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KJELL IVAR FLATBERG

Taxonomy, morphovariation, distribution and ecology of the *Sphagnum Imbricatum* complex with main reference to Norway

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ERRATA

Page 20	Text Fig. 8, line 2: "corcles" should be "circles".
Page 23	Text Fig. 9, line 3 from bottom: "species" should be "apices".
Page 38	Line 11 from bottom: "seemd" should be "seemed".
Page 59	Line 12: "$p<0.1\%$" should be "$p<0.001\%$".
Page 65	Line 19: "thrugh" should be "through".
Page 77	Line 18: "much more undulating the" should be "is much more undulating and the"
Page 81	Line 5 from bottom: "is concerned" should be omitted.
Page 82	Line 9 from bottom: "easily" should be "sometimes".

TAXONOMY, MORPHOVARIATION, DISTRIBUTION AND ECOLOGY OF THE *SPHAGNUM IMBRICATUM* COMPLEX WITH MAIN REFERENCE TO NORWAY

by

Kjell Ivar Flatberg

University of Trondheim, The Museum

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ABSTRACT

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The study deals with the Sphagnum imbricatum complex in Norway. Two taxa are distinguished at the subspecific level, viz. S. imbricatum Hornsch. ex Russ. ssp. austinii (Sull.) Flatb. and ssp. affine (Ren. & Card.) Flatb. Their taxonomical interrelationships are reviewed, and the Norwegian distributions are mapped. A survey of the most common plant communities occupied by the two taxa is presented, and the local and regional distributions are discussed in relation to habitat preference and environmental factors.

Morphovariational trends are studied with the aid of herbarium, mixed-stand and unmixed-stand material, and by transplantation and cultivation experiments. Current leaf dimorphism is demonstrated in ssp. affine. Comments are included on the palaeobotanical history of S. imbricatum in Europe.

Kjell Ivar Flatberg, Department of Botany, University of Trondheim, N-7055 Dragvoll, Norway.

* Botanical Series No 15.

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ABSTRACT

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Kjell Ivar Flatberg, Department of Botany, University of Trondheim. N-7055, Dragvoll, Norway.

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[1] Botanical Series No 19.

CONTENTS

TAXONOMY

In a previous paper (Flatberg 1984), I have outlined the taxonomy of the *Sphagnum imbricatum* complex, which globally consists of two separate species, viz. *S. portoricense* Hampe and *S. imbricatum* Hornsch. ex Russ. The former is endemic to atlantic parts of Central and North America (Andrus 1974), whereas the latter has a disjunct circumpolar distribution in the northern hemisphere.

Sphagnum imbricatum is polymorphous, and 3 infraspecific taxa can be separated at the subspecies level, viz. ssp. *imbricatum* restricted to eastern Asia, ssp. *austinii* (Sull.) Flatb. to the pacific and atlantic coasts of North America and to western Europe, and ssp. *affine* (Ren. & Card.) Flatb. which is amphiatlantic and confined to western Europe and eastern North and Central America. Ssp. *affine* is represented by two mainly substituting varieties, viz. var. *flagellare* (Roell) Flatb. which is confined to Europe and northern parts of atlantic North America (mainly Canada), and var. *affine* confined to atlantic parts of North and Central America. Also ssp. *austinii* exhibits some morphological variation related to regional aspects. Var. *arcticum* Flatb. is restricted to tundra areas of arctic and subarctic North America and adjacent parts of Asiatic Russia. The world distributions are mapped and further commented on in Flatberg (1984).

In Norway (and Europe) *S. imbricatum* is represented by ssp. *austinii* var. *austinii* and ssp. *affine* var. *flagellare*. In Europe the two taxa largely behave as distinct species separated by several morphological characteristics, and seemingly do not overlap genetically. The morphological peculiarities of the two European taxa are summarized in Table 1, and some of them are illustrated in Figs. 1-4.

The morphology and ecology of the two taxa in Fennoscandia have been commented on by Malmer (1962a:65-66, 1966:5-6) and Vorren (1972:8). Those workers distinguished between a "bog" and a "fen" type of *S. imbricatum*, which no doubt correspond to ssp. *austinii* and ssp. *affine*, respectively, judging from the information given by them and the material I have

Table 1. The main morphological characteristics distinguishing *Sphagnum imbricatum* ssp. *affine* and ssp. *austinii* in Europe.

Taxon	ssp. *affine* (var. *flagellare*)	ssp. *austinii* (var. *austinii*)
Habit	shoots in lax mats	shoots in densely compact cushions
Colour	green to usually yellowish brown	dark rustbrown
Number of pendent branches in each fascicle	usually 2-3	usually 1
Comb-lamellae in upper part of stem leaves	absent	pronounced
Comb-lamellae in branch leaves	few and often obscure in upper part, distinct in lower part except in wet-growing ecads	numerous and densely arranged throughout
Hyalocyst septae in upper third marginal part of stem leaves	several cells usually septated in 2-4(6) parts	only a very few cells usually septated in 2 parts
Inner stem cortical comb-lamellae	very pronounced, except in rare wet-growing ecads	absent
Circular pores in the mid and upper half of median cc part of branch leaves	absent	a few pores present except in rare wet-growing ecads
Stem leaf shape	broadly spathulate	mostly narrowly spathulate
Branch leaf shape	broadly ovate to semicircular	mostly narrowly ovate to ovate-elliptical

examined. Lid (1925), in his account of Sect. *Sphagnum* (his *Cymbifolia* group) in Norway, did not mention the existence of the two taxa as outlined above, nor did Isoviita (1966) or Nyholm (1969).

In the following text, the subspecific epithets are mainly left out, i.e. *affine* means ssp. *affine* var. *flagellare*, and *austinii* means ssp. *austinii* var. *austinii*.

The nomenclature for vasculars follows Lid (1974), *Bryopsida* mainly Nyholm (1954-1969), *Sphagnopsida* mainly Isoviita (1966), *Marchantiopsida (Hepaticae)* Arnell (1956), and lichens Krog et al. (1980). The mire terminology used is in accordance with common Fennoscandian practice, see e.g. Sjörs (1948), Malmer (1962a), Fransson (1972).

Measurements of pH were made with a Radiometer, PHM 29b. The SEM studies were done on a JEOL JSM 25S instrument. An ABC 80 computer was used for the statistical calculations.

Each of the collecting localities mentioned in the text is geographically localized using the UTM grid reference system to a particular square of 1 x 1 km (e.g. NR 42,26). Unless otherwise mentioned, the material referred to in the text, is - or will be - deposited at herb. TRH.

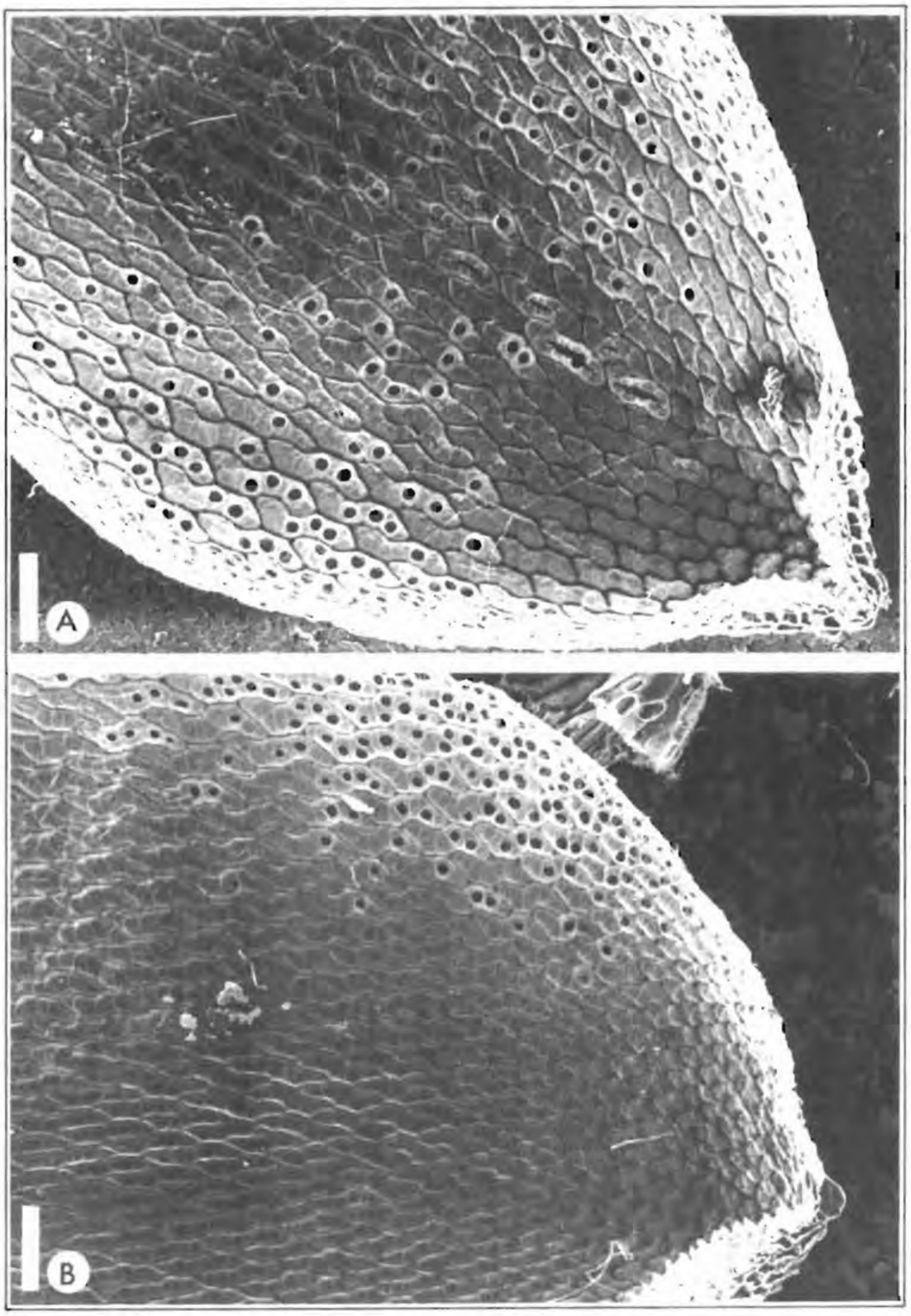


Fig. 1. Upper half of the concave surface of branch leaves of *Sphagnum imbricatum*. A: Ssp. *austinii*. B: Ssp. *affine*. SEM micrograph. Scale is 100 µm.

MORPHOVARIATION

In this study main emphasis is laid on leaf characteristics. I have found that the size and shape of leves in several *Sphagna* exactly reflect the peculiarities of the growing habitats occupied, and that these parameters can be profitably used to define the intraspecific and phenotypic response to alterations along local ecogradients. These parameters have also proved to be useful aids in studies of interspecific variation between related taxa, and for demonstrating regional intraspecific variation. In the *S. imbricatum* complex, the shape of leaves expressed through the breadth/length (B/L) ratio, has found by tests to be the parameter that most effectively expresses inter- and intraspecific peculiarities within the complex. However, the leaf length (L) parameter also provides valuable information.

