium rivulare	0	2	0	0	0	0	0	1	0	7	0	2	0	1
Brachythecium rutabulum	12	6	0	0	0	0	0	10	8	28	13	25	7	5
Brachythecium salebrosum	4	15	0	4	0	11	9	10	8	25	13	23	**54**	17
Brachythecium starcei	0	0	0	0	0	0	0	0	0	7	0	0	0	0
Brachythecium velutinum	0	0	0	0	0	0	4	1	0	0	0	2	2	1
Callicladium haldanianum	0	2	0	0	0	0	0	1	0	0	0	2	0	0
Calliergon cordifolium	44	25	60	44	**73**	56	61	**66**	33	28	23	11	5	1
Calliergon stramineum	0	0	7	20	0	0	0	1	0	0	0	0	0	0
Calliergonella cuspidata	8	17	13	4	21	11	**35**	14	8	12	3	11	7	5
Cephalozia spp.	4	4	0	0	0	11	13	3	0	2	3	2	0	1
Chiloscyphus polyanthos	4	15	13	8	29	0	17	6	0	7	3	2	5	4
Climacium dendroides	48	40	0	4	21	22	35	23	0	35	6	15	0	12
Dicranum fuscescens	4	0	0	0	0	0	0	1	0	0	0	1	2	1
Dicranum majus	0	0	0	0	0	0	0	3	0	0	0	0	0	0
Dicranum scoparium	24	15	13	0	29	11	9	15	25	22	13	14	5	19
Drepanocladus uncinatus	40	46	13	12	47	11	13	19	8	13	19	16	32	28
Hedwigia ciliata	0	6	0	0	0	0	0	1	0	0	3	0	0	4
Homalothecium sericeum	0	0	0	0	0	0	0	0	0	2	0	0	0	0
Hylocomium splendens	0	2	0	0	0	0	0	1	0	7	0	3	2	0
Hypnum cupressiforme	4	17	0	0	36	0	22	3	8	8	19	16	17	26
Hypnum lindbergii	**60**	27	0	0	0	0	0	1	0	0	7	1	0	0
Hypnum pallescens	12	21	0	0	21	0	9	15	8	15	13	11	2	22
Leptodictyum kochii	4	4	0	0	0	0	0	19	0	7	3	4	0	5
Leptodictyum riparium	8	2	0	4	0	0	4	1	0	0	0	0	0	0
Lophocolea heterophylla	16	12	33	4	36	11	4	6	0	13	0	11	15	5
Lophozia spp.	0	0	27	0	0	0	0	1	0	7	0	0	0	0
Marchantia polymorpha	0	0	0	0	0	0	0	3	0	0	0	0	0	0
Mnium hornnum	0	2	0	0	0	0	**22**	0	0	0	0	0	0	0
Paraleucobryum longifolium	0	8	0	0	0	0	0	0	8	2	0	0	5	10
Pellia epiphylla	0	17	0	0	0	22	0	4	0	0	0	0	0	1
Pellia neesiana	0	6	0	12	0	0	13	12	0	3	10	2	2	0
Plagiomnium affine	0	0	0	0	0	0	0	0	0	5	0	3	0	0
Plagiomnium cuspidatum	4	10	0	0	0	0	0	8	8	25	0	7	10	13
Plagiomnium ellipticum	4	0	0	4	**53**	**56**	9	18	8	45	19	9	34	5
Plagiomnium medium	0	4	0	0	0	0	0	0	17	17	0	4	0	0
Plagiothecium cavifolium	4	2	0	0	0	11	0	6	0	3	3	5	0	5
Plagiothecium denticulatum	8	25	13	20	40	33	17	14	8	17	13	13	10	10
Plagiothecium laetum	12	13	33	0	21	0	0	12	8	22	19	9	20	13
Plagiothecium ruthei	4	0	0	0	0	0	0	9	0	2	3	0	2	4
Pleurozium schreberi	12	23	13	4	0	0	4	6	0	8	3	6	0	15
Pohlia nutans	12	13	20	4	0	11	4	14	0	5	10	5	2	5
Polytrichastrum formosum	16	8	0	4	0	11	4	0	0	3	0	0	0	1
Polytrichastrum longisetum	0	6	13	0	**47**	0	9	3	0	0	0	0	0	1
Polytrichum commune	8	10	**40**	20	0	0	4	6	0	3	3	1	0	3
Polytrichum strictum	0	2	0	0	0	0	0	1	0	0	0	0	0	1
