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Studies in *Myrica gale* L., with main emphasis on its occurrence in the inner parts of the Gauldalen area in Central Norway

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STUDIES IN MYRICA GALE L., WITH MAIN EMPHASIS ON ITS OCCURRENCE IN THE INNER PARTS OF THE GAULDALEN AREA IN CENTRAL NORWAY

by

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ABSTRACT


The distribution of *Myrica gale* L. in Fennoscandia is discussed, primarily in relation to climatic factors. Lower limits for the summer temperature and for the actual length of the growing period are proposed as the main climatic factors responsible for the horizontal and vertical distribution. However, low winter temperatures, the occurrence of late-spring frost, and a combination of low precipitation amount/frequency and high summer temperatures can also lead to its absence from some districts. The distribution of *Myrica* in the Trøndelag region, Central Norway, is described, and its occurrence at the highest localities in Norway, in the Gauldalen area, Sør-Trøndelag county, is treated in detail. Aspects of its paleo-history in Norway are mentioned, and the possible dispersal by man is discussed.

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INTRODUCTION

In Norway, *Myrica gale* L. is a predominantly lowland species occurring more or less continuously along the coastal strip from the Swedish border in Østfold county in the southeast, to the Vågsfjorden and Vesterålen areas in Troms and Nordland counties in the north where it reaches its northern known limit at about 69° lat. (e.g. Benum 1958, Fægri 1960). In southeastern Norway, it is found in several places far inland, the northern limit being at Ytre Rendal. It is also found in two places in the Trysil district where it reaches 470 m a.s.l. (Nyhuus 1937). In western parts of southeast Norway it reaches the area surrounding Lake Mjøsa, the Krøderen area in Buskerud county, and Tokke in Telemark county.

*Myrica* is also found in several places far inland in Central Norway. In this Trøndelag region, the southeastern-most localities are at Tydalen, Holtålen in Gauldalen, and Rennebu in Orkladal. According to herbarium specimens it reaches its uppermost known altitudinal limit in Norway at 600 m a.s.l. in Holtålen, but it is reported from a locality at Vinje in Telemark at about the same altitude.

A map showing the Fennoscandian distribution of *Myrica* was published by Hultén (1971), and a similar version is given in Fig. 7. Jalas and Suominen (1976) published a map of the European distribution.

THE DISTRIBUTION IN THE GAULDALEN AREA, SØR-TRØNDELAG COUNTY

In the Gauldalen area *Myrica* is almost entirely restricted to pre-alpine parts of the coniferous belt. Three of the nine known *Myrica* localities in the area are situated below 350 m a.s.l., the remainder being above 400 m a.s.l. (Fig. 1). The lowland records are all from northwestern parts of the area. As the behaviour of *Myrica* at its upper altitudinal limit in Norway is of some interest, the two Holtålen localities will be dealt with in more detail.
Fig. 1.

The distribution of *Myrica gale* in the river Gaula basin in Sør-Trøndelag county. A and B indicate the two Holtålen localities, and C localities at Berkåk.

**Locality A**

Sør-Trøndelag. Holtålen. NW of Breidtjønn, 580-590 m a.s.l. (Figs. 1, 2-4 and 6), UTM-reference: PQ 05 84.

At this locality, *Myrica* grows at only one place, a south-facing sloping fen situated in the upper part of a valley depression. The locality is mostly surrounded by a mixed woodland of *Betula pubescens* and a few scattered *Pinus sylvestris*. Spruce forests occur here at their upper limit in the area, whereas the birch timber line lies at about 650-750 m a.s.l. *Myrica* covers a continuous area of about 10 x 14 m, and consists of female plants only. The stand is therefore undoubtedly made up of only one clone.
Fig. 2. Locality A of *Myrica gale* at Holtålen (580-590 m a.s.l.) in Gauldal, Sør-Trøndelag county (see text).

Fig. 3. The setting of locality A (indicated with an arrow).
I discovered the species at this locality in 1957. The number of plants has apparently remained essentially unchanged since then. This Myrica stand occupies a habitat which is partly mesotrophic to eutrophic fen, partly transitional to a wet mineral soil ericaceous community. A species list made on 10 Sept. 1978 gave the following composition of the stand: Andromeda polifolia, Betula nana, B. pubescens (juv.), Calluna vulgaris, Carex dioica, C. lasiocarpa, C. panicea, C. rostrata, Comarum palustre, Cornus suecica, Drosera rotundifolia, Equisetum palustre, E. sylvaticum, Eriophorum angustifolium, E. vaginatum, Euphrasia frigida, Lycopodium annotinum, Molinia caerulea, Nardus stricta, Narthecium ossifragum, Picea abies (juv.), Potentilla erecta, Scirpus cespitosus ssp. cespitosus, Selaginella selaginoides, Sorbus aucuparia (juv.), Succisa pratensis, Thalictrum alpinum, Tofieldia pusilla, Vaccinium myrtillus, V. uliginosum, Viola palustris. The following species were recorded in the bottom layer: Aneura pinguis, Calliergon stramineum, C. trifarium, Campylium stellatum, Drepanocladus intermedius, Hylocomium splendens, Pleurozium schreberi, Scaphidoium scorpioides, Sphagnum angustifolium, S. auriculatum, S. contortum, S. fuscum, S. papillosum, S. subnitens, S. warnstorffii.

Fig. 4. *Myrica gale* at locality A in Holtålen.
Locality B


*Myrica* forms small stands of only male plants at three places within an area of about 200 x 300 m. The largest stand covers about 7 x 8 m, the smallest one about 5 x 6 m. The locality lies on a south-facing slope, and consists of small mire sites of mostly mesotrophic character in woods and groves of *Picea abies, Betula pubescens* and scattered *Pinus sylvestris* (Fig. 5). As the grazing of domestic animals has now largely ceased there, the mire sites are being rapidly invaded by small birches and willows.

Fig. 5. Locality B of *Myrica gale* at Holtålen (600 m a.s.l.) in the Gauldalen area, Sør-Trøndelag county.

Like locality A, this is situated close to the upper limit of pre-alpine spruce forests. All three stands are associated with small soligenous mire sites, being mostly transitional between mire and moist mineral soil communities on shallow peat.

At the 600 m a.s.l. locality (Fig. 5), the following species were recorded on 9 Sept. 1978, within the limits of the *Myrica*
stand: Agrostis canina, Anemone nemorosa, Betula nana, B. pubescens (juv.), Calluna vulgaris, Deschampsia caespitosa, Juniperus communis, Melampyrum pratense, Molinia caerulea, Nardus stricta, Narthecium ossifragum, Picea abies (juv.), Vaccinium myrtillus, V. uliginosum, Viola epipsila. The bottom layer was not recorded, but was very poorly developed because of a dense field layer.

The sexual state of the Myrica stands was carefully examined at both localities in Holtålen. My experience with Myrica elsewhere in Norway has shown that it is not always strictly dioecious. Female catkins with some male inflorescences intermingled can occasionally be found, and vice versa. This was not the case in Holtålen.

THE ELEMENT OF COASTAL PLANTS IN INNER PARTS OF THE GAULDALEN AREA

Many Norwegian coastal plants are known to penetrate deeply into eastern parts of the Gauldalen area. Among the vascular plants which reach this particular area in Holtålen are: Blechnum spicant, Carex hostiana, C. pulicaris, C. tumidicarpa, Erica tetralix, Juncus effusus, Lycopodium inundatum, Narthecium ossifragum, Rhynchospora alba, Thelypteris limbosperma. The more important bryophytes are Bazzania trilobata, Leucobryum glaucum, Plagiothecium undulatum, Racomitrium aquaticum, Rhytidiadelphus loreus, Sphagnum molle, S. quinquefariurn, S. strictum. Of all these, Blechnum spicant, Narthecium ossifragum, Plagiothecium undulatum, Rhytidiadelphus loreus and Sphagnum quinquefariurn occur more commonly throughout the area where forests and mire vegetation are present, and they sometimes reach above the timber line. They all descend to the floor of the main Gauldalen valley, which at Holtålen has a lower limit of about 250 m a.s.l., but they are mainly concentrated between 400 and 650 m a.s.l. Lycopodium inundatum, Rhynchospora alba, Bazzania trilobata and Sphagnum molle are found only at a few localities in the valley bottom at between 265 and 330 m a.s.l. Carex pulicaris, C. tumidicarpa and Juncus effusus are primarily found in the zone between 350 and 600 m a.s.l. On the other hand, Carex hostiana, Thelypteris limbosperma, Leucobryum glaucum, Racomitrium aquaticum and Sphagnum strictum are not recorded below 560 m a.s.l. in this area.
Erica tetralix has been found at two places in Holtålen. One locality is on a mire with a very favourable humid climate in the main valley bottom area at 330 m a.s.l., the other is on a sloping fen 590 m a.s.l. 2 km southeast of Myrica locality A. Erica tetralix is common in the neighbouring area of Midtre Gauldal some 20 km to the northwest, where it has an altitudinal range of 450-700 m a.s.l. (Ouren 1961).