Largely using these two parameters, I have performed 6 kinds of study to elucidate the leaf morphovariation within the *S. imbricatum* complex in Norway. These are: (1) herbarium studies, (2) a mixed stand study of *austinii* and *affine*, (3) a transplantation experiment, involving the transfer of *affine* from a fen site to a bog *austinii* cushion, (4) morphogradient studies of *austinii* and *affine*, (5) a cultivation experiment involving *austinii*, and (6) a mixed stand study of male and female shoots of *affine*.

Some qualitative aspects are also dealt with. In the leaf B/L ratio and L studies, the following standardized methods have been used for selecting and removing of leaves from individual shoots, for measuring them and for obtaining of mean values used in constructing the graphs. About 20-30 leaves from typical shoots of specimens or samples selected for study, were removed from the middle part of 4-6 divergent branches of separate fascicles, and about 15-20 stem leaves were removed from a stem piece (2-3 cm long) just beneath the capitulum region. The leaves were semipermanently mounted on slides in glycerin. Using a Reichert Visopan screen microscope, 10 branch leaves and 10 stem leaves were selected avoiding aberrant leaves. The maximum breadth (B) and length (L) values were measured, and the mean B/L and L values were calculated. When only one shoot was used for the measurements (for herbarium specimens, see below),

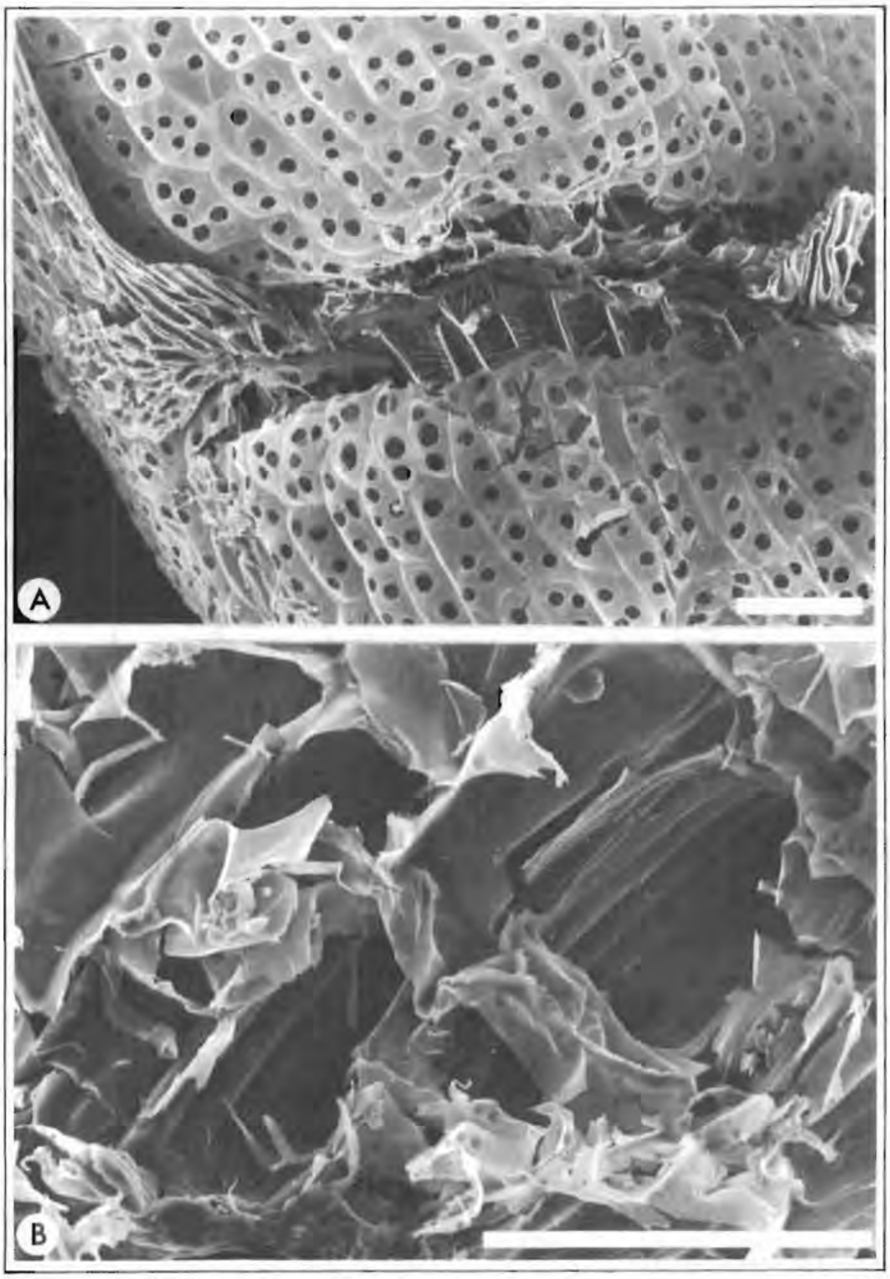


Fig. 2. Structure of the inner stem cortical cells where they face the wood cylinder, in *Sphagnum imbricatum*. A: Ssp. *affine*. B: Ssp. *austinii*. In ssp. *austinii* the outer cortical layers are removed; in ssp. *affine* the surface cortical layer with pores is partly present, but at the base of a stem leaf the cortical layers are removed and the inner wall cortical comb-lamellae can be seen; these are absent in ssp. *austinii*. SEM micrographs. Scale are 100 µm.

Fig. 3. Hyalocyst comb-lamellae in leaves of *Sphagnum imbricarum* ssp. *austinii*. A: Branch leaf in longitudinal section; the convex surface of the leaf to left. B: Stem leaf as seen from the convex surface in the median upper 1/3 of the leaf; the hyalocyst membranes are partly resorbed. SEM micrographs. Scale is 10 µm in A, 100 µm in B.

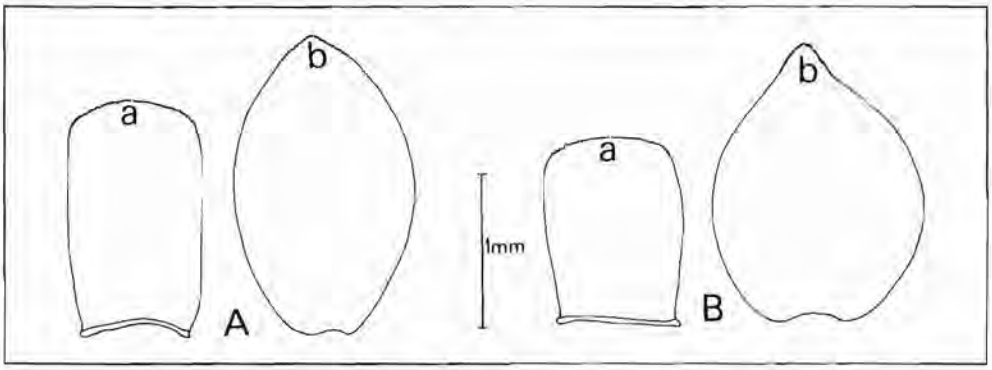


Fig. 4. Typical leaf shapes of *Sphagnum imbricatum*. A: Ssp. *austinii*. B: Ssp. *affine*; a: stem leaves, b: branch leaves.

these mean values constitute the basis for the graph constructions. When three, five or more shoots from each sample were used (see below), the mean values referred to are the mean of the mean values of the shoots used. The mean leaf B/L and L values thus obtained for each sample (or specimen) are depicted in graphs, the B/L ratios being given in scattergrams. About 9100 leaves were measured.

A. Herbarium material

During the revision work on Norwegian herbarium material belonging to the *S. imbricatum* complex, 62 specimens of *austinii* and 97 specimens of *affine* collected by several persons, were selected so as to cover the distributional ranges in Norway. Those specimens formed the basis for the leaf measurements involving B/L ratio and L values.

One shoot - or a part of one shoot - of each specimen was used. Although it would have been advisable to use several shoots from each specimen, doing so would in several cases have involved a substantial reduction of the herbarium specimen. Furthermore, it cannot always be ascertained that a particular herbarium specimen contains shoots which definitely constitute a single homogenous sample from one and the same microsite in the field. The sampling procedure differs from collector to collector, and commonly also with regard to the same collector from time to time, and from place to place. The graphs in Figs. 5 and 6 therefore in reality represent a great number of individual shoots collected in different and mostly unknown microhabitats scattered throughout the distributional ranges of *affine* and *austinii* in Norway. But it should be borne in mind, that when only one shoot from each specimen is used to calculate the B/L and L values, those values are likely to deviate somewhat from the typical pattern to be found in the population at the microsites in question. Nevertheless, it is reasonable to assume that such a substantial number of shoots of each of the two taxa must to some degree reflect the general morphological relationship between them. Likewise, the results must be assumed to have built-in morphovariational trends reflecting phenotypic responses to different local ecogradients, perhaps also to regional gradients.

B/L values

The leaf B/L ratio plottings (Fig. 5) show that *austinii* and *affine* concentrate at opposite ends of the scattergram; *affine* groups with the highest, and *austinii* with the lowest values. When regarded as an entirety, the plots form a more or less continuous cluster, i.e. in Norwegian material there exists a considerable overlap between the two taxa with regard to the leaf B/L ratio characteristic. Figure 5 therefore suggests that it would in several cases be difficult to determine to which of the two taxa a specimen belonged on the basis of the leaf shape (B/L) characteristic alone. The *affine* dots are more dispersed than the *austinii* dots. This apparent difference may be partly caused by that *austinii* being represented in this study by fewer specimens than *affine*. But both species when looked at in isolation show considerable dispersal as regards their plots, clearly indicating a morphoresponse to different environments at the collecting sites. But the scattergram does not tell us which factors promote the intra-subspecific variation as regards the leaf B/L values in the herbarium material of the two taxa.