Pseudobryum cinclidioides	4	4	20	24	**73**	**67**	43	48	0	13	13	5	0	0
Ptilidium ciliare	0	0	13	0	57	0	4	0	8	3	0	0	0	0
Ptilidium pulcherrimum	0	12	**33**	0	0	0	0	0	0	0	0	0	5	13
Rhizomnium pseudopunct.	0	0	0	0	**40**	0	4	7	0	0	0	2	0	1
Rhizomnium punctatum	0	8	0	8	0	11	17	8	0	3	6	2	0	0
Rhodobryum roseum	0	0	0	0	0	0	0	0	0	5	0	1	0	3
Rhytidiadelphus subpinnatus	0	0	0	0	0	0	0	0	8	7	0	6	0	1
Scapania spp.	8	12	0	0	0	0	0	1	0	3	0	0	0	0
Schistidium apocarpum	0	4	0	0	0	0	0	0	8	0	0	0	2	1
Sphagnum angustifolium	0	0	20	24	0	33	0	1	8	0	0	0	0	0
Sphagnum centrale	0	2	7	4	0	0	0	0	0	0	0	0	0	0

Sphagnum fallax	0	0	7	16	0	0	0	0	0	0	0	0	0	0
Sphagnum fimbriatum	0	0	7	**40**	0	0	0	14	0	3	0	0	0	0
Sphagnum flexuosum	0	0	0	4	0	0	0	2	0	0	0	1	0	0
Sphagnum girgensohnii	0	0	0	4	0	11	0	1	0	2	0	4	0	0
Sphagnum riparium	0	0	7	28	14	22	0	2	8	0	0	0	0	0
Sphagnum squarrosum	0	6	**67**	**60**	21	33	4	23	17	5	0	2	0	0
Sphagnum subsecundum	0	0	7	0	0	0	0	1	0	0	0	0	0	0
Sphagnum teres	0	0	27	20	**53**	0	4	1	0	0	0	0	0	0
Tetraphis pellucida	0	0	0	0	0	0	0	9	0	5	3	1	0	3
Thuidium spp.	0	0	0	0	0	0	0	1	0	3	0	1	0	0
Cladonia coniocrea	0	0	0	0	0	0	0	1	0	0	0	0	2	1
Cladonia fimbriata	0	4	0	0	0	0	0	0	0	0	0	0	0	0
Cladonia spp.	4	0	0	0	0	0	0	0	0	0	0	0	0	3

Abbreviations:
Cx.m.*Carex–Alnus glutinosa* community on mineral soil
Lys.*Lysimachia vulgaris–Calamagrostis purpurea–Alnus glutinosa* community
Phr.*Phragmites australis–Alnus glutinosa* community
Cx.p.Paludified *Carex–Alnus glutinosa* community
Eq.*Equisetum fluviatile–Alnus glutinosa* community
Thel.*Thelypteris palustris–Alnus glutinosa* community
Iris*Iris pseudacorus–Alnus glutinosa* community
At.Ca.*Athyrium filix-femina–Calla palustris–Alnus glutinosa* community
Sci.*Scirpus sylvaticus–Alnus glutinosa* community
At.Fi*Athyrium filix-femina–Filipendula ulmaria–Alnus glutinosa* community
At.for.*Athyrium filix-femina–Alnus glutinosa* community
Fil.*Filipendula ulmaria–Alnus glutinosa* community
Urt.*Urtica dioica–Alnus glutinosa* community
Rub.*Rubus idaeus–Alnus glutinosa* community

Appendix 3. Mean abundance % (integr.) of species in studied black alder communities. See the abbreviations in Appendix 2.

Liite 3. Keskimäärinen kasvilajien peittävyys tutkituissa tervaleppäyhteisöissä. Lyhenteiden selitykset liitteessä 2.

Site type code	A1	A2	B1	B2	B3	B4	B5	B6	B7	C1	C2	C3	C4	C5
Site type	Cx.m.	Lys.	Phr.	Cx.p.	Eq.	Thel.	Iris	At.Ca	Sci.	At.Fil.	At.for.	Fil.	Urt.	Rub.