Narthecium ossifragum dominates many of the sloping fens in the surroundings of the Myrica locality A. Sphagnum strictum and Leucobryum glaucum occur sporadically, and Racomitrium aquaticum has been found at one place. Here, Leucobryum glaucum, Racomitrium aquaticum and Erica tetralix are at their known eastern limit in the Gauldal area. At Myrica locality B (N of Grytbakk) Narthecium ossifragum is also an important constituent of the sloping mires, and Sphagnum strictum (680 m a.s.l.) reaches its eastern limit in the Gauldal area.

The habitats occupied by Myrica in Holtålen are like those common for the species elsewhere in western Norway.

THE CLIMATE IN INNER PARTS OF THE GAULDALEN AREA

The meteorological stations in Holtålen measure precipitation only. The mean annual amount of precipitation in the valley bottom is about 820-840 mm (Table 1). This is fairly representative for the main valley of Gauldal generally, as all the stations situated there report values between 800 and 900 mm (DNMI 1982). But in Holtålen the precipitation in the valley bottom is not representative for the pre-alpine areas where Myrica is found. The precipitation amount and frequency during the growing period are known to be on average higher in the pre- and sub-alpine areas than in and near the valley bottom. This is especially the case for areas north of the river Gaula. A typical feature on many summer and especially autumn days with prevailing westerly winds, is a belt of fog or clouds which covers the landscape down to about 450 m a.s.l. It was also told by the farmer at Grytbakk (locality B), that this area commonly has local showers during the summer, brought not only by westerly winds but also by southeasterlies.
Table 1. Climatic data from selected meteorological stations in Fennoscandia used to estimate the climatic conditions in areas where Myrica gale L. is present and absent. The meteorological data are from Braun (1963), Braun & Bälden (1970) and ONM (1962). For Finland and Sweden, the snow data are from Eds & Mannerfelt (1965) and Butter (1971). The temperatures for the Finnish and Swedish stations are reduced to sea level according to Laszlo-Kovacs (1970a).

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<th>Municipality</th>
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<th>July</th>
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Mean temperature: Jan. = 1.7°C, July = 16.5°C, Tetraph = 11.9°C
Annual precipitation: Trondheim = 41.9 mm, Vågåmo = 32 mm, Øvre Rendal = 32 mm
No. of days with precip. > 0.1 mm: Trondheim = 95 days, Vågåmo = 86 days, Øvre Rendal = 86 days
No. of days with snow cover: Trondheim = 124 days, Vågåmo = 126 days, Øvre Rendal = 126 days
The meteorological station at Vennafjell, Selbu (671 m a.s.l.) - north of the Gauldalen area - records a mean annual precipitation of 1175 mm. But the element of humid-demanding species is much less conspicuous in the Vennafjell area than in the pre- and sub-alpine areas north of the river Gaula in the middle and inner parts of Gauldalen. The annual amount of precipitation and/or precipitation frequency is therefore likely to be higher there.

The summer macrotemperature at the Myrica localities in Holtålen has to be estimated from values recorded at meteorological stations outside the area. This was done by converting to the 600 m level the mean July temperature and the tetratherm (June to September) from a selection of the nearest meteorological stations measuring temperature. A temperature decrease of 0.6°C for each 100 m of ascent, was then used as the conversion factor (the same factor has been used in all similar conversions mentioned in this paper). The stations used (Table 1) were: Røros (628 m a.s.l.), Stugudal (615 m a.s.l.), Vennafjell (671 m a.s.l.), Selbu (197 m a.s.l.), Berkåk (424 m a.s.l.), and Voll, Trondheim (127 m a.s.l.). Temperatures measured at those stations, converted to the 600 m level, give a mean July temperature of 11.8°C and a tetratherm of 9.5°C on average (Table 2).

This tetratherm value corresponds well with the timberline for spruce in the area which is about 600 to 650 m a.s.l., whereas the spruce treeline itself lies at about 700 to 750 m a.s.l. If the tetratherm value of 9.5°C is converted to these altitudes, the timberline comes to lie at 9.2 - 9.5°C, and the treeline at 8.6 - 8.9°C. Skre (1972) has found the climatic altitudinal limit for vegetative growth of spruce to lie at a tetratherm value of 8.8°C, and Mork (1933) established that the lower limit for ripening of spruce seeds lies at a tetratherm value of 9.5 - 10°C. But the sheltered and south-facing position of the two Myrica localities in Holtålen must imply a local summer temperature there that is much more favourable than the atmospheric macrotemperature in the area.

The mean length of the snow-free period at the two Myrica localities is unknown. But my own experience with locality A over several years indicates that the snow-cover period extends from about 1. November to mid-May, i.e. nearly 200 days.

Using the same meteorological stations as above, the mean annual temperature for January can be estimated to be approximately -6.7°C at 600 m a.s.l. in Holtålen.
DISCUSSION OF THE CLIMATIC AND EDAPHIC FACTORS INFLUENCING MYRICA DISTRIBUTION IN THE GAULDALEN AREA

The following factors may be important for the occurrence of *Myrica* at its pre-alpine localities in Holtålen: (1) The precipitation amount and frequency is high in the area; (2) the localities are well protected against winds, which maintains high microhumidity in the immediate surroundings of *Myrica* during the growing period; (3) the south-facing position gives a favourable summer microclimate; (4) the thick, stable snow cover protects against the winter temperature extremes; (5) the localities are supplied by water from melting snow during late spring and early summer, the period when Trøndelag has least precipitation.

I believe the thick, stable snow cover means that the winter temperature can be left out of consideration when discussing the distribution of *Myrica* in the Gauldalen area. The upper distribution limit at 600 m a.s.l. is not likely to be caused by precipitation or air humidity factors, although the wind-protected sites of *Myrica* in the pre-alpine spruce forest do have a very favourable humid local climate and may well have higher mean air humidity during the growing period than most higher mires in the area. Mire and wetland sites suitable for *Myrica* are indeed common at higher altitudes. The best evidence for excluding humidity as a decisive factor is that *Narthecium ossifragum, Erica tetralix, Thelypteris limbosperma* and *Sphagnum strictum* all ascend to higher altitudes than *Myrica* in the Gauldalen area. *Narthecium ossifragum* and partly also *Erica tetralix*, can moreover grow at fairly exposed habitats there. All these species are undoubtedly absent from the area surrounding the Gulf of Bothnia because they require high precipitation and/or air humidity during the growing period, even though *Myrica* grows there. It is thus reasonable, from a climatic point of view, to assume that the summer temperature is in some way responsible for the upper limit of *Myrica* in inner parts of the Gauldalen area.

The seemingly total absence of *Myrica* below 400 m a.s.l. in eastern parts of Gauldalen is, however, not easily explained in solely climatic terms as both the summer temperature and the length of the growing period should be more favourable there than at higher altitudes.
The annual amount of precipitation and the air humidity are undoubtedly on average less favourable at lower altitudes in this area, but they are still relatively high. This is also seen by the frequent occurrence of humid-demanding species like Blechnum spicant, Plagiothecium undulatum, Rhytidiodelphus loreus and Sphagnum quinquefarium which descend to the valley bottom in the whole area. On the other hand, it seems likely that some other humid-demanding species have their lower altitudinal limit in the Gauldalen area defined by precipitation/humidity factors. This especially concerns Erica tetralix, Thelypteris limbosperma, Leucobryum glaucum and Sphagnum strictum.

It should be emphasized that few mire sites are available below 400 m a.s.l. in eastern parts of the Gauldalen area. This is mostly due to the topography. Steep hillsides rise straight from the valley bottom leading to a dominance of coniferous, and partly also deciduous forests. Furthermore, mires and mire vegetation are only occasionally found in the more or less flat valley-bottom areas along the entire stretch of the main Gauldalen valley. The only place where mires are common there is in the western parts of Holtålen where mires of varying topography, vegetation and nutrition occur on both sides of the river Gaula between 265 and 340 m a.s.l.

Lycopodium inundatum, Rhynchospora alba and Sphagnum molle are found on some of these mires at their eastern distributional limit in the Gauldalen area. Erica tetralix grows abundantly and is associated with for example, Rhynchospora alba. It is quite incomprehensible that Myrica is not found growing on one or more of these mires. As Erica tetralix and Narthecium ossifragum are found there, the humidity should be more than sufficient for Myrica. I will return to this problem later.

THE DISTRIBUTION IN THE TRØNDELAG REGION

The distribution of Myrica in part of Trøndelag and Møre and Romsdal was mapped by Ouren (1974) using squares of 20 x 20 km in the UTM grid system as a basis. Subsequent records are also included in the present map (Fig. 6). Thorough botanical investigations connected with, for example, the Norwegian national plan for
Fig. 6. The known distribution of *Myrica gale* in the Trøndelag region, Central Norway. Circles: Herbarium specimens. Squares: Field-card and literature records. Stars: Verbal information. Dots with line: Inexact localization, alternative square(s) indicated. The capitals A to C refer to localities in the river Gaula basin in Sør-Trøndelag county.
mire nature reserves, and the provisional preservation of river systems, have also given valuable information concerning the location of areas where Myrica is actually lacking.