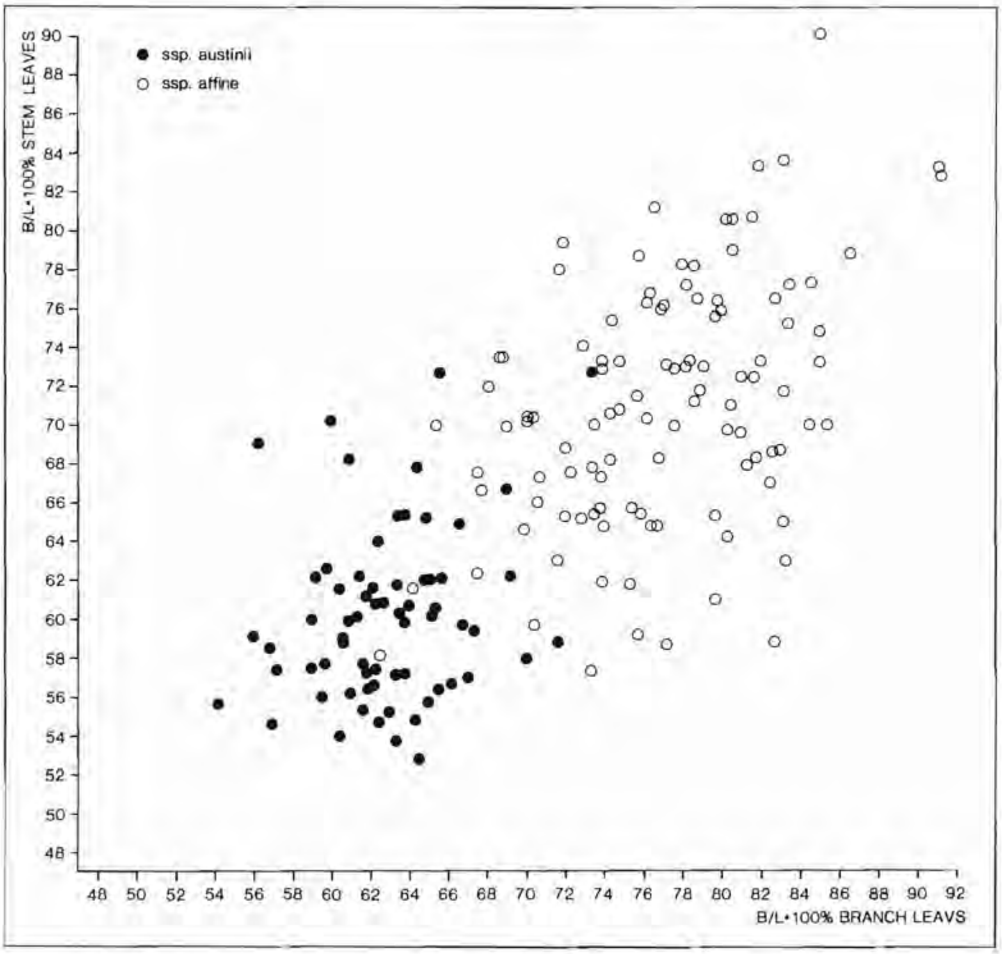


Fig. 5. The relationship between *Sphagnum imbricatum* ssp. *austinii* and ssp. *affine* with regard to leaf breadth/ length (B/L) ratios, based on Norwegian herbarium material. See the text for the methods used.

L values

The length of the stem leaves in herbarium material of *affine* and *austinii* differs significantly (a "t-test" gave $t=8.60$ and $P<0.001$), whereas the branch leaves do not ($t=1.04$ and $P>0.10$). *Affine* shows a larger scatter of the branch leaf lengths than *austinii*. See Fig. 6.

B. The mixed stand study

Locality: Møre & Romsdal Co., Eide, Svanvikmyra, about 300 m N of Vassgardvatnet, ca. 25 m, MQ 20,74. July 2, 1980 KIF.

Method for quantitative leaf B/L and L studies: Three mixed samples of the two taxa (marked A, B and C) were collected at their interfaces, each sample representing different vertical levels in relation to the water table in the field, with A as the most dry-growing, C as the most wet-growing, and B as an intermediate sample. Their relative positions were: A: Medium-level hummock. B: Low-level hummock. C: Transitional between hummock and lawn. Only shoots growing in intimate contact with each other were used. In each of the three samples, 5 typical shoots of each taxon were selected, avoiding newly developed shoots. The shoots were examined with regard to the B/L and L parameters in the manner described above.

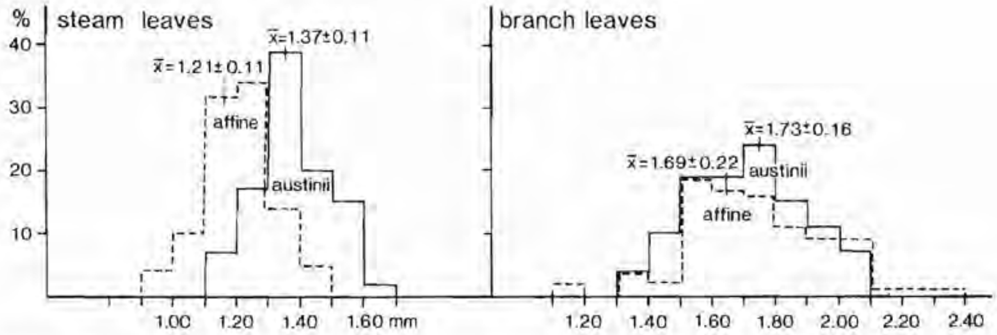


Fig. 6. Frequency histograms of the distribution of leaf lengths in Norwegian herbarium material of *Sphagnum imbricatum* ssp. *austinii* and ssp. *affine*. Same material as in Fig. 5.

The mixed stand locality of *austinii* and *affine* was situated in a broad, lagg-like, slightly soligenous fen soak, draining between the *Pinus*-dominated forest on mineral soil and the open, treeless plain in a bog complex of atlantic type. The high-level bog hummocks were dominated by *Racomitrium lanuginosum* and *austinii* in the bottom layer, while *affine* was one of the dominating species in the fen soak, where it occupied lawns and low hummocks of a poor to intermediate minerotrophic character. Some 10 m away from the sharp fen plant limit separating the fen and bog areas, and in the fen, a relatively low-level hummock of *austinii* (ca. 1.5 x 1.5 m in extent) occurred. About half to two-third of the hummock was surrounded by a mat of *affine*, which had an interface with the lower edge of the *austinii* hummock establishing an intimate contact between shoots of the two taxa. A 0.25 m^2 square analysis was performed covering about half *austinii* and half *affine*, and this gave the following composition (degree of cover according to the Hult-Sernander scale): *Andromeda polifolia* (1), *Calluna vulgaris* (5), *Erica tetralix* (2), *Oxycoccus microcarpus* (1), *Drosera rotundifolia* (1), *Narthecium ossifragum* (1), *Potentilla erecta* (3), *Trientalis europaea* (1), *Carex lasiocarpa* (1), *C. pauciflora* (1), *Eriophorum angustifolium* (1), *E. vaginatum* (1), *Scirpus cespitosus* ssp. *cespitosus* (3), *Sphagnum* * *affine* (4), *S.* * *austinii* (5), *S. capillifolium* (1), *S. rubellum* (1).

Although this kind of minerotrophic site is undoubtedly uncommon for *austinii* in Norway I have observed the taxon at other places in minerotrophic hummocks surrounded by fen lawns and carpets (see later). The chances of that the two taxa occurring together in the field is, indeed very small according to my experience. Despite careful search, I have succeeded in finding only this one mixed stand in Norway.

In the upper part of the hummock, *austinii* had a typical rustbrown and compact appearance, but in the medium and lower parts, where it had an interface with *affine*, the shoots were more lax and more greenish brown. At first glance the shoots were not easy to distinguish from shoots of *affine*. The individual shoots of *austinii* could be distinguished, however, by a more slender habit, and by possessing only 1 pendent branch in each fascicle, whereas *affine* had 2-3. Only female shoots of both taxa were recorded.

B/L values

The two taxa are quantitatively separable on the basis of the leaf B/L parameter (Fig. 7), although not clearly so in sample C. The stem leaves seem to be more unreliable than the branch leaves for distinguishing the two taxa. Some ambiguity is apparent when the two taxa are compared reciprocally in the three samples. In samples A and B, *austinii* has distinctly narrower leaves than *affine*, whilst the opposite is the case in sample C. *Affine* behaves fairly stably in all three samples, whereas *austinii* has relatively broader leaves in sample C than in the drier growing samples A and B.

For comparison, a bog hummock sample of *austinii* and a sample of *affine* from an extremely poor fen hummock on the same mire, were also included (Fig. 7).

L values

In the mixed stands A and B - the two most dry-growing ones - *austinii* and *affine* possess about the same stem leaf lengths (Fig. 8). The mean length of the stem leaves is slightly greater in *austinii*, but the differences are not significant (Table 2). However, in the most wet-growing of the mixed samples (C), *austinii* has significantly shorter stem leaves than in the associated *affine*, and also has shorter stem leaves in mean than *austinii* in samples A and B. The bog hummock sample of *austinii* from the same mire possesses longer stem leaves than in either of the *austinii* mixed samples. The comparatively short stem leaves of *affine* from the extremely poor fen hummock, are also noticeable.

The branch leaves (Fig. 8), behave somewhat differently, the mean length of *affine* leaves being greater than those of *austinii* in all three mixed samples, but significantly so only in the samples A and C (Table 2). The most pronounced difference is found in the most wet-growing sample (C). *Austinii* has the longest branch leaves in the intermediate sample (B), and the

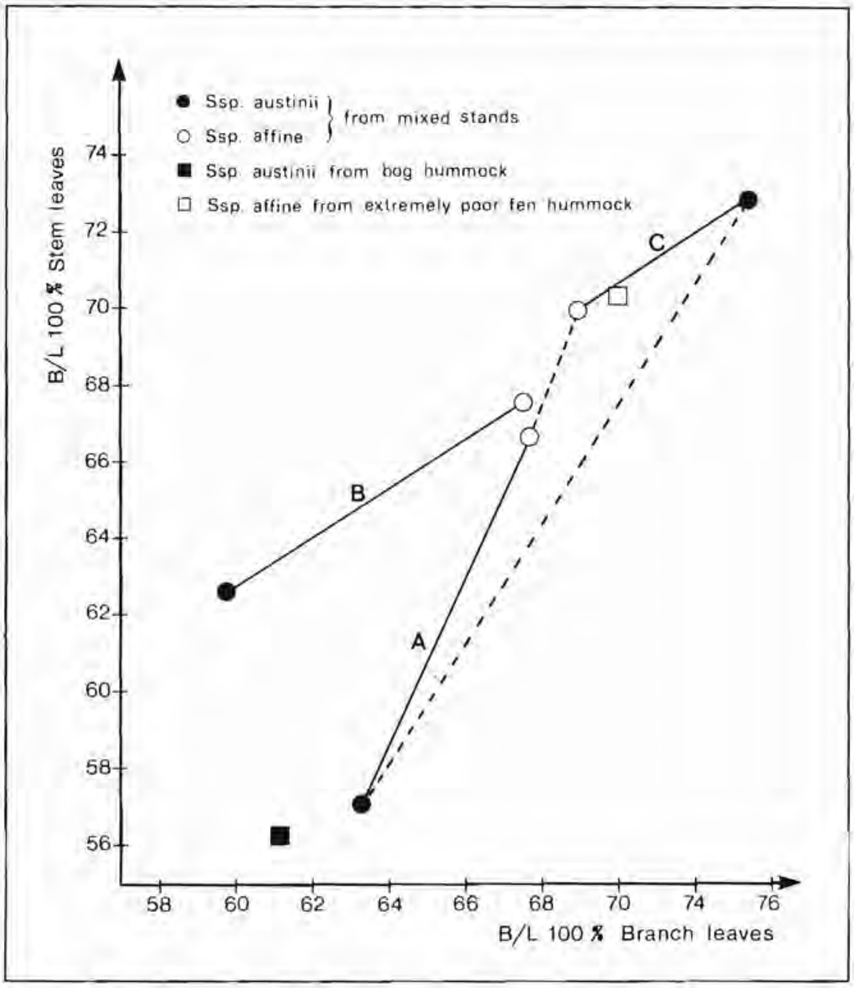


Fig. 7. The relationship between *Sphagnum imbricatum* ssp. *austinii* and ssp. *affine* with regard to leaf breadth/length (B/L) ratios as studied in three mixed stands. The solid lines connect mixed stand plots of each taxon, the broken lines indicate the total alteration found in each taxon. The squares indicate samples from the same mire as the mixed stand. See the text for material and methods.

shortest ones in the wettest sample (cf. also the stem leaves). The branch leaves in the ombrotrophic sample of *austinii* are shorter than in the B sample of the same. However, the *affine* sample from the extremely poor fen hummock has shorter branch leaves than either of the mixed samples of the taxon from the mire.