Nr. of Stands	16	28	5	8	5	3	8	40	8	27	17	64	15	49
Nr. of Sites	25	52	15	25	14	9	23	145	12	60	31	122	41	78
Nr. of Species	137	230	69	88	69	90	115	189	88	184	105	165	104	214
Species														
Ace plat	0	0	0	0	0	0	0	0.01	0	0.02	1.46	0.08	0	0.54
Aln glut	62	73.94	38	61.2	57.86	63.89	59.35	63.79	56.67	53	66	60.89	67.68	60.06
Aln inca	0.84	1.38	0.07	0.01	0.07	0	0	2.14	0.18	5.2	2.94	2.18	2.19	2.99
Bet pend	0	0.23	0	0	0	0	0.01	0.07	0.08	0.07	0	0	0	0.12
Bet pube	0.2	5.66	0.53	2.89	2.23	0.76	1.45	4.65	1.6	3.44	1.1	2.28	0.21	1.35
Cor alba	0	0	0	0	0	0	0	0.07	0	1.09	2.42	0.01	0.09	0.01
Fra exce	0	0	0	0	0	0	0	0	0	0.02	0.1	0.64	0	0.9
Jun comm	0	0.03	0	0	0	0	0.02	0.02	0	0.08	0	0.09	0	0.62
Lon xylo	0	0	0	0	0	0	0	0	0	0	0	0	0.05	0
Myr gale	0	0	1.55	2.54	0	0	0	0	0	0	0	0	0	0
Pic abie	1.25	0.83	0.15	0.1	0.05	0	0.11	1.04	0.02	1.65	2.31	1.54	0.02	3.94
Pin sylv	0	0.03	0	0	0	0	0	0.05	0	0.01	0	0	0.24	0.06
Pru padu	0.05	0.5	0	0	0.01	0	0.01	3.28	0.33	7.23	8.77	3.46	2.1	7.47
Rha fran	0.35	1.79	0.53	0.02	1.53	0.04	0.15	2.52	2.45	1.29	1.19	0.76	0.98	0.83

Rib alpi	0	0	0	0	0	0	0	0.01	0	0	0.01	0.04	0	0.03
Rib nigr	0.01	0	0	0	0	0	0.01	0.24	0.03	1.12	0.01	0.03	0.01	0.01
Rib spic	0.1	0.15	0	0.04	0	0	0.02	1.18	0.1	1.44	0.76	1.35	1.51	1.07
Sal auri	0	0.02	0	0.02	0	0.6	0.05	0	0.18	0	0	0	0	0
Sal capr	0.2	0.65	0	0	0	0.11	0.06	0.01	0.52	0.22	0.24	0	0.17	0.06
Sal cine	0.02	0.62	0.07	0	0.01	0.49	0.36	0.02	0	0	0	0.02	0	0
Sal myrs	0	1.22	0	0.01	0.11	0	0.2	0.32	0.17	0.85	0.1	0.26	0.37	0.03
Sal pent	0	0.64	0	0	0.14	0.16	0.1	0.14	0	0.06	0.14	0	0	0
Sal phyl	1.2	0.9	0.87	0.02	0.09	0.58	0.59	0.04	0.03	0.25	0	0.23	0	0
Sam race	0.02	0.81	0	0	0	0	0	0.18	0	0.51	0.78	0.41	0.3	0.9
Sor aucu	0.19	0.42	0	0.01	0.04	0.02	0.65	1.92	1.37	2.33	2.25	0.81	0.86	5.62
Vib opul	0	0	0	0	0	0	0	0.01	0.02	0	0	0.16	0	0.01
Ado mosh	0	0	0	0	0	0	0	0	0.02	0	0	0	0	0
Aeg poda	0	0	0	0	0	0	0	0	0.05	2.63	0	0.19	0.05	0.37
Agr cani	0	0.01	0.11	0	0	0	0	0.46	0	0.02	0	0	0	0
Agr capi	5.54	0.96	0	0.06	0	0	0	0	0	0.01	0.14	0.51	0.01	1.3
Agr giga	0	0	0	0	0	0	0	0	0	0	0	0	0	0.61
Alc vulg	0	0.58	0	0	0	0	0	0	0	0	0	0	0	0.01
Ali plan	0.07	0.02	0	0.02	0	0	0	0	0	0	0	0	0	0
Alo aequ	0	0	0	0	0	0	0	0.01	0	0	0	0	0	0
Ane nemo	0	0	0	0	0	0	0	0	0.17	0.24	0	6.15	0	3.47
Ang sylv	0	0.06	0	0	0	0	0	0	0.02	0.32	0	0.24	0.02	0.05