A high occurrence of Myrica, corresponding to that in the Gauldalen area, is situated at Berkåk, Rennebu, in the south-eastern part of the Trøndelag region, where Myrica is found at 5 localities between 420 and 500 m a.s.l. (C in Figs. 1, 6 and 7). In Neadalen, north of the Gauldalen area, Myrica is found between 200 and 380 m a.s.l., and reaches its eastern limit there at Gressli in Tydalen (D in Figs. 6 and 7). From this district there is also an interesting report of a Myrica locality at about 700 m a.s.l. (Tydal, Skarpdalsvollen, PQ 41 06). According to a dependable old woman acquainted with the locality, Myrica was seen there some time before the First World War, and her grandmother had used it in clothes as a protection against moths during the winter (T. Ouren, in litt. 1983). However, Myrica was not found there during a visit made by T. Ouren in 1973. Fægri (1960) also reported Myrica from Lierne in Nord-Trøndelag (S in Fig. 7).

Myrica is rare on the mainly tree-less coastline of Trøndelag. From the windy island Frøya (E in Fig. 7) where spontaneous coniferous forests are not found now, it is found only two places. It occurs more commonly on the neighbouring island of Hitra (F in Fig. 7), but its distribution there is almost totally restricted to lowland mires surrounded by pine forests. Myrica is not found in the boggy Havmyrene area, in the inner, exposed part of the island (A. Skogen, pers. comm.), even though most of this area is as low as 100 - 200 m a.s.l.

It is also worth mentioning some areas where Myrica is not found. For example, it is seemingly absent from the pre- and sub-alpine, and partly very humid, inland area between Neadalen in the south and Lierne in the north. Some of this area has been thoroughly investigated floristically in recent years, e.g. upper Forradal in Nord-Trøndelag (G in Fig. 7) where many coastal plants are found, such as Narthecium ossifragum, Juncus squarrosus, Thelypteris limbosperma, Lycopodium inundatum, Rhynchospora alba, Leucobryum glaucum, Sphagnum strictum and S. angermanicum (Moen et al. 1976). The very boggy upper Forradal area is almost entirely higher than 400 m a.s.l., and spruce forms the timber line at about 500 - 550 m a.s.l. (Moen et al. 1976:65).
Fig. 7. The approximate distribution of *Myrica gale* in Fennoscandia (solid line). Localities/districts for *Myrica* mentioned in the text are marked with large, filled circles. Open circles denote localities/districts mentioned in the text where *Myrica* is not found. The line with stars is the mean July isotherm of 13°C, that with dots, the mean July isotherm of 15°C. The line with squares is the isopleth of mean annual precipitation of 500 mm. Distribution after Fægri (1960) and Hultén (1971). Temperature after map DNMI (1973). Precipitation after Kalliola (1973:62).
The absence of *Nyrica* from the Momyr and Nord-Fosen areas in Sør-Trøndelag (H in Fig. 7) is also surprising. Apparently suitable mire vegetation occurs abundantly here between 150 and 350 m a.s.l., and spruce forms the upper timber line at (300)- 350 - 400 m a.s.l. (Moen & Selnes 1979, Selnes 1982). Many coastal plants are also found in these areas, e.g. *Narthecium ossifragum, Erica tetralix, Juncus squarrosum, Sphagnum strictum, S. angermanicum* and *Leucobryum glaucum*. *Lycopodium inundatum* and *Rhynchospora alba* are also found sporadically up to about 200 m a.s.l. (Moen & Selnes 1979).

In the Trondheim area, *Myrica* is common wherever mire vegetation is present within the spruce forest zone below 350 m a.s.l. Up to this altitude it grows more or less continuously, occupying various kinds of mire sites and being fairly indifferent to exposure. For example, on the northwest-facing side of Gråkallen it reaches an upper altitudinal limit of 340 m a.s.l. on a sloping fen just beneath the upper spruce timber line. The upper limit of *Myrica* in the Trondheim area is at 420 m a.s.l.

**DISCUSSION ON THE CLIMATE RELATING TO THE TRØNDELAG DISTRIBUTION**

All the known localities in the Trondheim area seem to occur where the mean annual precipitation exceeds 750 mm (DNMI 1982). If the mean July and tetratherm values recorded at the meteorological station at Voll (Table 1) are converted to 350 m a.s.l., the values obtained are 13.1°C and 10.8°C, respectively (Table 2). The corresponding mean January temperature is -4.7°C. The number of days with a snow cover at Voll (127 m a.s.l.) is on average 106.8, and at Øvre Leirfoss, Trondheim (70 m a.s.l.) it is 134 (Table 1). But the snow cover at 350 m a.s.l. in the Trondheim area lasts about 30 to 60 days longer than is reported at these two lowland stations, but varies according to topography and exposure.

As a basis for the remaining discussion, I will define the climatic altitudinal limit for common occurrence of *Myrica* in the Trondheim area as a July temperature of 13.1°C, a summer tetratherm of 10.8°C and a snow cover lasting 150 - 180 days (all average values).

As with the Holtålen localities of *Myrica*, I believe the winter air temperature is of little significance for the distribu-
tion in the Trondheim area because of the thick, stable snow cover. It is also difficult to see how the precipitation amount and/or frequency should significantly influence the vertical distribution of *Myrica* in this area, as it grows at lowland sites which receive a lower precipitation amount and frequency than the 350 m a.s.l. level and higher. But the increasing amount of precipitation with increasing altitude is a strongly contributing factor for the long-lasting snow cover in higher parts of the area.

How do the data from the Trondheim area agree with other isolated occurrences of *Myrica* in the Trøndelag region? At Berkåk in Rennebu (C in Figs. 1, 6 and 7), *Myrica* grows in topogenous to slightly soligenous fen vegetation at localities situated between 420 and 430 m a.s.l., e.g. at the small lake Buvatnet, where the species is growing at the southern and northern ends of the lake in exposed vegetation. But at the 500 m a.s.l. locality, *Myrica* is growing on a small southeast-facing sloping fen. All the localities lie within the boundaries of the spruce forest zone in the area.

The meteorological station at Berkåk (424 m a.s.l.) must be assumed to be representative for the climate where *Myrica* actually grows. Records show an annual precipitation of 782 mm, 169.1 days with precipitation > 0.1 mm, a July temperature of 13.1°C, a tetramerth of 10.7°C, and a snow cover lasting 170.6 days (all average values, see Table 1).

There is a strong similarity here with the climatic conditions at the upper limit for common occurrence of *Myrica* in the Trondheim area, especially as regards the summer temperature. The precipitation amount and frequency is undoubtedly lower than at the 350 m level there, but the period with a snow cover is probably about the same or slightly longer. It is also interesting that the Berkåk localities of *Myrica* at the 420 to 430 m level are not restricted to especially favourable habitats as regards wind protection and sun exposure, whereas the locality at the 500 m level has a favourable exposure.

If the meteorological stations at Selbu (197 m a.s.l.) and Stugudal in Tydal (615 m a.s.l.) are used as references (Table 1), and the summer temperatures there are converted to an altitude of 380 m a.s.l., which is the level for the highest known locality for *Myrica* in the Neadle area, a mean July temperature of 13.6°C and a mean tetramerth of 11.2°C is obtained. On the basis of the defined summer temperature limit for common occurrence of *Myrica* in the
Trondheim area, the potential summer climate limit for it is not reached in the Neadalven area. Future records of *Myrica* at higher altitudes than 380 m can therefore be expected in this area, if the summer temperature alone is considered decisive. As already mentioned, there exists an old record of *Myrica* in this area from a locality situated at about 700 m a.s.l. The meteorological station, Stugudal (615 m a.s.l.), should be representative for this locality. The mean July and tetratherm values measured there are 11.8°C and 9.4°C, respectively, when converted to the 700 m level. Those are almost exactly the same as the values calculated for the *Myrica* locality at 600 m in Holtålen.

If the summer temperatures calculated for the common upper limit of *Myrica* in the Trondheim area are converted to the area containing *Myrica* in the middle and inner parts of the Gauldalen area, the corresponding altitudinal limit there should lie at about 380 m a.s.l. Of the seven known occurrences of *Myrica* there, six are situated above 380 m a.s.l., and the seventh is at 320 m a.s.l. This last locality lies at the south end of the lake Haukdalsvatnet (NQ 64 85) where *Myrica*, according to T. Ouren (pers. comm. 1983), grows abundantly in topogenous/limnogenous mire vegetation. Of the localities situated above 380 m a.s.l. those northwest of Digre (NQ 84 84, 430 m a.s.l.) and northeast of Granåsvold (NQ 92 88, 550 m a.s.l.) face southeast, and the remaining four localities face south.

Bearing in mind the Berkåk locality at 500 m a.s.l., it is obvious that *Myrica* tends to occupy localities with a locally favourable summer temperature when it is found above 400 m in the southeastern parts of the Trøndelag region. The valley bottom mires in Holtålen at 265 to 320 m a.s.l. where *Myrica* is absent, should have a summer temperature that satisfies its demands.