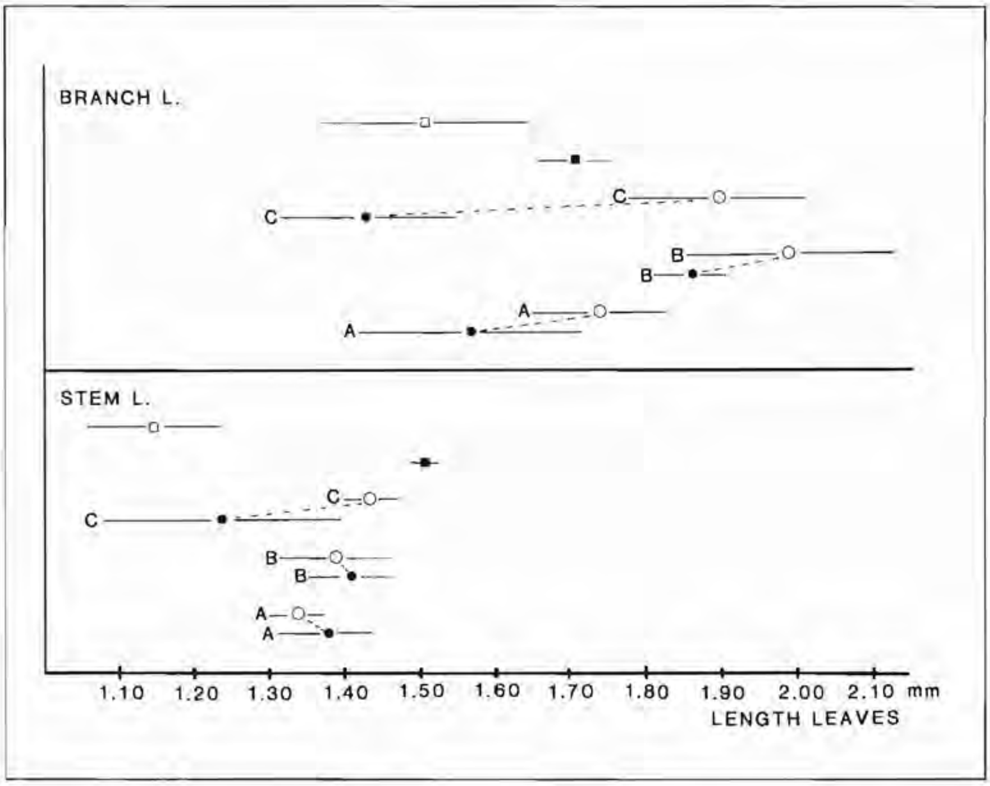


Fig. 8. The relationship between *Sphagnum imbricatum* ssp. *austinii* (filled corcles) and ssp. *affine* (open circles) with regard to leaf lengths in a mixed stand. The samples and symbols are the same as in Fig. 7. The lines denote the ± S.D. range. Same material as in Fig. 7.

Table 2. Statistical significance of differences between leaf lengths in the mixed stand of *S. imbricatum* ssp. *affine* and ssp. *austinii*. b: branch leaves, s: stem leaves. ***: $p<0.001$; **: $p<0.01$; *: $p<0.05$; -: $p>0.05$ (not significant); (*): p just above 0.05.

	2		3		4		5		6	
	b	s	b	s	b	s	b	s	b	s
1. aust. A	**	-	(*)	(*)	*	-	**	-	(*)	(*)
2. " B			***	*	*	*	(*)	-	-	-
3. " C					**	-	***	(*)	*	*
4. affine A							*	-	-	*
5. " B									-	-
6. " C										

Qualitative aspects

The mixed shoots of the two taxa differed in several qualitative characteristics. The most useful of the distinguishing characters were the number of pendent branches in each fascicle and the presence/absence of comb-lamellae in the stem leaves and on the inner stem cortical walls (see Table 1). In *austinii*, hyalocyst septae were absent or occurred only occasionally in the median upper part of the stem leaves, whilst a few 1-septated hyalocysts were usually present towards the margins. *Affine*, on the other hand, usually possessed 1-2-septated hyalocysts in the median upper part of the stem leaves and towards the margins several of the hylocysts were divided by septae into 2-4 (occasionally 5-6) parts. The structure of the cell membranes on the convex surface of the stem leaves also differed. While *affine* mostly possessed almost totally resorbed membranes, *austinii* partly had semiresorbed membranes with irregular pores and gaps which were not seen in *affine*. The hyalocysts in the upper half of the stem leaves were relatively broader in *affine*, and the chlorocysts were not so strongly curved as in *austinii*. However, in the wet-growing sample C, no real difference between the two taxa was seen as regards this characteristic. A few (usually 1 to 2) unringed and circular pores, were usually present in the distal half of the hyalocysts in the upper concave half of the branch leaves in *austinii* (see Fig. 1), but none were recorded in *affine*.

The comb-lamellae in the upper half of the branch leaves of *austinii* were more numerous and distinct than in *affine*. No difference was observed as regards the structure and number of pores on the convex surface of the branch leaves, and the characteristic triple-pores (Flatberg 1984) were present in both taxa. The chlorocysts in transverse section also proved to be identical in shape, being characteristically shaped like isosceles triangles in both taxa.

The number of pores in the surface layer of the stem cortex, sometimes given diagnostic value in Sect. *Sphagnum*, showed no real difference. The number of surface pores in each cell ranged from (1)2-5(8) in both taxa.

C. The transplantation experiment

The *affine* material used for the transplantation experiment was collected at the following locality: Sogn & Fjordane. Solund. NE of Hardbakke, ca. 60 m, KN 76,78. July 31, 1978 KIF. See Fig. 9. And the transplantation experiment was carried out at the locality: Sør-Trøndelag. Klæbu. Lysklettmyra, ca. 160 m, NR 74,21.

The transplantation started on August 15, 1978. The collecting date for *affine* sample 1 was August 7, 1980, for *affine* sample 2 and for *austinii* for reference September 9, 1981.

Methods: Twenty capitula of the *affine* collection were removed from their shoots and transplanted in a dispersed fashion among shoots of *austinii* in two neighbouring hummocks. Shoots of the latter were replaced by capitula of the former (Fig. 9).

The sites where *affine* was collected and transplanted differed considerably in trophic and water-table conditions. A topogenous, intermediate and low-level lawn constituted the collecting site, whereas the transplantation site was of bog hummocks dominated by *austinii* in the bottom layer and situated in an eccentrically-domed bog (cf. square No. 1, Table 7).

Climatically the transplantation locality is characterized by considerably colder winters (but including a more permanent snow cover), by less macrohumid surroundings, and by a lower precipitation frequency during the year, than at the collecting locality situated on the extreme west coast of Norway. The two localities are about 380 km apart. About two and three years after transplantation (see above), five shoots of *affine* were recollected on each occasion from one of the hummocks (these are called samples 1 and 2, respectively). Five shoots of *austinii* growing in close contact with the transplanted shoots of *affine* were also collected on the last occasion. Those *austinii* shoots, and five shoots from the original collection of *affine*, constituted the basis for the morphological comparisons. Branch and stem leaves from each of the *affine* and *austinii* samples were removed, examined and measured in the manner previously outlined. In the case of the recollected