Ant sylv	0	0.03	0	0	0	0	0	0	0	0.1	0.01	0.13	0.05	0.11
Ath fili	0	0.4	0	0	0.03	0.11	0	20.71	5.05	18.15	40.9	0.26	1.11	1
Bid trip	0.03	0.01	0	0	0	0	0.09	0	0	0	0	0	0	0
Cal arun	0	1.73	0	0	0	0	0	0	0	0	0	0	0	0.29
Cal cane	0	4.1	0	0.2	0.51	0.02	0.02	0.01	0.93	0.17	0	0.58	0.01	0.26
Cal purp	1.07	19.22	0.03	0.15	0.03	2.27	2.71	0.25	0.31	0.99	0.87	0.6	0.25	0.29
Cal palu	0.59	0.14	0.33	1.8	0.01	12.56	19.48	22.17	0.02	0.01	0	0	0	0
Clt palu	0.27	1.1	0	0.03	0.36	0.29	0.03	1.8	0.58	2.96	0.5	1.23	0.03	0.04
Cal sepi	0	0	0	0	0	0	0	0	0	0.01	0.01	0	0	0.07
Car amar	0	0	0	0	0	0	0.23	0.04	0	0.07	0	0	0	0
Car prat	0.06	0.15	0	0.01	0	0.02	0.01	0	0.05	0	0.01	0	0	0
Car acut	0.02	0.87	4.03	5.2	0.03	7.78	3.49	0	0	0	0	0	0	0
Car aqua	0	0	0	17	0	0	0.01	0	0	0	0	0	0	0
Car brun	0	0	0	0	0	0	0	0	0	0.01	0	0	0	0
Car cane	0.09	0.03	0	0.14	0.21	0.02	0.03	0.53	0	0.09	0.06	0.09	0	0.08
Car echi	0	0	0	0	0	0	0	0.02	0	0	0.01	0	0	0
Car elat	0	0.1	0	0	0	0	0.05	0	0	0	0	0	0	0
Car elon	0.01	0.01	0	0.01	0	0	0.03	0.89	0.2	0.27	0.06	0.01	0.3	0
Car flav	0.01	0	0.03	0	0	0	0	0	0	0	0	0	0	0
Car lasi	0	0	3.47	6.69	0	0	0	0	0	0	0	0	0	0
Car nigr	3.22	0.14	0.18	0.22	0.19	0.07	0.02	0.02	0.02	0	0	0	0	0
Car pall	0	0	0	0	0	0	0	0	0	0.05	0	0.01	0	0.01
Car pseu	0	0	0	0	0.01	0.02	0.03	0	0	0	0	0	0	0
Car rost	1.01	0.27	0.41	24.6	0.36	3	2.13	0.43	0.04	0	0	0	0	0
Car vesi	32.14	1.26	0	9	0	0.02	3.39	0.01	0	0	0.01	0	0	0
Chr alte	0	0	0	0	0	0	0	0.03	0.88	1.41	0	0	0.2	0
Cic viro	0.24	0.02	0.01	0.05	0.06	0.78	0.59	1.16	0	0	0	0	0	0
Cir alpi	0.01	0	0	0	0	0	0	0.29	0	0.17	0.18	0	0	0.56
Cir hele	0	0	0	0	0	0	0	0	0	0.27	0	0	0	0.01
Cir palu	0.01	0.01	0	0.01	0	0	0	0.02	0.02	0.03	0	0.04	0.02	0.01
Cir vulg	0	0.01	0	0	0	0	0	0	0	0	0	0	0.02	0.01
Cre palu	0	0	0	0	0	0	0	0	1.67	0.97	0	0.01	0	0
Des cesp	0.11	8.66	2.67	0.58	0.09	0.02	0.01	3.09	0.28	1.57	1.13	1.55	1.14	8.76
Des flex	0.02	0	0	0	0	0	0	0.07	0	0.01	0	0	0	0
Dry cris	0	0	0.01	0	0	0	0.01	0	0	0	0	0	0	0
Dry cart	0.14	0.26	0	0.02	0.01	1.33	1.17	3.61	0.27	0.7	3.88	0.12	0.66	4.84
Dry expa	0	0	0	0	0	0	0	0.05	0	0.03	5.52	0	0	0.06
Dry fili	0	0	0	0	0	0	0	0	0	0.5	0	0.33	0	0

Ely repe	0	0	0	0	0	0	0	0.02	0	0.02	0	0	0	0.01
Epi angu	0.01	0	0	0	0	0	0	0	0	0.25	0.01	0.02	0.05	1
Epi mont	0.01	0	0	0	0	0	0	0	0	0	0.01	0	0.01	0