According to Y. Mejland (field-cards 1942, herb. O), *Myrica* is found in Lierne (S in Fig. 7) at 4 localities, viz. Brandsfjellet (= Brandsfjellet, exact site unknown), Eidet (= Eide, VM 34 47), Sandmoen (VM 19 51/52) and Skutbakk (VM 30 56). Those localities define an altitudinal range from about 360 to 440 m a.s.l. for the species in Lierne. However, the Brandsfjellet locality may lie even higher. Temperatures measured at the meteorological station Nordli III (Table 1), converted to the 440 m level, give the following mean values: January -10.2°C, July 12.9°C, and the tetratherm 10.0°C. The same station records a mean snow cover of 148.9 days, and an annual precipitation of 991 mm. This implies that in Lierne *Myrica* is ex-
posed to a mean July temperature at or just below the "critical" value for the 350 m level in the Trondheim area, whereas the tetra-
therm is somewhat lower. The Lierne occurrences of *Myrica* are those among the Trøndelag ones which are exposed to the lowest winter

temperatures. As, however, the actual area carrying *Myrica* has much

snow and has a fairly lengthy snow cover, I find it hard to believe that the winter temperature should have a restricting effect upon

*Myrica* there.

When a "critical" summer temperature of 13.1°C (July) and

10.8°C (tetratherm) is postulated for the occurrence of *Myrica* in

the Trøndelag region, its extreme rarity on the island of Frøya, and

its restriction to pine-forested parts of the island of Hitra, can be rationaly explained. The meteorological station at Titran on

Frøya (6 m a.s.l., Table 1) gives a mean July temperature of 13.2°C,

and a tetratherm of 12.0°C. The corresponding values for Sandstad,

Hitra (22 m a.s.l., Table 1) situated on the relatively sheltered

southeastern part of the island, are 13.9°C and 12.3°C. For comparis-

son, the meteorological station at Moldstad on the island of Smøla

(Møre & Romsdal county) records values of 13.3°C and 11.8°C. Smøla,

like Frøya, lacks coniferous forests, and *Myrica* is recorded there

from only one place, where it probably was introduced by man (Høeg


These summer temperature values are all above the "criti-
cal" values defined for *Myrica* in the Trondheim area, and the actual

growing period is also longer because of the high temperature and

the thin snow cover during most of the winter. But it is reasonable
to assume that the strong and frequent winds which characterize the

naked coastal landscape of Frøya, Smøla and Hitra (above the pine-

forest limit) have a considerable cooling effect upon the ground

surface and the vegetation growing there during the summer. This

will not be revealed by measurements made by meteorological stations.

I believe it is unlikely that a mire and wet heathland species like

*Myrica* should be damaged by drought in a maritime area characterized

by high atmospheric humidity and high precipitation frequency. I thus

consider that the summer temperature in some way is also the most

likely climatic factor responsible for the rarity of *Myrica* on Frøya,

and for its restriction to the lowland, forested parts of Hitra.

A rational climatic explanation for the absence of *Myrica*
in the upper Forradal area in eastern Nord-Trøndelag, and the Momyra

and Nord-Fosen areas near the coast of Sør-Trøndelag remains to be
found. The meteorological station at Feren (405 m a.s.l., Table 1) situated at the eastern end of Lake Feren just east of upper Forradal, records a mean July temperature of 13.1°C and a tetratherm value of 10.5°C. The corresponding values recorded at Sulstua (Table 1), northeast of the area in question, are 12.9°C and 10.3°C when converted to 400 m a.s.l. Hence, the summer climate in the upper Forradal area - almost entirely situated above 400 m a.s.l. - does not wholly satisfy the demands of Myrica as defined for the Trondheim area. But the upper Forradal area contains so many local pockets of wind-protected and south-facing mire sites that Myrica should be expected to grow there in places, as in the Gauldalen area at corresponding altitudes. The length of the actual growing period may therefore be of some importance. Although the station at Feren (Table 1) does not record more than 952 mm annual precipitation, it is supposed by Moen et al. (1976:23) that the upper Forradal basin must have a larger annual precipitation than the Feren station. In any case, the snow cover is long-lasting in the area, and snow melting continues into June (Moen et al. 1976). Climate data for the Momyr and Nord-Fosen areas are given by Moen & Selnes (1979), and Selnes (1982). Summer temperatures are calculated from measurements made at the meteorological station Vallersund (Table 1), and results in the following values converted to the 100 m level: mean July temperature 13.2°C, and mean tetratherm 11.7°C, i.e. the "critical" 13.1°C and 10.8°C values for the 350 m level in the Trondheim area, are reached at very low altitudes, just about 100 m a.s.l. Too low summer temperatures can therefore explain the absence of Myrica from the Momyr and Nord-Fosen areas. But, in common with upper Forradal, why is Myrica not found in at least some mire pockets with a locally favourable summer climate, as it is in the Gauldalen area? Such pockets should be available.

The Momyr and Nord-Fosen areas are very wet, the meteorological station at Måmyr (250 m a.s.l.) reporting no less than 2047 mm as the mean annual amount (Table 1). The snow cover is also long-lasting (Selnes 1982). The length of the actual growing season may therefore also be a factor of importance in this district, i.e. it may be too short.
THE DISTRIBUTION IN NORWAY AND CLIMATIC CONDITIONS

The climatic conditions at the northern distribution limit in the counties of Nordland and Troms, on the northwestern coast, and at the inland limits in southeastern Norway are of particular interest for the discussion of the Norwegian distribution of *Myrica*.

The meteorological station at Bø (Table 1) should reflect very well the climate at one of the *Myrica* localities situated at the northern limit of its distribution in Norway (locality I in Fig. 7). The mean July temperature (13.1°C) and the tetratherm (10.9°C) there are almost exactly the same as those previously defined as being "critical" for the Trondheim area. Furthermore, the annual precipitation is about the same (953 mm) as in the Trondheim area, but the precipitation frequency is higher. Due to its coastal exposure and high winter temperature the snow-cover period is probably shorter at Bø than in the Trondheim area at the 350 m level, but no figures are available. The meteorological stations at Evenskjer and Sandsøy (Table 1) should reflect the summer climate prevailing at the two northernmost known localities on the islands of Rolla and Bjarkøy in the Vågsfjord area (J in Fig. 7). Evenskjer is situated just south of Rolla, and Sandsøy just north of Bjarkøy. The calculated average of the mean records at these two stations gives a July temperature of 13.0°C, and a tetratherm of 10.8°C. Evenskjer has a snow cover lasting 141.7 days, and Sandsøy 126.0 days. Both the summer temperature and the annual amount of precipitation are almost identical with conditions at the Berkåk locality (Table 1), but the snow-cover period is shorter, and the annual precipitation frequency somewhat less. The winter temperature is favourable. According to NORMANN (1982:158-159), *Myrica* on Rolla grows on the mire Årsandmyra in a margin community bounded by a forest of *Alnus incana* towards west and north. Only male plants are found, and the species covers an area of about 20 m².

The absence of *Myrica* from the exposed and mainly treeless Lofoten archipelago (Flatberg 1976) (K in Fig. 7), can be explained in the same way as its extreme rarity on the island of Frøya on the Trøndelag coast. The mean July and tetratherm values recorded at the meteorological stations at Sørvågen, Svolvær and Kvalnes (Table 1) clearly indicate a borderline district for the occurrence of *Myrica* in Lofoten as regards summer temperature. When the wind-exposed topography is also taken into consideration, it is understand-
able that *Myrica* is absent there, despite the humidity, winter temperature and length of the actual growing period being more favourable than further north in the Vågsfjord area.

In southeastern Norway, the northernmost known locality of *Myrica* is in Rendalen in the main valley of Østfold, on the large topogenous mire, Østamyra (250-260 m a.s.l.) east of the river Glomma (L in Fig. 7). According to Moen (1970:62, and pers. comm. 1983), *Myrica* grows abundantly at some places along the western side of the mire in fairly wet topogenous and oligotrophic fen sites, associated with species like Carex rostrata, C. limosa, Scheuchzeria palustris and Phragmites communis. *Rhynchospora alba* (at its known northern limit in southeastern Norway), and *Alnus glutinosa* (near its northern limit in southeastern Norway) were also found growing on this mire (Moen 1970).

The meteorological station, Ytre Rendal (Table 1) can be assumed to be representative for the macroclimate in Østamyra area. The mean July temperature is high (14.7°C), whereas the tetramertherm value is fairly low (10.8°C). The annual precipitation in the area is very low; the two stations Øvre Rendal (just north of Østamyra) and Åkrestrømmen (just south of Østamyra) record 440 and 455 mm respectively as an annual average. In the view of this, the precipitation frequency is surprisingly high (see Øvre Rendal, Table 1), and is comparable, for example with the figure recorded at the Voll station in Trondheim, and higher than at Berkåk. However, the snowcover period is shorter than at Berkåk, viz. 114.3 compared with 170.6 days. As the winter temperatures are very low (mean January temperature of -8.6°C at the Ytre Rendal station), and the snow cover is comparatively thin due to the low annual precipitation, *Myrica* must, in some years at least, be exposed to hard winter conditions at Østamyra. This strengthens the impression that *Myrica* is not specially sensitive to frost effects during its rest period in winter.

In the Trysil area (M in Fig. 7), *Myrica* is found at Mellåneset, Jordet, about 440 m a.s.l., and at Sør-Fugløsen (434 m a.s.l.) in mire vegetation surrounding the lake and on a small south-west-facing mire just east of the lake (470 m a.s.l.) (Nyhuus 1937: 43). *Rhynchospora alba* and *Lycopodium inundatum* were also recorded by Nyhuus (1937) at Mellåneset. Measurements at the meteorological station at Trysil (356 m a.s.l., see Table 1), converted to 470 m
a.s.l., give a mean July temperature of 13.7°C, and a tetratherm value of 11.2°C.