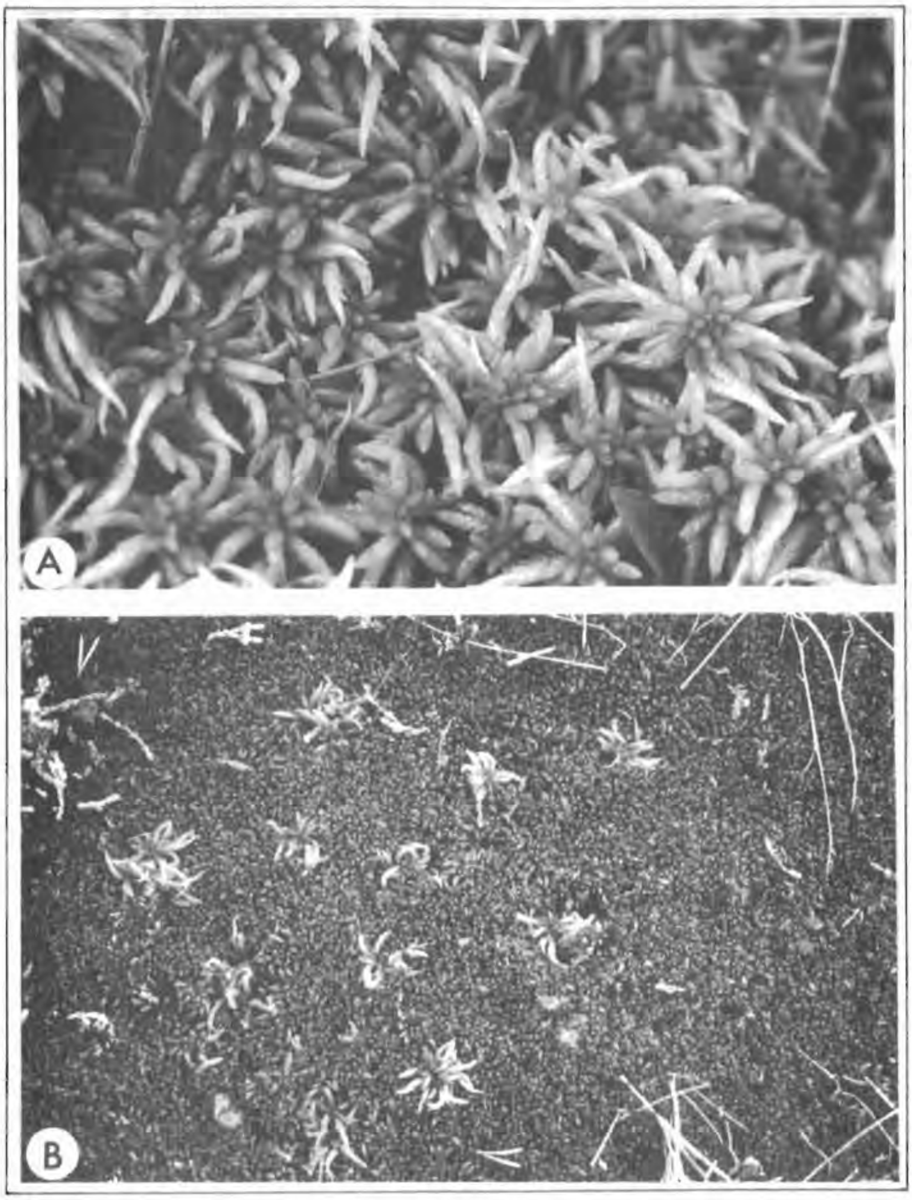
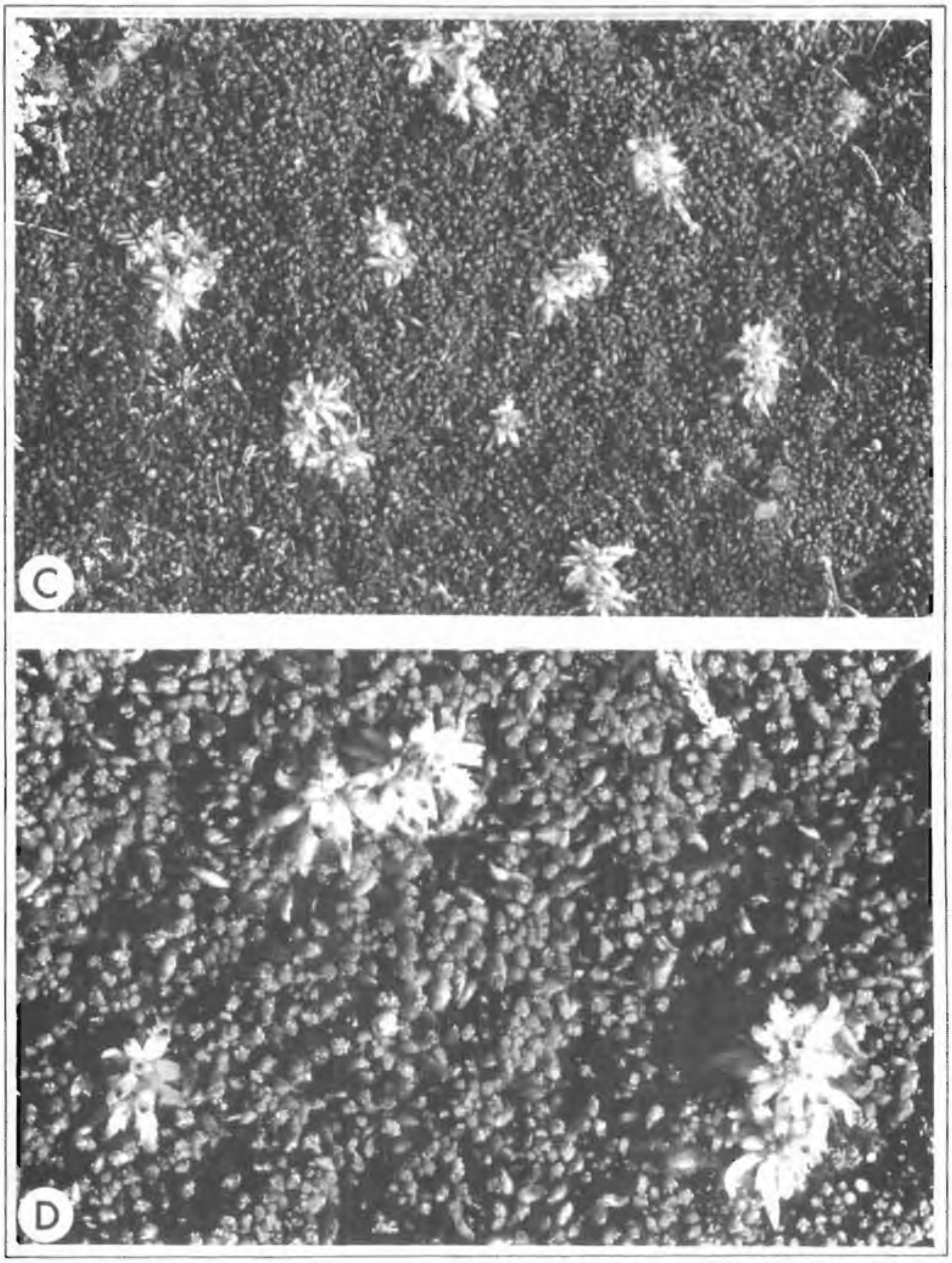


Fig. 9. Habit of *Sphagnum imbricatum* ssp. *affine* before and after the transplantation period. A: Ssp. *affine* at the original collecting site. B: Capitula of ssp. *affine* just after transplantation among shoots of ssp. *austinii* in a bog hummock. C-D: same microsite as B, but photographed just before the recollecting of *affine* shoots after about 2 years of the transplantation period. Note the elevated position of the *affine* capitula in C and D as compared with ssp. *austinii*, and the dark-coloured burnt-looking branch species of *affine*. See the text for material, localities and other details.


C
D

transplants of *affine*, care was taken to only include leaves of branches and the stem region immediately beneath the capitula.

The capitula of *affine* and *austinii* differed noticeably in colour and habit before and just after transplantation (Fig. 9 A,B). In *affine* the capitula were pale green but in *austinii* they were rust brown. Two years after transplantation (Fig. 9 C,D), the capitula of *affine* had changed colour to pale yellowish green brown, but were still noticeably different from the capitula of *austinii*. Another prominent feature was the somewhat elevated position of the *affine* capitula, indicating a faster growth rate than in the associated *austinii*. The five shoots in the *affine* sample 1 were on average about 20 mm long when recollected. Compared with the original *affine* shoots, the branch fascicles and the stem leaves were markedly more densely arranged, and the divergent branches were shorter; the branch leaves were still less imbricate than those of *austinii*. The capitulum branches of *affine* also looked burned at their tips (Fig. 9 D).

When sample 2 of *affine* was recollected, i.e. about three years after transplantation, the five shoots collected were about 25 to 30 mm long on average. Despite a preceding wet summer, the *affine* capitula had become distinctly smaller with shorter branches than the previous year, and they did not look especially robust. However, the capitula still contrasted markedly in colour from the accompanying capitula of *austinii*, as they were still pale yellowish green brown.

B/L values

The scattergram (Fig. 10) shows that *affine* had changed its leaf B/L ratio only slightly during the first two years of the transplantation period, as compared with the original material, although somewhat relatively broader stem leaves were in evidence. However, sample 2 of *affine* (three years after transplantation) shows a rather drastic change towards of relatively broader leaves. In all three samples of *affine*, the B/L ratio differs considerably from that of *austinii*. The transplantation period has not led to the two taxa approaching each other as regards the B/L parameter, but indeed the reverse.

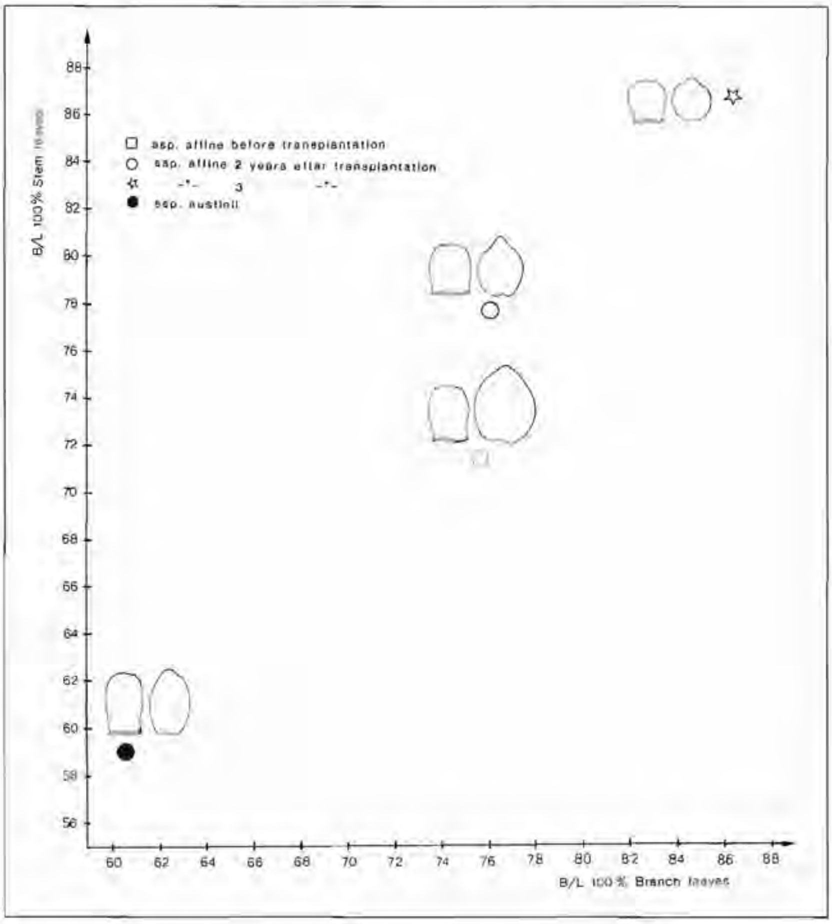


Fig. 10. The relationship between *Sphagnum imbricatum* ssp. *austinii* and ssp. *affine* with regard to breadth/length (B/L) ratios as a result of the transplantation experiment. See the text for details.

L values

The most marked trend is the shortening of the leaves in *affine* during the transplantation period (Fig. 11). Again the most pronounced change occurred during the third year of the period. The branch leaves, in particular, became shorter in *affine*, and at the end of the period were nearly half as long as at the start. Both the branch and the stem leaves of *affine* were shorter in the transplanted samples 1 and 2, than in the accompanying *austinii*. The difference in leaf lengths between the *austinii* and the *affine* transplants is significant (Table 3).

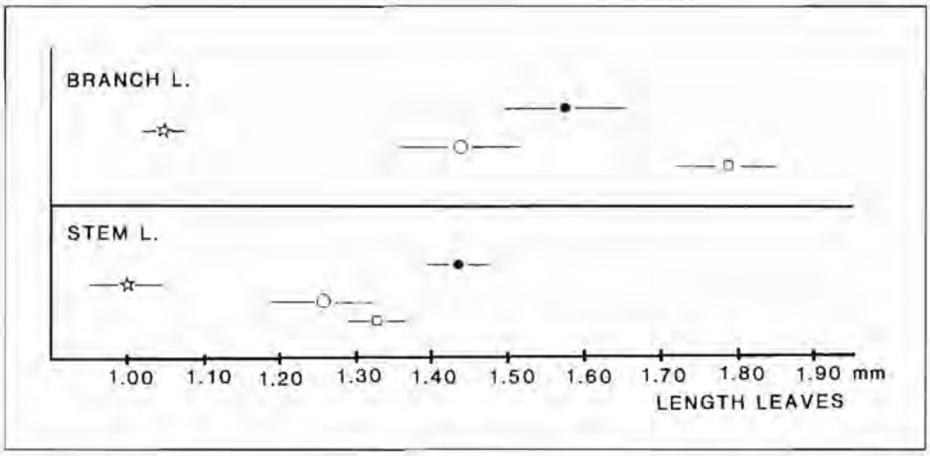


Fig. 11. The relationship between *Sphagnum imbricatum* ssp. *austinii* and ssp. *affine* with regard to leaf lengths as a result of the transplantation experiment. The symbols are the same as in Fig. 10; the lines give the ± S.D. range. See the text for details.