Epi palu	0.02	0.01	0	0.02	0	0	0.01	0.02	0.05	0.01	0	0	0	0.01
Equ arve	1.3	2.57	0	0	4.29	0	0.01	1.85	0.1	0.48	1.2	0.28	0.67	0.03
Equ fluv	0.04	0.34	1.08	0.68	70	0.09	0.91	0.29	0	0.03	0	0.02	0	0
Equ sylv	0	0.97	0	0	0	0	0	0.25	0.83	2.82	0.08	2.64	0	0.33
Fil ulma	0.22	0.2	0.69	0.08	0.37	1.57	1.98	1.03	3.77	36.84	2.03	62.05	3.24	1.52
Fra vesc	0	0.01	0	0	0	0	0	0.02	0	0.01	0.01	0.01	0.25	0.32
Gal trif	0.25	0.09	0	0	0	0	0	0.02	0.17	0.02	0.04	0.02	0	0.17
Gal palu	2.37	1.63	0.07	0.22	0.53	0.04	0.6	0.75	0.08	0.15	0.42	0.07	0.03	0.04
Gal ulig	0	0.11	0	0	0	0	0	0	0	0.01	0	0	0	0
Ger sylv	0	0	0	0	0	0	0	0	0	0.34	0	0.24	0	0.01
Geu riva	0.01	0.11	0	0	0	0	0.01	0.08	0.85	1.63	1.3	0.27	0.13	0.01
Gle hede	0.09	0.01	0	0	0	0	0	0	0	0	0	0	0.03	0.08
Gly flui	0.62	0.01	0	0	0	0	0	0	0	0	0	0	0	0
Gly maxi	25.2	0.16	0	0	0	0	0	0.17	0	0	0.01	0	0.39	0
Gym dryo	0	0	0	0	0	0	2.3	0.14	0	0.27	0.28	0.01	0	0.44
Hum lupu	0	0	0	0	0	0	0	0	0	0.03	0	0	0	0.24
Hup sela	0	0	0	0	0	0	0	0.01	0	0	0.01	0	0	0
Imp noli	0	0.01	0	0	0.07	0	0	1.69	0.21	9.98	0.27	2.21	0.82	0.02
Iri pseu	0	0.02	0.03	0.02	2.76	3.93	34.96	0.01	0.1	0	0	0	0	0
Jun fili	1.66	1.04	0.01	0.04	0	0	0.01	0.01	0	0	0	0.04	0	0
Lac sibi	0	0.02	0	0	0	0	0	0	0	0	0	0	0	0
Lem mino	0	0	0	0.02	0	0.3	3.97	0.03	0	0	0	0	0	0
Leo autu	0	0.06	0	0	0	0	0	0	0	0	0	0.01	0	0
Luz mult	0	0	0	0	0	0	0	0	0	0	0	0	0	0.01
Luz pilo	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0.02
Lyc anno	0	0	0	0	0	0	0	0.02	0	0.01	0	0	0	0
Lyc euro	0.08	0.05	0.04	0.08	0.04	0.07	0.08	0.14	0.03	0.01	0	0.01	0	0.01
Lys thyr	1.81	0.61	1.6	1.73	0.64	7.49	0.99	9.82	0.23	2.93	0.49	0.24	0	0.16
Lys vulg	0.72	18.63	0.63	0.28	1.19	0.82	0.41	0.62	0.03	0.33	0.03	1.19	0.04	0.64
Lyt sali	0.7	0.3	0.16	0.34	0.43	0.02	2.08	0.07	0	0.01	0.01	0.04	0	0.01
Mai bifo	0	0.07	0	0	0	0	1.31	0.03	0.02	0.75	1.15	0.07	0	3.06
Mat stru	0	0	0	0	0	0	0	0.14	0	0.09	0	0	0	0
Mel prat	0	0.21	0	0	0	0	0	0	0	0	0	0	0	0
Mel sylv	0	0.07	0	0	0	0	0	0	0	0	0	0	0	0.01
Mel nuta	0	0.01	0	0	0	0	0	0	0.02	0.19	0	0.01	0	0.02
Men arve	0.14	0.12	0	0	0	0	0	0	0	0.01	0.01	0	0	0.13
Men trif	0	0	0.03	0.85	12.2	0.08	0.05	0.54	0	0	0	0	0	0
Mil effu	0	0	0	0	0	0	0	0	0	0.05	0	0	0	0.43
Moe trin	0	0.01	0	0	0	0	0	0	0	0	0.01	0	0.07	0.02
Myo scor	1.35	0.2	0	0	0	0	0.01	0.4	0.04	0.64	0.7	0.01	0.1	0.03