The data for snow cover and the amount and frequency of annual precipitation at the Trysil station are nearly the same as at Berkåk 68 m higher. The Trysil station records a lower mean January temperature than is known at any of the other Norwegian localities of Myrica with meteorological data available (-10.1°C, Table 1). But the fairly high annual precipitation amount, indicates the presence of a protecting snow cover during the winter.

If the "critical" 13.1°C (July) and 10.8°C (tetratherm) values for the 350 m level in the Trondheim area are used as basis for defining the climate limit for Myrica in the Trysil area, it should be found there up to about 570 m a.s.l. As mires and mire vegetation are very abundant between 470 and 570 m a.s.l. in Trysil, lack of suitable habitats cannot satisfactorily explain its absence. The actual length of the growing period, may therefore be postulated as a climatic factor which might prevent Myrica from occupying its potential summer temperature area in Trysil (compare the relatively long snow-cover period at the Trysil station, Table 1).

On the basis of the "critical" summer temperature defined for the Trondheim area, Myrica should be able to grow as far north as Alvdal and Tynset in the main valley of Østerdalen. Stormyra (475 m a.s.l., N in Fig. 7), between Alvdal and Tynset, closely resembles Østamyr in Rendalen in size, topography and vegetation. At the meteorological stations Alvdal (485 m a.s.l.) and Tynset II (483 m a.s.l.) average values of 13.4°C and 10.7°C are obtained for the mean July temperature and the tetratherm, respectively. These stations also report a snow-cover period almost identical to the Trysil and Berkåk stations (Table 1). An occurrence of Myrica at Stormyra should therefore theoretically be possible on the basis of the climatical parameters mentioned and when comparison is made with the behaviour of the species in the Trondheim area. However, Myrica as well as other coastal plants such as Lycopodium inundatum and Rhynchospora alba, are absent there (Singsetaas 1981). Stormyra should have about the same annual amount of precipitation as Østamyr in Rendalen, but the precipitation frequency is considerably lower, as is also the winter temperature (Table 1). As pointed out by Singsetaas (1981) the peat at Stormyra can some years be frostbound well into the early summer. Consequently, plants growing with their roots in partly frozen or strongly cooled peat will not fully benefit from
the favourable June air temperature. The snow-cover period is also longer in the Alvdal-Tynset area than in the Rendalen area (Table 1).

Another outlying district for *Myrica* in southeastern Norway is the Krødsherad, Sigdal, Flesberg area in Buskerud county (O in Fig. 7). Torbergsen (1980) reports *Myrica* to an altitude of 420 m a.s.l. in Krødsherad (Forsmyr, NM 46 66), and up to about 440 to 480 m a.s.l. in Flesberg (Svarttjern area, NM 37-39 37-38). According to a herbarium specimen (O, C), *Myrica* is found in Sigdal at a locality 430 m a.s.l. (Klampelia, NM 3 4). Torbergsen (1980) reports fairly topogenous and exposed mire sites as the habitat for *Myrica* at the localities mentioned in Krødsherad and Flesberg.

To estimate the summer temperature conditions at the Krødsherad locality, I have used the meteorological stations Nesbyen I/II (165 m a.s.l.), Åsen (369 m a.s.l.) and Modum (135 m a.s.l.) (Table 1). When averages from those three stations are converted to the 420 m level, a mean July temperature of 14.6°C and a tetratherm of 12.0°C is obtained (Table 2). This should allow *Myrica* to reach an altitude of 620 to 670 m a.s.l. in this district when comparison is made with the corresponding figures for the Trondheim area. As for precipitation, Grimeli at Krødsherad (367 m a.s.l.) reports a mean annual amount of 846 mm, which should be fairly representative for the Krødsherad locality of *Myrica*.

When the meteorological stations Kongsberg III (172 m a.s.l.), Knutehytta (717 m a.s.l.), Lyngdal (290 m a.s.l.) and Veggli (243 m a.s.l.) (Table 1) are used to estimate the summer climate at Flesberg, a mean July temperature of 14.3°C, and a tetratherm of 11.9°C at the 480 m level is obtained (Table 2). On the basis of the Trondheim area, *Myrica* should be found up to about 650-660 m at Flesberg. The Knutehytta station (717 m a.s.l.) actually records mean July and tetratherm values above the "critical" 13.1°C and 10.8°C values for the Trondheim area.

The snow-cover period at the station Lyngdal (290 m a.s.l.) is 138.0 days. It is not unlikely that the snow cover at about 500 m will last at least 14 days longer in this district. Mires are also common above 500 m at Flesberg. The apparent lack of *Myrica* in the main valley of Numedal is also interesting. At Flesberg on the valley floor, three mires situated at about 190 m a.s.l. were investigated by Torbergsen (1980), but all lacked *Myrica*, despite the pre-
sence of other coastal species such as *Drosera intermedia*, *Rhynchospora alba* and *R. fusca* (see later).

In Telemark county *Myrica* should theoretically be found up to at least 650 m a.s.l., when the summer temperature is considered and the meteorological stations at Vefall (68 m a.s.l.) and Dalen (77 m a.s.l.) are used as a reference. It is actually found up to 560 m a.s.l. at Tokke (ML 5 9; herb. O) (P in Fig. 7) and 541 m a.s.l. at Siljan (NL 3 8; field-card herb. O), and also has been reported from a locality at Vinje (NM 3 0) at 600 m a.s.l. (information from herb. O, but no herbarium specimen exists). I recorded *Myrica* up to 450-470 m a.s.l. on the mire complex Langemyr in Nissedal (ML 82-84 45-47) (Flatberg 1971). *Myrica* was also abundant here in exposed topogenous sites, and gave no impression of being at an outlying locality. *Drosera intermedia* and *Rhynchospora alba* were also found on the same mire, as well as many humidity-demanding species, like *Erica tetralix*, *Juncus squarrosus*, *Sphagnum strictum* and *S. angermanicum*. The precipitation in this area is high, and the Postmyr station in Drangedal (464 m a.s.l.) — where *Myrica* is actually growing — records an annual amount of 1138 mm. This also indicates a fairly long-lasting snow cover in the more elevated parts of the district.

An area in southeastern Norway where *Myrica* is not found, but where the summer temperature should satisfy its demands, is the main valley of Gudbrandsdalen (Q in Fig. 7) north of lake Mjøsa. As an example, the meteorological station at Vinstra (241 m a.s.l.) records a mean July temperature of 15.5°C and a tetratherm of 12.8°C. The corresponding values for the Vågåmo station (371 m a.s.l.), (Table 1) further north are 14.5°C and 12.0°C. A mean of these values gives a more favourable summer climate than, for example, at the *Myrica* locality in Rendalen. In addition, the snow cover lasts about as long in the two areas. The Gudbrandsdalen area differs from Rendalen mainly in having even less annual precipitation, lower winter temperatures, and especially a lower precipitation frequency (Table 1). However, the main valley of Gudbrandsdalen is generally poor in mires and mire vegetation, although suitable mires do exist, such as the mire complex Selbyrene (Sel, NP 2 5) situated at about 300 m a.s.l.

It was pointed out earlier that in Trøndelag *Myrica* mostly avoids naked coastal areas exposed to strong winds. This is not the case in outer parts of Hordaland county. There, *Myrica* is frequently
found on the ericaceous coastal heaths at Mongstad on the Lindås peninsula, where it appears in mire and moist heath vegetation exposed to westerly winds, although actually occurring most abundantly in sheltered depressions (own observations 1971, 1978, 1982). The meteorological station at Byrknesøy (7 m a.s.l.) just north of Mongstad, reports a mean July temperature of 14.3°C and a tetratherm of 13.0°C (Table 1). It therefore seems likely that along the western coast of Norway Myrica requires a higher atmospheric summer temperature in places exposed to wind than in sheltered localities. The "exposed" limit there seems to be fairly well correlated with a mean July temperature of about 14.0°C.

THE FENNOSCANDIAN DISTRIBUTION AND CLIMATIC CONDITIONS

The meteorological stations of Sunderbyn, Högsön, Heparanda and Kemi (Table 1) can be used to estimate the climate at the northern limit of Myrica around the Bothnian Bay (T in Fig. 7). When the mean temperatures at these stations (see Laaksonen 1979a) are converted to sea level and to 100 m a.s.l., a mean January temperature range of -9.6°C to -11.1°C, a mean July temperature range of 16.2°C to 15.6°C, and a tetratherm range of 12.3°C to 11.8°C is obtained; these temperature ranges should give a representative picture of the macroclimate under which Myrica is found growing in the area. According to Elveland (1976:150-151), winters poor in snow cause a layer of frozen peat to last far into the summer on the mires in the Bothnian Bay area. The northern limit of Myrica around the Bothnian Bay coincides well with the isopleth for a continuous snow cover of 180 days (Hultén 1971:42, 150). The annual amount of precipitation varies between about 400 to 600 mm in the area of Myrica distribution in the Bothnian Bay (see e.g. Sjörs 1965:10, Kalliola 1973:62).