Table 3. Statistical significance of differences between leaf lengths in the transplantation experiment with *S. imbricatum* ssp. *affine*. b = branch leaves, s = stem leaves. ***: p<0.001; **: p<0.01; *: p<0.05; -: p>0.05 (not significant).

	2		3		4	
	b	s	b	s	b	s
1. *affine* at start of transplantation period	***	-	***	***	**	**
2. *affine* after 2 years of transplantation period			***	**	*	**
3. *affine* after 3 years of transplantation period					***	***
4. *austinii* growing among transplanted *affine*						

Qualitative aspects

Affine altered only slightly slightly in morphological details during the transplantation period, and differed consistently from the *austinii* partner in the characteristics used to distinguish the two taxa. The number of pendent branches in each fascicle - the easiest way to separate the two in the field - was 2-3 in *affine* both at the start and the end of the transplantation period, whilst consistently 1 in the *austinii* shoots. Microscopic examination showed that the septation pattern in the upper half of the stem leaves was quite different. *Affine* (before, as well as at the end of the transplantation period of three years) had 2-4(6)-septated hyalocysts in the marginal regions, and partly also in the median part of the leaf. In *austinii* only some submarginal hyolocysts were recorded as 1-septated, and those in the median upper part of the leaf were for the most part unseptated. The leaf pores of the two taxa also differed in every sample. In *austinii* numerous circular to fairly irregular pores and membrane gaps occurred in the midmedian part of the stem leaves on the convex surface, while the hyalocyst membranes as a rule were totally resorbed in the same position in the *affine* leaves examined. Distal-end hyalocyst pores, which were present in the upper half of the concave surface of the branch leaves in *austinii*, were not observed in the *affine* transplants or in the original sample of *affine*. Hyalocyst comb-lamellae were abundant in the stem leaves of *austinii*, but were not found in leaves from the *affine* samples. To test the impression gained from the microscope examination that the hyalocysts in the distal half of the branch leaves of *austinii* looked relatively narrower than in any of the *affine* samples, the following measurements were performed in three of the samples: The breadth/length ratio (B/L) of 75 cells (5 cells in each of 3 leaves from each of 5 shoots) from the median upper fourth part of the leaves was measured. The mean (± S.D.) values obtained were: *affine* at the start of the transplantation period: B/L = 31.7 ± 5.3 %; *affine* two years after transplantation: B/L = 32.3 ± 5.4%. *Austinii* growing among the transplanted *affine*: B/L = 24.5 ± 5.4 %. These results confirm the visual impression obtained when microscoping the leaves.

D. Morphogradient studies

The theory behind the morphogradient studies performed, is that the morphological variation met with in a population of a particular *Sphagnum* at a given place, is likely to be a phenotypic response to the alterations along the various ecogradients acting there. A morphogradient is therefore defined as the continuous morphological variation observed in one or more attributes in a *Sphagnum* population at a particular microsite affected by alterations in one or more ecogradients. The ecogradients referred to here are the same main gradients as those which have been shown to determine the local distribution of mire plants and mire communities in general, viz. (1) the "wet-dry" gradient, mainly expressing different levels relative to the water table, (2) the "poor-rich" gradient, expressing different trophic levels of peat and the mire water, and (3) the "mire margin-expanse" gradient, which is a complex and compound gradient expressing different ecological factors, such as degree of exposure or shade, thickness of peat, content of dissolved oxygen in the mire water, and so on. The terminology follows, for example, Malmer (1962a), but I have found it more expedient to use ecogradient instead of ecological gradient and morphogradient instead of morphological gradient.

The method I have adopted for morphogradient studies in mire *Sphagna* is as follows: Mire microsites are selected where the actual taxon or taxa to be studied show a continuous distribution which at the same time defines different levels along one or more of the local ecogradients operating there and whose effect on the morphological behaviour is to be studied.

I have found that the "wet-dry" ecogradient is the local ecogradient which causes most of the morphovariation met with in the majority of mire *Sphagna*. It is also the easiest ecogradient to define in relative terms in the field. The second most important local ecogradient to cause morphovariation in *Sphagnum* is usually the "poor-rich" gradient. This gradient is, however, often difficult to define in practice as it commonly interacts to same degree with the "wet-dry" ecogradient. The "mire margin-expanse" ecogradient as such is unsuitable for morphogradient studies of the kind outlined. A "shade-exposure" ecogradient - which constitutes part of the "mire margin-expanse" gradient - can, however, be defined in several cases (see later).

At the microsites selected for the morphogradient studies, small homogenous samples of the actual *Sphagnum* are collected at the places within the distribution that reflect the extreme levels recognized along the ecogradient(s) whose effect is to be studied there. One or more samples representing intermediate levels should also be included. The samples represent a kind of population strata.

As the different levels along a particular ecogradient at a mire habitat often are difficult to define exactly in ecological terms without thorough and time-consuming measurements, I have found it adequate and justifiable to use the vegetational gradients to define the ecogradients and the levels along them from where the samples are collected. Experience has shown that the vegetational gradients, defined step by step by presence and absence of different indicator species, in most cases reflect the behaviour of the underlying ecogradients in a reliable and a fairly subtle way in mires (see e.g. Malmer 1962a). Although the floristic composition can usually be used in this way to define the levels of the extreme samples along a particular ecogradient in a satisfactory manner, I have in several cases found it useful to introduce a physiognomical classification in addition, as, for example, when operating with low-, medium- and high-level samples along the "wet-dry" ecogradient in hummocks, lawns and carpets; but the hummock, lawn and carpet levels themselves are floristically defined. In the case of the "shade-exposure" ecogradient, the floristic composition is found to be of little use. A rough subjective and relative estimate of the "average" light conditions acting on the capitulum surface has therefore been used to define the levels along the gradient, for example, "highly shaded" and "moderately exposed" samples. The shade effect along this ecogradient may, for example, be caused by the dense cover of a field or shrub layer. Ecological measurements like pH, specific conductivity, level of the water table, light intensity would undoubtedly in several cases supply valuable additional information about the behaviour of the underlying ecogradient(s). But the method outlined - although it may look simple and rough - has in practice proved to work satisfactorily in revealing the main morphovariational trends as a response to the alterations along different ecogradients. The method is also suitable for making comparisons between morphogradient studies performed at different localities at a different stage in the vegetative season, as it will to a large degree be independent of the climatical and ecological conditions prevailing when the sampling is undertaken.

In the laboratory the morphogradient samples collected at a particular microsite are examined, measured and compared with respect to the behaviour of selected morphological characteristics.

In the case of *affine* and *austinii*, I have performed morphogradient analyses at 25 microsites at 19 different localities in Norway, in order to elucidate the local morphovariation. The phenotypic response to the alteration along three ecogradients was investigated, viz. the "wet-dry", the "poor-rich", and the "shade-exposure" gradients. Most emphasis has been laid on the "wet-dry" ecogradient. I have not succeeded in tracing microsites where the effect of the "poor-rich" ecogradient was able to be studied independently of a simultaneous variation along the "wet-dry" ecogradient. Two or three samples have been collected from each of the microsites selected for morphogradient studies, e.g. one sample for each extreme level recognized along the ecogradient(s) in question, and sometimes one additional sample from an intermediate level. The distance between the two extreme samples in one and the same morphogradient investigated has never exceeded 2 m. As regards size, the samples collected for the morphogradient studies constituted a diameter of between 5 and 10 cm in the field as looked at from above.

The relative level of the samples along the ecogradients in question was defined in the way outlined above. In a few cases, some ecological measurements have also been included (see the survey of the individual morphogradients).

Most emphasis has been laid on the leaf characteristics in the morphogradients investigated. I have found the B/L ratio of the leaves to be that characteristic which best reflects the general pattern of variation met with in the morphogradients. The leaf length (L) has also given valuable information about the variational patterns, as have other leaf characteristics and, in a more general way, some other qualitative aspects.

I have used 3 shoots from each sample for the leaf measurements in all of the morphogradient analyses.

Below the term morphogradient is also used to designate the microsites where the morphogradients have been performed.

The *austinii* morphogradients

Thirteen morphogradients containing *austinii* have been investigated; they are termed AU. Ten of the gradients (AU 1-3, AU 7-13) are from exclusively ombrotrophic sites, while gradients AU 5 and 6 are from minerotrophic sites and AU 4 is from a mixed ombrotrophic and minerotrophic site. Except for AU 11 and 13 - which are affected by the "shade-exposure" ecogradient - all the other gradients are affected by the "wet-dry" ecogradient. But some effect of the "poor-rich" ecogradient cannot be wholly disregarded in gradients AU 5 and 6, and is obvious in AU 4.

Locality list and characterization of the *austinii* morphogradients:

AU 1: Møre & Romsdal. Fræna. Svanvikmyra, ca. 10-20 m, MQ 20,74-75. July 2, 1980.
Site exposed, ombrotrophic in an atlantic bog. The "wet-dry" gradient studied using two samples: a = Top of high-level hummock. b = Mat fringing a mud-bottom area, presumably corresponding to a high-level carpet.

AU 2: Møre & Romsdal. Molde. W of Nordheim, ca. 30 m, MQ 19,56. July 30, 1980.
Site exposed, ombrotrophic in an atlantic bog. The "wet-dry" gradient studied using three samples. a = Top of hummock. b = Medium-level lawn. c = High-level carpet.

AU 3: Sør-Trøndelag. Klæbu. Lysklettmyra, ca. 160 m, NR 74,21. September 19, 1980.
Site exposed, ombrotrophic, in an eccentrically domed bog. The "wet-dry" gradient studied using two samples. a = Top of hummock. b = High-level lawn.

AU 4: Møre & Romsdal. Fræna. NE of Søholt, ca. 25-35 m, LQ 98-99,74-75. July 1, 1980.
Site exposed, situated in an atlantic bog. Combined effect of the "wet-dry" and the "poor-rich" gradients studied using two samples. a = Top of ombrotrophic hummock. b = Extremely poor minerotrophic, low-level lawn at the margin of a "fen window" (pH = 4.0).

AU 5: Møre & Romsdal. Eide. Svanvikmyra, ca. 20 m, MQ 20,74. July 2, 1980.
Site exposed, exclusively minerotrophic of poor to intermediate character and situated in a fen soak draining through an atlantic bog. The "wet-dry" gradient studied using two samples. a = Top of low-level hummock. b = High-level lawn just beneath the lower *Calluna* limit.