Oxa acet	0	1.17	0	0	0	0	0.3	1.84	0.05	2.39	9.21	1.64	0.13	13.79
Par quad	0	0	0	0	0	0	0.04	0.17	0.17	0.18	0.01	0.38	0	0.39
Per amph	0.4	0.02	0	0	0	0	0	0	0	0	0	0	0	0
Per lapa	0.13	0	0	0	0	0	0	0	0	0	0	0	0	0.01
Peu palu	0.48	1.06	2.07	2.79	0.26	0.38	0.2	0.41	0.05	0.07	0.01	0.21	0	0.13
Pha arun	0.08	0.68	0	0	0	0	0	0	0	0	2.41	0.01	0	0.03
Phe conn	0	0	0	0	0	0	0	0.07	0.03	0.28	0.44	0.02	0	0.35
Phr aust	0	0	73.93	0.01	0	0	0.01	0	0	0	0	0	0	0
Pla majo	0	0	0	0	0	0	0	0	0	0	0	0	0	0.01
Poa nemo	0	0.41	0	0	0	0	0	0	0	0	0	0	0	0.01
Poa prat	0.04	0.11	0	0	0	0	0	0	0	0	0	0	0	0
Poa triv	0.22	0	0	0	0	0	0	0	0	0.02	0.01	0	0	0.01
Pot erec	0.01	0.02	0	0	0	0	0	0	0	0.02	0	0	0	0.02
Pot palu	1.8	0.86	0.81	0.82	0.77	0.04	0.72	0.82	0.18	0	0	0.09	0	0
Pru vulg	0.02	0.02	0	0	0	0	0	0	0	0.02	0.03	0	0	0.01
Ran acri	0	0.03	0	0	0	0	0	0	0	0.01	0.01	0.02	0.01	0.07
Ran auri	0.01	0	0	0	0	0	0	0	0.02	0.3	0	0.03	0	0

Ran repe	2.28	1.89	0	0	0	0.02	0.04	0.69	0.18	0.67	2.26	0.11	0.18	0.17
Ran rept	0.02	0.01	0	0	0	0	0	0	0	0	0	0	0	0
Rub idae	0.02	0.5	0	0	0	0.56	0.07	0.44	0.18	1.74	5.31	1.35	3.13	48.85
Rub saxa	0	0.01	0	0	0	0	0.01	0.02	0.05	1.18	0.01	0.26	0	0.03
Rum acsa	0.01	0	0	0	0	0	0.01	0	0	0.01	0.01	0.03	0	0.38
Rum hydr	0	0	0	0	0	2.33	0	0	0	0	0	0	0	0
Sci sylv	0	0	0	0	0.36	0	0.03	0.03	75	0.04	0	0.05	0.32	0
Scu gale	0.27	0.27	0	0	0.04	0.02	0.02	0.06	0.08	0	0.01	0.01	0.01	0.01
Sil dioi	0	0	0	0	0	0	0	0	0	0.02	0.09	0.72	0	3.54
Sol dulc	1.14	0.18	0.01	0	0.43	9.31	2.27	5.35	2.93	0.35	0.46	0.4	0.27	0.01
Sol virg	0	0	0	0	0	0	0	0	0	0.01	0	0	0	0.01
Sta palu	0.33	0.01	0	0	0	0	0	0.01	0	0.01	0	0	0	0
Ste medi	0.03	0.6	0	0	0	0	0	0	0	0.01	0.01	0.01	0	0.03
Ste nemo	0	0	0	0	0	0	0	0	0	0.21	0.35	0.18	0	0.34
Ste palu	0.29	0	0	0	0	0	0	0.01	0	0	0	0	0	0
Tar offi	0.12	0.13	0	0	0	0	0	0	0	0	0.01	0.01	0.02	0.05
Tha flav	0.03	0	0	0	0	0	0	0	0	0	0	0.09	0	0.26
Tha simp	0.29	0.02	0	0	0	0	0	0	0	0	0	0	0	0
The palu	0	0	0	0	0	33.33	0.6	0	0	0	0	0	0	0
Tri euro	0	0.12	0	0	0	0	0	0.34	0.18	0.28	0.6	0.11	0	4.06
Tus farf	0.09	0.01	0	0	0	0	0	0	0	0	0	0	0	0
Typ lati	0	0	0	0.62	0	0.49	1.74	0	0	0	0	0	0	0
Urt dioi	0.21	0.55	0	0	0	0.02	0.01	0.52	1.02	2.49	4.13	2.73	76.68	0.62
Vac oxyc	0	0	0.08	1.1	0.01	0	0	0	0	0	0	0	0	0
Vac myrt	0	0.01	0	0.01	0	0	0.05	0.05	0	0.19	0	0.01	0	0.02