The northern limit in the southern, inland half of Finland ("the lake region"), corresponds fairly well with a mean July temperature between 16.5°C and 17.0°C, and a tetratherm between about 14.0°C and 14.5°C (Kalliola 1973, Laaksonen 1979a; see also the meteorological stations Tampere (V), Kuopio (W) and Joensuu (X) in Table 1 and Fig. 7). Myrica has not been found in districts with a mean January temperature below -10°C (Kalliola 1973:60). No correlation exists between the various January isotherms and the northern limit of Myrica in "the lake region" of Finland, nor between the
Myrica distribution and the precipitation in Finland (Kalliola 1973:62, Tuhkanen 1980:79-80). At the northern limit in "the lake region", Myrica is not found in districts with a mean annual precipitation below 550 mm (Kalliola 1973:62). This contrasts with its occurrence at several places along the coastal strip adjacent to the Gulf of Bothnia where the annual precipitation is below 550 mm (see e.g. Sjörs 1965:10). But it should be emphasized that the immediate surroundings of the Gulf of Bothnia have a more maritime climate than further inland.

The northern limit of Myrica around the Bothnian Bay coincides well with the isopleth for a continuous snow cover of 180 days (Multén 1971:42, 150). According to BjörkBäck, Stockholm (in litt. 1983), Myrica in Jämtland county, Sweden, has its westernmost locality at Offerdal (Y in Fig. 7), where it is found growing at lake Groningen (63°25'N, 14°05'E, 330 m a.s.l.). This locality is also the upper altitudinal limit for Myrica in Jämtland.

The mean temperatures at the meteorological station at Östersund (Table 1) - which should be representative for the climate in central parts of Jämtland - give a January temperature of -10.1°C, a July temperature of 14.3°C, and a tetratherm of 11.2°C, when converted to the 330 m level. The snow cover in the area concerned lasts about 180-200 days, and the annual precipitation is about 500 mm (Sjörs 1965:10-11).

SYNOPTICAL DISCUSSION

It is a well-known phenomenon among several vascular plants that the July temperature necessary for their presence is higher in a continental area with a low winter temperature than in an atlantic area with a higher winter temperature (see e.g. Iversen 1944, Hintikka 1963). This has commonly been attributed to the presence of a longer growing period in atlantic than in continental areas, which enables a plant to succeed in accumulating the energy necessary for completing its growth even though the summer temperature is lower. The apparent increasing demand of Myrica for, especially, a more favourable July temperature seen when its distribution is traced eastwards from western parts of Norway to Finland, could therefore be thought to reflect this behaviour. If so, one should expect the accumulated summer heat during the growing period to be nearly the
same at all outlying localities of *Myrica* in Fennoscandia. However, when the Fennoscandian distribution of *Myrica* is compared with the isopleths for respiration units, as defined and calculated by Skre (1979) on the basis of the behaviour of spruce (*Picea abies*), it is seen that *Myrica* does not behave in this manner. The distribution of *Myrica* along the western coast of Norway mainly coincides with the isoline of the 4 respiration units, but the high occurrences situated near the upper timber line of spruce in Gauldalen coincide with the isoline of the 3 respiration units. In southeastern Norway, Sweden and the Gulf of Bothnia area, the distribution of *Myrica* mainly follows the isoline of the 5 respiration units. However, in inland areas of Finland the distribution fits the isoline of the 6 units better.

The same trend is also seen when the known distribution limits for *Myrica* are related to ETS-values (the effective temperature sum of the vegetative period, denoting the number of days with a mean temperature of 5°C or more) as defined and calculated by Laaksonen (1979b). The ETS-values corrected to the actual levels for outlying localities of *Myrica* in Fennoscandia, are given in Table 2.

There exists good conformity in ETS-values between the northernmost localities in Norway, the 350 m level in the Trondheim area, and the Berkåk localities at the 420–430 m level. But the ETS-values at some of the outlying localities in southeastern Norway, Jämtland and the Bothnian Bay area are considerably higher. Inland parts of Finland have the highest values. The values at the outlying localities on the islands of Frøya and Hitra are also high. The lowest value (585) is held by the outlying localities in Lierne (440 m a.s.l.) and Holtålen (600 m a.s.l.) in Trøndelag. The same is also seen for Sweden and Finland when the *Myrica* distribution is compared with isopleths for potential evapotranspiration (PE) (Tuukkanen 1980:77). The Jämtland and Bothnian Bay limits of *Myrica* coincide with the 420 to 430 mm PE isopleth, whereas "the lake region" limit in Finland partly fits the 460, partly the 480 mm isopleth.

The seemingly different behaviour of *Myrica* with respect to demands for summer warmth in Fennoscandia during the growing period can be explained in several ways: (1) It consists of different ecotypes with dissimilar climatic demands. (2) Some climatic parameter other than the summer temperature, (a) defines its distributional limits in eastern Fennoscandia, or (b) affects the potential growing habitat in such a way that *Myrica* is not able to effectively
Table 2. The mean air temperature and ETS values (see text and Laaksonen 1979a,b) at some outlying localities or districts for Myrica gale L. in Fennoscandia. The values quoted or calculated derive from recordings made at those meteorological stations which are presumed to be the most representative ones in each case; the figures given are approximate (see text and Table 1).

<table>
<thead>
<tr>
<th>Locality/district</th>
<th>Kind of limit</th>
<th>Altitude (m a.s.l.)</th>
<th>January (°C)</th>
<th>July (°C)</th>
<th>Tetratherm (°C)</th>
<th>ETS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vågsfjord, Troms county</td>
<td>northern</td>
<td>&lt;50</td>
<td>-2.6</td>
<td>13.0</td>
<td>10.8</td>
<td>750</td>
</tr>
<tr>
<td>Bø, Nordland county</td>
<td></td>
<td>&lt;50</td>
<td>-1.0</td>
<td>13.1</td>
<td>10.9</td>
<td>762</td>
</tr>
<tr>
<td>Lierne, Nord-Trøndelag county</td>
<td>altitudinal</td>
<td>440</td>
<td>-10.2</td>
<td>12.9</td>
<td>10.0</td>
<td>585</td>
</tr>
<tr>
<td>Trondheim, Sør-Trøndelag county</td>
<td>absolute alt.</td>
<td>420</td>
<td>-5.2</td>
<td>12.7</td>
<td>10.4</td>
<td>692</td>
</tr>
<tr>
<td>Berkåk, Sør-Trøndelag county</td>
<td>absolute alt.</td>
<td>350</td>
<td>-4.7</td>
<td>13.1</td>
<td>10.8</td>
<td>743</td>
</tr>
<tr>
<td>Holtålen, Sør-Trøndelag county</td>
<td>altitudinal</td>
<td>500</td>
<td>-6.9</td>
<td>12.6</td>
<td>10.2</td>
<td>666</td>
</tr>
<tr>
<td>Frøya, Sør-Trøndelag county</td>
<td>western</td>
<td>450</td>
<td>-6.7</td>
<td>13.1</td>
<td>10.7</td>
<td>704</td>
</tr>
<tr>
<td>Hitra,</td>
<td>altitudinal</td>
<td>600</td>
<td>-6.7</td>
<td>11.8</td>
<td>9.5</td>
<td>585</td>
</tr>
<tr>
<td>Trysil, Hedmark county</td>
<td>altitudinal</td>
<td>500</td>
<td>-0.5</td>
<td>13.3</td>
<td>11.7</td>
<td>920</td>
</tr>
<tr>
<td>Rendal,</td>
<td>northern</td>
<td>470</td>
<td>-10.8</td>
<td>13.7</td>
<td>11.2</td>
<td>791</td>
</tr>
<tr>
<td>Krødsherad, Buskerud county</td>
<td>altitudinal</td>
<td>255</td>
<td>-8.6</td>
<td>14.7</td>
<td>10.8</td>
<td>933</td>
</tr>
<tr>
<td>Flesberg,</td>
<td>northern</td>
<td>420</td>
<td>-8.3</td>
<td>14.6</td>
<td>12.0</td>
<td>887</td>
</tr>
<tr>
<td>Tokke, Telemark county</td>
<td>northern</td>
<td>480</td>
<td>-6.2</td>
<td>14.3</td>
<td>11.9</td>
<td>877</td>
</tr>
<tr>
<td>Jämtland county</td>
<td>western, alt.</td>
<td>500</td>
<td>-6.1</td>
<td>13.3</td>
<td>11.3</td>
<td>845</td>
</tr>
<tr>
<td>The Bothnian Bay</td>
<td>northern</td>
<td>330</td>
<td>-10.1</td>
<td>14.3</td>
<td>11.2</td>
<td>830</td>
</tr>
<tr>
<td>Finland, &quot;lake district&quot;</td>
<td>northeastern</td>
<td>100</td>
<td>-8-11</td>
<td>16.5</td>
<td>13.5</td>
<td>1065-1170</td>
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</table>
utilize the warmth sum available during the growing period, and as defined above on the basis of atmospheric temperatures. (3) It has not yet managed to occupy its potential summer climate area all over Fennoscandia.

Only cultivation and laboratory experiments can say whether there exists Myrica ecotypes adapted to different climates, so this will not be further commented on in this context.