AU 6: Sør-Trøndelag. Hitra. E of Lauvåsen, ca. 75 m, MR 97,54. September 26, 1980.
Site exposed, minerotrophic, poor to intermediate. The "wet-dry" gradient studied using 2 samples. a = Medium-level hummock, situated 43 cm above the water table (pH = 4.20). b = Medium-level lawn, situated 13-15 cm above the water table (pH = 4.30).

AU 7: Sør-Trøndelag. Hitra. W of Sandstad, ca. 60 m, NR 03,44. September 25, 1980.
Site exposed, ombrotrophic in a small bog. The "wet-dry" gradient studied using 2 samples. a = High-level hummock. b = Transitional between hummock and stagnant *S. tenellum* lawn hollow.

AU 8: Sør-Trøndelag. Hitra. At Middammen, ca. 50 m, MR 78,46. September 25, 1980.
Site exposed, ombrotrophic in a small bog. The "wet-dry" gradient studied using 2 samples. a = Medium-level hummock, situated 45 cm above the water table. b = Stagnant *S. tenellum* lawn, situated 5.5 cm above the water table.

AU 9: Sør-Trøndelag. Hitra. At Laksvatnet, ca. 30 m, MR 97,49. September 25, 1980.
Site exposed, ombrotrophic in a small atlantic bog. The "wet-dry" gradient studied using 2 samples. a = High-

level hummock. b = Transitional level between hummock and a naked peat hollow.

AU 10: Sør-Trøndelag. Snillfjord. E of Slåttvik, ca. 80 m, NR 10,42. September 25, 1980.
Site exposed, ombrotrophic in a small atlantic bog. The "wet-dry" gradient studied using 2 samples. a = Medium-level hummock. b = Transitional level between hummock and a naked peat hollow, probably corresponding to a high-level carpet or a low-level lawn.

AU 11: Hordaland. Lindås. SW of Ringås, ca. 30 m, KN 96,38. April 6, 1980.
Site ombrotrophic in an atlantic bog. The "shade-exposure" gradient studied using two samples from a low-level hummock. s = Under a dense field layer of *Calluna*. e = exposed (without *Calluna*) ca. 30 cm from sample s.

AU 12: Locality and date as AU 11.
Site exposed, ombrotrophic in an atlantic bog. The "wet-dry" gradient studied using two samples. a = Medium-level hummock. b = Naked peat corresponding to a carpet level.

AU 13: Sør-Trøndelag. Trondheim. Høstadmyra, ca. 100 m, NR 56,31. May 7, 1982.
Site ombrotrophic in an eccentric bog. The "shade-exposure" gradient studied using two samples from a medium-level hummock. s = Under a dense field layer of *Calluna*. e = Exposed (without *Calluna*), ca. 50 cm from sample s.

B/L values

Some clear trends are in evidence. In general a strong correlation exists between the alteration in the B/L values for the stem and the branch leaves in the individual morphogradients, although this is less pronounced in one of the purely minerotrophic gradients (AU 5), and in the "shade-exposure" gradient AU 13 (Fig. 12). Hence, the angle of slope of the individual gradients is very similar. Since all the morphogradients, except AU 2, are based on only two samples, and are generally investigated at the extreme levels along the ecogradient(s) in question at each microsite, little can be said about reciprocal changes in the branch and the stem leaves along the individual gradients in the field. In gradient AU 2 - based on three samples - the B/L value of the stem leaves increases more rapidly than that of the branch leaves in the drier phase of the gradient, whereas the opposite is seen in the wetter phase.

The hummock samples have pronouncedly narrower leaves than samples from the lawn and the high carpet levels, both within the same microsites and overall. There is also virtually no overlap in the B/L values between the samples from the hummock and the lawn/carpet levels. Another marked feature is the tendency of the bog hummock plots to cluster, even though samples come from localities in different parts of Norway. The plots representing the hollow samples are more dispersed. The two minerotrophic hummock plots (AU 5a, AU 6a) have somewhat higher B/L values (especially as regards the stem leaves) than the plots from the ombrotrophic hummocks, except for AU 11e. But no corresponding tenable difference can be traced when bog and fen samples from lawn/carpet levels are compared. The effect of the "poor-rich" ecogradient upon leaf shape in *austinii* is therefore visible only in the hummock part of the morphogradients studied; it is obscured at wetter levels. Increasing wetness and richness along respectively the "wet-dry" and the "poor-rich" ecogradients, therefore apparently results in convergence of the B/L values along the corresponding morphogradients. But more morphogradients should be performed to obtain a more reliable picture of the effect of the "poor-rich" ecogradient. The two "shade-exposure" morphogradients included, AU 11 and 13, show a similar variational trend, although they are in no way coincident, i.e. shade promotes relatively broader leaves. The morpho-gradient studies therefore indicate that increased richness, shade and wetness have a consistent effect on the leaf shape in *austinii*, i.e. the leaves get relatively broader.

Some typical leaf shapes of selected *austinii* morphogradients are given in Fig. 18.

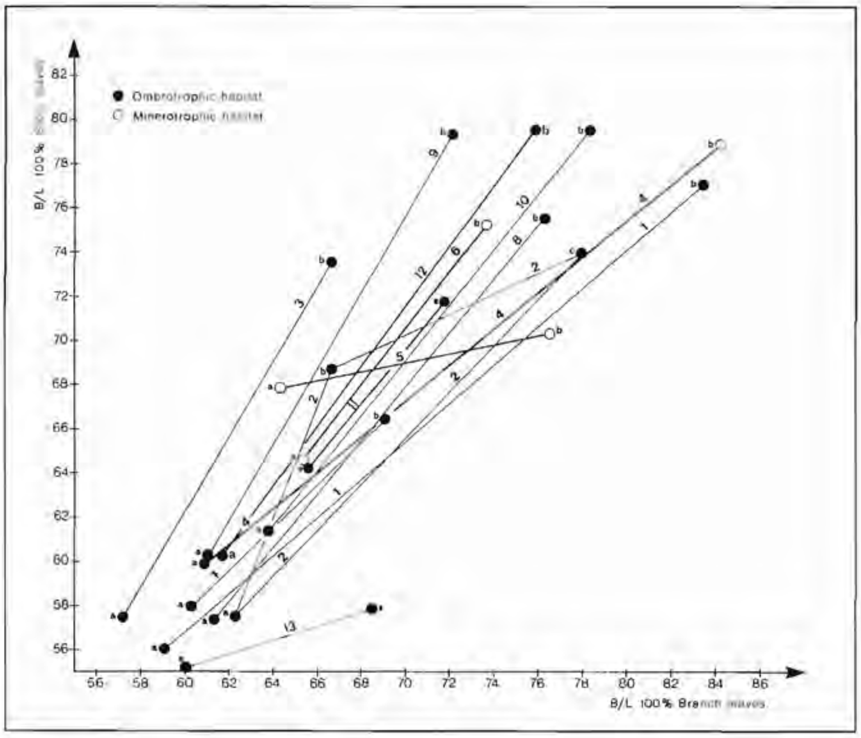


Fig. 12. Morphogradients of *Sphagnum imbricatum* ssp. *austinii* with regard to leaf breadth/length (B/L) ratios. The lines connect plots representing samples from the same morphogradients; a = the driest-growing samples, b or c = the wettest-growing samples; e = exposed samples; s = shaded samples. See the text for the localities of the individual morphogradients and methods.

L values

The variational trend found in the majority of the morphogradients(Fig. 13) is unambiguous as regards the stem leaves, i.e. increased wetness and apparently also increased shade (AU 11, AU 13), promotes shorter stem leaves in terms of mean values, but the values are not always statistically significant (Table 4). The same trend is also obvious in the branch leaves (Fig. 13), except for the two exclusively minerotrophic morphogradients (AU 5 and 6), which show an opposite behaviour; but the values are not statistically significant (Table 4). The effect of the "shade-exposure" ecogradient upon the length of

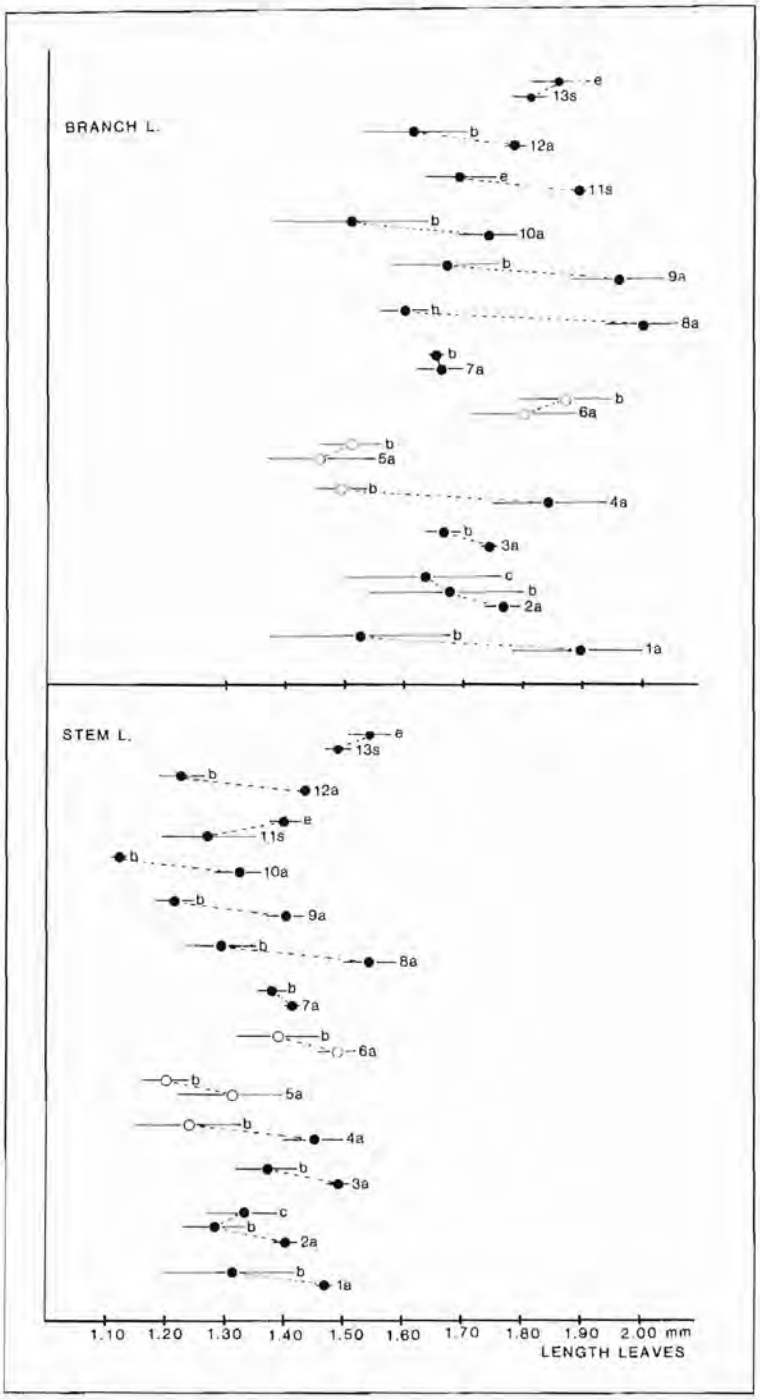


Fig. 13. Morphogradients of *Sphagnum imbricatum* ssp. *austinii* with regard to leaf lengths. Material and symbols are the same as in Fig. 12; the lines give the ± S.D. range. See the text for details.

the branch leaves is not clear. When all the ombrotrophic plot values (a) on one side are compared with all the ombrotrophic plot values (b and c) (Fig. 13), the overlap is small both the branch leaves and in the stem leaves. But a considerable overlap is seen in each of the two groups of plots in both kinds of leaves.