Vac viti	0	0	0	0	0	0	0.01	0.11	0	0	0	0	0	0.01
Ver cham	0	0.02	0	0	0	0	0	0	0	0	0	0	0	0.01
Vio epip	0	0.07	0	0	0	0	0	0.15	0.08	0.14	0.01	0.1	0	0
Vio palu	0.11	6.44	0.11	2.68	12.59	2.62	0.31	7.54	2.08	4.86	8.06	2.2	1.23	2.42
Vio rivi	0.01	0.01	0	0	0	0	0	0	0	0	0	0.01	0	0.01
Vio selk	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0.19
Amb serp	0.05	0.02	0.03	0.02	0	0	0	0.02	0	0.01	0.01	0.03	0.23	0
Atr undu	0	0.32	0	0.01	0.01	0	0.01	0.02	0	0.03	0.11	0.17	0	0.02
Bar barb	0	0.21	0	0	0	0	0	0	0.08	0.09	0	0	0	0.04
Bra oedi	0.01	0.03	0.07	0.02	0.14	0	0.13	0.05	0	0.7	0.89	0.42	0.02	0.36
Bra popu	0.08	0.04	0	0	0	0	0	0	0	0.07	0	0.01	0	0.04
Bra refl	0.35	0.45	0.03	0.04	0.18	0	0.07	0.2	0.03	1.42	0.32	0.58	0.34	1.11
Bra rivu	0	0	0	0	0	0	0	0.04	0	0.37	0	0.01	0	0.04
Bra ruta	0.11	0.09	0	0	0	0	0	0.46	0.58	2.61	0.06	0.86	0.15	0.09
Bra sale	0.02	0.05	0	0.01	0	0.02	0.02	0.11	0.02	2.92	0.23	0.46	3.6	0.17
Bra star	0	0	0	0	0	0	0	0	0	0.02	0	0	0	0
Bra velu	0	0	0	0	0	0	0.13	0	0	0	0	0	0	0
Cal hald	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0
Cal cord	0.95	0.18	0.29	0.2	3.56	0.52	3.61	3.23	1.75	1.79	0.6	0.31	0.01	0
Cal stra	0	0	0.01	0.07	0	0	0	0.01	0	0	0	0	0	0
Cal cusp	0.02	0.35	0.4	0.01	0.04	0.06	0.42	0.66	0.02	0.37	0.01	0.14	0.1	0.02
Cep spp.	0.01	0.01	0	0	0	0.02	0.03	0.02	0	0	0.01	0	0	0
Chi poly	0.04	0.53	0.03	0.09	0.06	0	0.07	0.04	0	0.04	0.17	0	0.01	0.02
Cli dend	0.82	1.29	0	0.2	0.04	0.04	0.38	0.39	0	1.49	1.04	0.62	0	0.07
Dic fusc	0.08	0	0	0	0	0	0	0	0	0	0	0	0	0
Dic maju	0	0	0	0	0	0	0	0.05	0	0	0	0	0	0
Dic scop	0.09	0.03	0.08	0	0.08	0.02	0.03	0.05	0.05	0.14	0.05	0.04	0.01	0.27
Dre unci	0.54	0.29	0.03	0.06	0.18	0.02	0.03	0.08	0	0.12	0.22	0.13	0.09	0.22
Hed cili	0	0.01	0	0	0	0	0	0	0	0	0.03	0	0	0.01
Hom seri	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hyl sple	0	0	0	0	0	0	0	0	0	0.04	0	0.01	0.02	0
Hyp cupr	0.02	0.27	0	0	0.09	0	0.19	0.01	0.02	0.09	0.31	0.15	0.23	0.63
Hyp lind	4.94	0.41	0	0	0	0	0	0	0	0	0.01	0	0	0
Hyp pall	0.13	0.45	0	0	0.06	0	0.03	0.11	0.02	0.15	0.12	0.05	0	0.39
Lep koch	0.01	0.01	0	0	0	0	0	0.09	0	0.02	0.02	0.01	0	0.02

Lep ripa	0.02	0	0	0.01	0	0	0.01	0.02	0	0	0	0	0	0
Lop hete	0.04	0.03	0.07	0.04	0.07	0.02	0.01	0.01	0	0.06	0	0.03	0.03	0.01
Loz spp.	0	0	0.05	0	0	0	0	0.04	0	0.02	0	0	0	0
Mar poly	0	0	0	0	0	0	0	0.01	0	0	0	0	0	0