As mentioned previously, mires situated in relatively continental areas where low winter temperatures are combined with a fairly thin snow cover often experience a protracted period of frozen ground after the snow has gone. The vascular plants growing there will therefore not be able to benefit fully from the atmospheric temperatures acting there during the early summer, i.e. they will need a higher ETS during the growing period to complete their growth than plants in areas where the peat is not frozen or where it thaws just after the snow goes in spring. It may also be suggested that Myrica requires a higher temperature in the close surroundings of its roots for initiation of vegetative growth than many other mire plants, since it is partly dependent on the activity of nitrogen-fixing bacteria living in symbiosis on its roots (Bond 1951). However, the temperature threshold for biotic activity in Myrica is, I believe, unknown. The retarding effect of ground frost upon growth during early summer, can, however, not be disregarded as an important factor when attempting to explain the apparent higher demand for summer warmth in continental than in more maritime areas of Fennoscandia. In a continental area with hard winters, Myrica may also have to use more energy during the summer to produce frost-resistant shoots and buds than in an oceanic area with mild winters. But it is difficult to see why these factors should cause Myrica to demand more summer warmth in the inland parts of Finland than in the area near the Bothnian Bay area. The favourable autumn temperature in the Bothnian Bay area (see Elveland 1976:17-18) - caused by the maritime effect of the Baltic Sea - may compensate better for the growth-retarding effect of the frozen soil during early summer than in inland parts of Finland. However, it is doubtful whether this factor alone can explain the different behaviour of Myrica in those two areas (see later).

The high ETS-values at the Myrica limit on the islands of Frøya and Hitra, can be explained in the way previously outlined,
i.e. the frequent and often strong winds prevailing there, reduce the effect of the available summer heat.

As already mentioned, there are good reasons for believing that *Myrica* requires a certain minimum length of the growing period, and that this seems to be at least partly independent of the summer temperature, provided this exceeds a certain lower threshold value. In most outlying districts for *Myrica* in Fennoscandia the actual length of the growing period is not determined by threshold values in the air temperature being exceeded, but by the length of the snow-free period.

To clarify this problem, some mire and wetland species with a similar distribution to *Myrica* in Fennoscandia, viz. *Alnus glutinosa*, *Lycopodium inundatum*, *Rhynchospora alba* and *R. fusca*, will be discussed. Contrary to *Myrica* all these species show distribution limits in Fennoscandia that by and large reflect an equal energy demand with regard to summer heat. Their distribution (see Hultén 1971) mainly corresponds with the isoline of 5 respiration units (Skre 1979) throughout Fennoscandia, but with a trend which shows that *A. glutinosa* and *R. alba* are somewhat less demanding in northeastern Fennoscandia than elsewhere. This means that these species in part penetrate much further north in northeastern Fennoscandia than *Myrica*, whereas along the western coast of Norway their behaviour is the opposite, i.e. they apparently demand more summer warmth than *Myrica*. This is also supported by the fact that in Trøndelag *Myrica* is found higher than any of these fours, especially *A. glutinosa*. They all lack on Freya, where *Myrica* grows.

The different distribution of these four species in northeastern Fennoscandia compared with *Myrica* is, as far as the climate is concerned, likely to indicate either (1) they manage with a shorter growing period than *Myrica*, or (2) they are less sensitive to low winter temperatures.

As previously mentioned, *Myrica* is not found in areas with a mean January temperature below -10°C to -11°C. It may therefore have a frost damage limit in some districts in northeastern parts of Fennoscandia. Such a limit will not be solely dependent on the air temperature during the winter, but will also be influenced by the thickness of the snow cover, which again depends on the annual precipitation and how much of it falls as snow.

If the length of the growing period is the factor which prevents *Myrica* from occupying its potential summer climate area
north of the Bothnian Bay area, its limit there corresponds well with a continuous snow cover of about 180 days (Table 1). The duration of the snow cover at the Trysil meteorological station (Table 1), indicates a similar figure at the *Myrica* localities there. At the westernmost of the Jämtland occurrences of *Myrica* (see previously), the snow-cover period lasts about 180 to 200 days. However, in all of those three isolated *Myrica* occurrences a snow-cover period of about 180 to 200 days coincides with a mean January temperature of about -10°C to -11°C. It is therefore difficult to decide which of the two factors is most decisive for *Myrica* in each case. However, in Trysil the winter temperature can be assumed to be of less importance than the length of the snow-cover period since the fairly high annual precipitation there (Table 1) compared with Central Jämtland and the Bothnian Bay area, suggests a better protective snow cover during winter. What can be said with some certainty is that precipitation conditions are unlikely to determine the western and altitudinal limits of *Myrica* in Jämtland, because both the precipitation amount and its frequency increase considerably towards the Norwegian border.

The mean January temperatures calculated for the highest occurrences of *Myrica* in Buskerud and Telemark counties (Table 2) are, however, not so extreme as those in Trysil, Jämtland and the Bothnian Bay. At the same time the fairly high annual precipitation in Buskerud and Telemark (Table 1) indicates a thick, protective snow cover during winter. I can therefore see no climatic factor other than the length of the snow-cover period which is likely to prevent *Myrica* from ascending to higher altitudes than it does in these counties.

In this connection, the vertical distribution of the mire species *Drosera intermedia* in Buskerud and Telemark is of some interest as it mostly reaches the same altitude as *Myrica* (about 450-500 m a.s.l., own observations 1970, see also Flatberg 1971:60 and Torbergsen 1980:44). Along the western coast of Norway (see Skogen 1979 for the Norwegian distribution) this species undoubtedly demands more summer heat than *Myrica*, and is never found as high as that. This behaviour is also reflected by the horizontal Fennoscandian distribution of *D. intermedia* (see Hultén 1971) which largely corresponds with the isoline for the 6 (or perhaps better, the 5 to 6) respiration units (Skre 1979). Furthermore, when compared with the upper timber line for spruce in the two counties, which lies at about
900 to 1000 m a.s.l. (compare the Holtålen localities of *Myrica* at the upper timber line for spruce there), it is obvious that *D. intermedia* occupies its potential summer climate area (in a vertical sense) in these mentioned counties, whereas *Myrica* does not.

If a mean January temperature of about -10°C defines a frost-damage limit for *Myrica* with a thin snow cover, this may explain the absence of *Myrica* from the main valley of Gudbrandsdalen which is characterized by a very low annual amount of precipitation, a comparatively short snow-cover period, and a mean January temperature of about -9 to -10°C (Table 1). But the absence of *Myrica* from the mires lying in the valley bottoms at, for example, Numedal, and Holtålen in Gauldalen, is not satisfactorily explained in this way. The winter temperatures are not so extreme there, and the larger amount of precipitation indicates a better protective snow cover. As all these valley areas (Gudbrandsdalen, Numedal and Gauldalen) have a relatively short snow-cover period, it may be suggested that its absence there is the result of a frost-damage effect during late spring and early summer after the snow has gone, and caused by frosty nights due to temperature inversions. The frost resistance of *Myrica* during that period is, however, unknown.

Against this hypothesis it can be argued that *Myrica* grows in Rendalen, which has a snow-cover period identical to that of Gudbrandsdalen and where temperature inversions are equally likely to occur. The difference in climate between Rendalen where *Myrica* is growing, and Gudbrandsdalen where it is not, is on the whole small (Table 1). The most striking difference lies in the precipitation frequency, which is considerably higher at Rendalen. This factor may be of importance. *Alnus glutinosa* ogd *Rhynchospora alba* also grow along with *Myrica* at Østamyra in Rendalen, and like it they also avoid the Gudbrandsdalen area.

Hence it follows, that the very low amount of precipitation - and especially the precipitation frequency - in combination with a high summer temperature can be of importance when an explanation is being sought for the absence of species like *A. glutinosa*, *Myrica* and *R. alba* from the Gudbrandsdalen area. It should also be emphasized that *A. glutinosa* and *R. alba* are found growing in north-eastern Fennoscandia with considerably colder winters than Gudbrandsdalen. It is difficult to see that such a factor as combined precipitation and summer temperature should be responsible for the northern limit of *Myrica* in "the lake region" of Finland. The sum-
mer temperature gradually decreases north of the *Myrica* limit, whereas the annual amount of precipitation in many districts is unaltered from that further south, where the species is growing (Kalliola 1973: 60, 62). One such district is Kuhmo in Ostrobotnia Kajanensis, the only place where *Erica tetralix* is found in Finland (Mäkinen and Tiikkainen 1966). But it should be emphasized that the numerous lakes in "the lake region" result in many favourable humid niches which may moderate the effect of the high summer temperatures there.

The restriction of *Myrica* to a narrow atlantic zone in mainland Europe south of Fennoscandia (for distribution, see Jalas and Suominen 1976:52) can, however, be rationally explained in terms of the combined climatic factor outlined. The eastern limit of *Myrica* there is not found to correlate with any particular precipitation parameter, but it coincides fairly well with the mean July isotherm of 18°C, except for the humid and precipitation-rich western coasts of Portugal and Spain where the eastern limit is better correlated with a mean July isotherm of 20°C, (for climate maps, see Størmer 1969). It thus seems as if *Myrica* endures a high summer temperature better in an area with high local atmospheric humidity.