Mni horn	0	0	0	0	0	0	2.48	0	0	0	0	0	0	0
Par long	0	0.16	0	0	0	0	0	0	0.02	0.05	0	0	0.08	0.21
Pel epip	0	0.3	0	0	0	0.04	0	0.01	0	0	0	0	0	0
Pel nees	0	0.08	0	0.14	0	0	0.03	0.07	0	0.01	0.13	0.02	0	0
Plm affi	0	0	0	0	0	0	0	0	0	0.04	0	0.26	0	0
Plm cusp	0.01	0.03	0	0	0	0	0	0.23	0.02	0.23	0	0.06	0.38	0.13
Plm elli	0.02	0	0	0.08	1.61	13.67	0.26	0.25	0.83	3.28	0.23	0.23	1.08	0.05
Plm medi	0	0.01	0	0	0	0	0	0	0.83	1.65	0	0.15	0	0
Pla cavi	0.01	0	0	0	0	0.02	0	0.02	0	0.18	0.02	0.02	0	0.02
Pla dent	0.03	0.18	0.03	0.04	0.15	0.07	0.31	0.09	0	0.15	0.07	0.03	0.02	0.14
Pla laet	0.22	0.25	0.09	0	0.06	0	0	0.05	0.08	0.81	0.08	0.07	0.09	0.04
Pla ruth	0.01	0	0	0	0	0	0	0.1	0	0.08	0.02	0	0	0.02
Ple schr	0.04	0.06	0.41	0.01	0	0	0.01	0.02	0	0.02	0.01	0.04	0	0.17
Poh nuta	0.06	0.06	0.04	0.01	0	0.04	0.01	0.14	0	0.01	0.05	0.02	0	0.04
Pol form	0.03	0.02	0	0.01	0	0.02	0.01	0	0	0.01	0	0	0	0
Pol long	0	0.05	0.03	0	0.16	0	0.03	0.02	0	0	0	0	0	0.13
Pol comm	0.06	0.05	0.08	0.1	0	0	0.22	0.08	0	0.02	0.03	0	0	0.06
Pol stri	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0
Pse cinc	0.01	0.01	0.13	0.51	12	1.41	0.5	6.03	0	2.4	0.32	0.76	0	0
Pti cili	0	0	0.05	0	0.19	0	0.02	0	0.02	0.05	0	0	0	0
Pti pulc	0	0.03	0.09	0	0	0	0	0	0	0	0	0	0.13	0.05
Rhi pseu	0	0	0	0	0.26	0	0.01	0.13	0	0	0	0.25	0	0
Rhi punc	0	0.04	0	0.1	0	3.33	0.28	0.95	0	0.09	0.04	0.03	0	0
Rho rose	0	0	0	0	0	0	0	0	0	0.02	0	0	0	0.21
Rhy subp	0	0	0	0	0	0	0	0	0.02	0.68	0	0.83	0	0
Sca spp.	0.02	0.04	0	0	0	0	0	0	0	0.05	0	0	0	0
Sch apoc	0	0.01	0	0	0	0	0	0	0.02	0	0	0	0	0
Sph angu	0	0	16.67	0.25	0	1.69	0	0.02	0.02	0	0	0	0	0
Sph cent	0	0	0.67	0.4	0	0	0	0	0	0	0	0	0	0
Sph fall	0	0	0.03	1.6	0	0	0	0	0	0	0	0	0	0
Sph fimb	0	0	0.01	7.8	0	0	0	1.06	0	0.01	0	0	0	0
Sph flex	0	0	0	3.6	0	0	0	0.01	0	0	0	0	0	0
Sph girg	0	0	0	0.04	0	0.56	0	0.03	0	0.17	0	0.02	0	0
Sph ripa	0	0	0.67	0.65	3.57	0.58	0	0.01	0.58	0	0	0	0	0
Sph squa	0	0.02	14.81	4.18	0.64	0.6	0.01	2.13	0.03	0.1	0	0.01	0	0
Sph subs	0	0	0.01	0	0	0	0	0.04	0	0	0	0	0	0
Sph tere	0	0	4.27	3.29	15.02	0	0.87	0.12	0	0	0	0	0	0
Tet pell	0	0	0	0	0	0	0	0.14	0	0.02	0.01	0	0	0.02
Thu spp.	0	0	0	0	0	0	0	0	0	0.02	0	0	0	0
Cla coni	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cla fimb	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0