The position of the *Myrica* limit in southern Finland is not in itself exceptional, as several summer-warmth demanding species have a similar limit, e.g. *Acer platanoides*, *Tilia cordata* and *Drosera intermedia* (Hultén 1971). The *Myrica* limit is also largely parallel to the boundary between the southern and middle Boreal phytogeographical zones of Ahti et al. (1968). As shown by Tuhkanen (1980), several climatic isopleths concerned with temperature parameters also coincide with this limit. The problem is that the *Myrica* limit in the Bothnian Bay area mainly follows the boundary between the middle and the northern Boreal zones, and species showing a similar distribution limit in southern Finland do not occur so far north in that area. It is therefore difficult to find a rational climatic explanation for the *Myrica* limit in southern Finland.

The conclusion may be drawn that, as far as the climate is concerned, the distribution limits of *Myrica* in Fennoscandia may be determined by several factors. Which factor or factors are decisive in each case seems to vary regionally. Concerning the summer temperature, there seems to be both a lower and an upper limit. Judging from the behaviour of *Myrica* in western Norway, a lower temperature limit there corresponds with a mean July temperature of about 13.0°C to 13.1°C, and a tetratherm for the four months from June to Septem-
ber of just under 11.0°C. This lower limit also corresponds with an ETS-value (in the sense of Laaksonen 1979b) lying between 700 and 770. It is, however, reasonable to assume that this lower summer temperature limit must lie somewhat higher in continental areas with a low winter temperature and a thin snow cover, due among other things to the frozen-ground effect in early summer. But as the ETS-values for the growing period are in part considerably higher at all the outlying occurrences of Myrica in eastern Fennoscandia than usually is the case in the western parts, other factors than certain threshold values for the summer temperature being exceeded, must be responsible for its horizontal and vertical limits there. A possible upper summer temperature limit will be dependent on precipitation conditions. Its absence from the Gudbrandsdalen area may, for example, be correlated with a climatic limit corresponding to a mean July temperature of about 15.0°C - 15.5°C and a mean annual precipitation of about 400 mm, perhaps also a precipitation frequency of about 140 days (Table 1).

If this is so, the presence of Myrica in the Bothnian Bay area, and several other places along the Baltic coast of Sweden with an annual precipitation under 500 mm and a mean July temperature of 16.0°C to 17.0°C, can be explained in terms of the local maritime climate. The actual length of the growing period as a delimiting factor for Myrica corresponds with a continuous snow-cover period of about 170 to 200 days.

A possible critical winter temperature for Myrica is likely to be a mean January temperature of about -10.0°C to -11°C, provided the snow cover is fairly thin.

A climatical explanation is still required for the high Myrica occurrences in the Trøndelag region, which are beyond the lower limit defined on the basis of the summer macrotemperatures. This is especially the case with the high-occurrences in the inner parts of the Gauldalen area. As previously mentioned, all the known localities of Myrica at altitudes above the "critical" climatic limit in Gauldalen (about 380 m a.s.l.) have a favourable south or south-eastern exposure. Moreover, the two highest localities in Holtålen at 590 and 600 m, are also well protected against winds. Hence, it is not unreasonable to suggest that a favourable local climate compensates for the inadequate macroclimate at these localities. Such mire niches with a favourable local summer climate are common in the pre- and subalpine districts of inner Gauldalen. In the case of Myrica,
the problem that arises is to find such niches which at the same time have a sufficiently long growing period, i.e. where the snow cover does not last too long. As earlier mentioned, the snow-cover period at one of the Holtålen localities is likely to be less than 200 days (see p. 15).

The occurrence of *Myrica* at 460 m a.s.l. in Lierne, at a locality which also does not have a summer macrotemperature which satisfies its requirements and which has the same calculated ETS-values as at the 600 m level in Holtålen (Table 2), is a support for the assumption made above. The continuous snow-cover period at the 400 m level (see Nordli III, Table 1) is just under 160 days, i.e. favourable summer-warmth niches with a sufficiently long growing period for *Myrica* are likely to occur. It is therefore possible to give a rational climatic explanation for the highest occurrences of *Myrica* in inner parts of Gauldalen and elsewhere in Trøndelag.

It should also be emphasized, that many lowland plants reach fairly high altitudes in inner parts of the Gauldalen area. For instance, *Eriophorum latifolium* reaches 800 m a.s.l., *Anemone nemorosa* 850 m a.s.l. (Ouren 1961), and *Campanula latifolia* 720 m a.s.l. (Ouren 1966:41). Furthermore, *Juncus effusus* reaches 610 m a.s.l. in Holtålen, and is there at its eastern limit in the Gauldalen area (Ouren 1966:44). According to Lid (1974), *J. effusus* is found up to about 600 m a.s.l. in Norway, and its Fennoscandian distribution is not unlike that of *Myrica* (Hultén 1971).

The prehistory of *Myrica* in the pre-alpine districts of inner Gauldalen is unknown. The scattered distribution pattern in favourable climatic niches may indicate a formerly more continuous distribution, with only relics being left at present in the most favourable niches. The occurrence of only male plants at the three separate stands of *Myrica* at locality B in Holtålen (Fig. 1), undoubtedly can indicate a formerly more continuous distribution in this area. *Myrica* frequently grows in large stands of either all male or all female plants, and according to Lloyd (1980) male plants are found in Wales about twenty times more frequently than female ones.

If *Myrica* was present in the Gauldalen area during part of the postglacial climatic optimum, it should not be difficult to obtain support for a relic theory. However, although there is pollen-analytical evidence for the presence of *Myrica* in some southern and southwestern districts of Norway as early as the transition between the Atlantic and the sub-Boreal periods - perhaps even earlier
(see Danielsen 1970:35, Pl. 3; Eide & Faus 1982, Fig. 5, p. 31), its marked expansion in southern Norway evidently did not take place before late sub-Boreal and early sub-Atlantic time (see e.g. Hafsten 1965, Danielsen 1970). I have not been able to trace any published pollen diagrams containing *Myrica* from Central or North Norway, North Sweden or Finland. However, this does not prove its former absence there as *Myrica* pollen is not always distinguished from *Corylus avellana* pollen in stratigraphic analyses. According to S. Selvik (pers. comm. 1983) *Myrica* pollen is recorded in a stratigraphic profile performed on peat from Lierne in Nord-Trøndelag, in the same area as the species is known to grow at present (see p. 24). It is, however, only found in the uppermost 5 cm of the profile, which clearly indicates a fairly recent arrival there.

The rarity of *Myrica* in lowland districts east of Trondheimfjorden in Nord-Trøndelag (Fig. 6), may reflect a late sub-Atlantic immigration to the Trøndelag region. From climatic and edaphic points of view, it is quite inexplicable that the species is so extremely rare in these districts. It is therefore reasonable to suggest that *Myrica* has not yet been able to occupy its potential summer-climatic area there. In this respect, Trondheimfjorden as a barrier, may have been an obstacle for effective dispersal. The fairly common occurrence of *Myrica* in areas south-east of Trondheimfjorden and its occurrence in Lierne to the northeast, may simply reflect immigration routes lacking significant dispersal barriers. Another coastal species, *Erica tetralix*, behaves in the same manner in eastern parts of the Trøndelag region. It is very common in places in the pre- and subalpine districts southeast of Trondheimsfjorden, but has been sought after in vain in the corresponding, and even more humid, eastern districts of Nord-Trøndelag (e.g. in the upper Forradal area, see Moen et al. 1976).

The possible dispersal of *Myrica* by man has so far been left out of consideration. Before the extracts of *Humulus lupulus* came into common use, *Myrica* was an important taste-contribution ingredient of home-made beer (Schüeber 1886, Hofsten 1960, Nordland 1969). It was also used for other purposes, for example, to combat moths in clothes. Names like "Postmyra" ("the *Myrica* mire") and "Postskogen ("the *Myrica* forest"), which also occur in the Gauldalen area, are excellent testimonies to those activities (see Ouren 1961, 1973). Høeg (1974:458) mentions that *Myrica* was collected at Haukdalsvatn in the Gauldalen area (p. 23) for beer production as late
as 1860-1870. Undoubtedly, many localities of *Myrica* were well known by our ancestors.

I have not succeeded in tracing old people who have been aware of the occurrence of *Myrica* at locality A in Holtålen (Fig. 1). But it should be emphasized that this locality - although it may look very remote at present - is in a mire-rich area that was previously intensively exploited for haymaking purposes. A deliberate introduction by man can, therefore, not be wholly excluded. The local historian and keen amateur botanist H. Kosberg, Ålen, has informed me (in litt. 1983) that he has not succeeded in tracing any tradition concerning *Myrica* with regard to locality B (Fig. 1) in Holtålen.

If *Myrica* was introduced by man into the inner parts of Gauldalen, it is also somewhat surprising that the localities known there at present, with one exception, are all situated in climatically-favourable south or southeast-facing sites. Furthermore, if they were planted at pre-alpine localities, why not also at mire sites in the main valley bottom (e.g. in Holtålen), where the species would be more available for its purpose? But such localities may be lost at present due to an unfavourable climate. Still I am inclined to believe that the Gauldalen localities of *Myrica* are spontaneous, but only detailed paleo-ecological investigations can clarify its pre-history there in detail.

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REFERENCES


DNMI 1973. Døgnets normaltemperaturer i Skandinavia i juli måned (map in scale 1:4 000 000).