Table 4. Statistical significance of differences between leaf lengths in the individual morphogradients of *S. imbricatum* ssp. *austinii* and ssp. *affine*. ***: $p<0.001$; **: $p<0.01$; *: $p<0.05$; -: $p>0.05$ (not significant).

austinii	Branch l.	Stem l.	*affine*	Branch l.	Stem l.
AU 1a-b	*	*	AF 1a-b	**	*
2a-c	-	-	2a-b	**	-
3a-b	*	*	3a-b	***	**
4a-b	**	*	4a-b	-	**
5a-b	-	-	5a-b	-	**
6a-b	-	-	6a-b	-	**
7a-b	-	-	7a-b	-	-
8a-b	**	**	8s-e	**	*
9a-b	*	**	9a-c	-	***
10a-b	*	**	10a-c	-	-
11s-e	*	*	11s-e	**	-
12a-b	**	*	12a-b	-	-
13s-e	-	-			

Other morphological aspects

In addition to changes in the size and shape of the leaves, a corresponding alteration was observed in the relative size of the hyalocysts of the branch leaves; they seemd to be relatively broader in the wet-growing samples than in the drier-growing ones. In order to test this impression, measurements were made in gradient AU 8: the B/L ratios of 5 hyalocysts in the upper third and median part of 15 branch leaves (3 leaves from the middle part of divergent branches in each of 5 shoots) were measured in both samples. The following mean (± S.D.) values were obtained: Sample AU 8a: B/L = 26.9 ± 5.5%; sample AU 8b: B/L = 34.1 ± 7.5%. Although a considerable overlap is present, the results support the visual impression obtained when the branch leaves were studied in the microscope.

Shoots from the bog hollow and the minerotrophic samples generally had a more lax mode of growth with less densely crowded branches, than in shoots from the bog hummock samples. In the bog hummock samples the branch leaves were also markedly more imbricately arranged than otherwise.

The number of pendent branches in each fascicle remained consistent, independent of the sampling levels. No significant colour change was noted in the "wet-dry" morphogradient samples, but a more greenish tinge was usually visible in the hollow samples. However, in the "shade-exposure" morphogradients (AU 11, AU 13) both the shade-growing samples consisted of nearly green shoots.

The branch leaves from the hummock level were mostly elliptical, but they were distinctly more ovate to semicircular in the more wet-growing samples (Fig. 18). Distal-end hyalocyst pores in the mid median part of the concave surface of the branch leaves were nearly always present in samples from the hummock level (included minerotrophic ones), but were often absent with increasing wetness. They were sometimes not found in leaves from lawn and carpet samples.

Comb-lamellae were recorded in the branch leaves in shoots from all of the samples, and no clear change was observed in the number of distinctness of the lamellae in keeping with the alteration along the different ecogradients. However, in the minerotrophic low-level lawn sample AU 4b, the comb-lamellae in several of the branch leaves were very difficult to see in the upper half of the leaves, though they were still distinct in the lower half.

In most morphogradients, the number of circular pores in each hyalocyst along the margin and submargin of the convex surface of the branch leaves decreased with increasing wetness. In some wet-growing samples, only 1-2 pores were observed in each hyalocyst at the mid-marginal part of the leaves, whereas up to 5-6 pores were commonly present at the same position in the drier growing samples.

No clear difference was recorded in the frequency and number of hyalocyst septae in the stem leaves. However, the more wet-growing samples usually possessed a larger number of cells with septae in the median upper half part of the leaves than the more dry-growing samples. Hyalocysts which were more than 1-septated only occurred exceptionally.

Although circular to irregular circular pores or membrane gaps were the common feature in the upper and mid-median parts of the stem leaves on the convex surface in shoots from the hummock samples, hyalocysts with predominantly resorbed membranes occurred on the same surface in the wetter growing samples. Hence, increased wetness leads to increased resorption of the hyalocyst membranes in the stem leaves of *austinii*.

No clear difference was found in the shape of the branch leaf chlorocysts in transverse section in response to changes along the "wet-dry" and "poor-rich" ecogradients, and no distinct differences in microscopical details were found in "shaded" and "exposed" samples of the two "shade-exposure" morphogradients.

The *affine* morphogradients

Twelve *affine* morphogradients have been investigated; they are termed AF. Ten of them (AF 1-7, AF 9 and 10, AF 12) are mainly affected by the "wet-dry" ecogradient, although certain aspects of the "poor-rich" gradient can also be assumed to have had some influence in at least a number of cases. The gradients AF 8 and AF 11 are affected by the "shade-exposure" ecogradient. Gradient AF 12 is from an ombrotrophic site, the remaining *affine* morphogradients being from minerotrophic sites, mostly from transitional poor or intermediate fen vegetation. However, in some cases the elevated hummock samples may have been trophically influenced by a somewhat poorer environment than was indicated by the floristic composition. Several of the vasculars commonly used as indicator species are deeply rooted in the underlying peat of the hummocks and their presence does not necessarily exactly reflect the trophic condititons under which the bottom layer including *affine* is growing. The pH measurements from the gradient site of AF 7 illustrate this problem (see below) in that they show a lower value at the hummock than at the lawn sampling level even though the floristic composition did not indicate a different trophic level. Some gradational effect of the "wet-dry" and "poor-rich" ecogradients upon the *affine* morphogradients in question, is therefore likely to occur, probably to a varying degree from one microsite to another.

Locality list and characterization of the *affine* morphogradients:

AF 1: Same locality and date as AU5.
Site exposed, intermediate minerotrophic, in a gently soligenous fen soak. The "wet-dry" gradient studied using two samples. a = Low-level hummock. b = High-level carpet.

AF 2: Møre & Romsdal. Fræna. SE of Holden, ca. 60 m, MQ 10,66. July 2, 1980.
Site exposed, transitional poor minerotrophic, situated at the periphery of a topogenous mire pond. The "wet-dry" gradient studied using two samples. a = Medium-level lawn. b = High-level carpet.

AF 3: Møre & Romsdal. Molde. W of Nordheim, ca. 30 m, MQ 19,56. June 30, 1980.
Site exposed, intermediate minerotrophic, situated at the edge of a mire brook. The "wet-dry" gradient studied using two samples. a = Transitional between hummock and high-level lawn. b = Low-level lawn.

AF 4: Hordaland. Sveio, Kvernaneset, ca. 40 m, KM 92,03. July 22, 1978.
Site exposed, intermediate minerotrophic, almost topogenous. The "wet-dry" gradient studied using two samples. a = High-level lawn. b = Carpet.

AF 5: Nord-Trøndelag. Namdalseid. At Meungselva, ca. 20 m, NS 94,24. July 21, 1979.
Site exposed, transitional poor to intermediate minerotrophic, slightly soligenous. The "wet-dry" gradient studied using two samples. a = Top of medium-level hummock. b = Lawn.

AF 6: Sør-Trøndelag. Snillfjord. At Fossdalsvatnet, ca. 110 m, NR 17,40. September 25, 1980.

Site exposed, intermediate minerotrophic, nearly topogenous. The "wet-dry" gradient studied using 2 samples. a = Low-level hummock (pH = 4.70). b = Low-level lawn (pH = 4.75).

AF 7: Sør-Trøndelag. Hitra. At Brattåstjønna, ca. 65 m, NR 03,44. September 25, 1980.
Site exposed, transitional poor minerotrophic, nearly topogenous. The "wet-dry" gradient studied using 2 samples. a = Medium-level hummock (pH = 4.45). b = High-level lawn just beneath the lower *Calluna* limit (pH = 4.85).

AF 8: Same locality and date as AF 6.
Site intermediate minerotrophic, slightly soligenous, situated in a medium-level lawn near the mire margin. The "shade-exposure" gradient studied using 2 samples. s = Shaded, situated beneath a small pine and with a dense field layer of herbs and graminids. e = Exposed, situated 1 m removed from e, with a sparse field layer.

AF 9: Sør-Trøndelag. Orkdal. W of Husdalsvatnet, ca. 180-185 m, NR 42,26. September 2, 1981.
Site exposed, intermediate minerotrophic, slightly soligenous. The "wet-dry" gradient studied using 3 samples. a = Medium-level hummock. b = High-level lawn. c = High-level carpet.

AF 10: Same locality, date and habitat as AF 9.
The "wet-dry" gradient studied using 3 samples. a = Medium-level hummock. b = High-level lawn. c = High-level carpet.

AF 11: Hordaland. Lindås. SW of Ringås, ca. 30 m, KN 96,38. April 6, 1982.
Site intermediate minerotrophic, slightly soligenous, situated in a medium-level lawn near the mineral soil. The "shade-exposure" gradient studied using two samples. s = Highly shaded, situated beneath a dense layer of *Juniperus* and *Calluna*. e = Slightly shaded, ca. 1 m removed from s.

AF 12: Same locality and date as AF 11.
Site ombrotrophic in an atlantic bog. The "wet-dry" gradient studied using two samples. a = Medium-level hummock. b = Low-level lawn.

B/L values

In addition to the plot values of the morphogradient samples, four plots of *affine* which represent individual samples from the same locality as gradients AF 6 and AF 8 are also included (Fig. 14). These samples approximately correspond in richness and wetness to sample AF 8s, but were collected at different micro-sites on the same mire. Another plot included comes from the same locality as AF 11, and represents a sample collected at a shaded microsite in a moist type of Bazzanio-Pinetum forest. These samples are included to find out how far the plot values obtained for the shaded gradient samples AF 8s and AF 11s are representative.

The incline of the individual lines (Fig. 14) of the "wet-dry" morphogradients of *affine* varies more than in the corresponding gradient lines of *austinii* (Fig. 12), but the variational trend in the majority of the *affine* morphogradients is nevertheless fairly uniform (e.g. gradient AF 1). Of the "wet-dry" gradients, AF 3 and AF 5 (at either end of the variational amplitude) deviate most clearly from this pattern. The ombrotrophic morphogradient AF 12 shows, however, the opposite behaviour from the usual pattern.

The common steep incline of the *affine* morphogradients as a response to the "wet-dry" ecogradient shows that increased wetness promotes relatively broader stem leaves, and only slightly to moderately broader branch leaves. In the ombrotrophic gradient AF 12, however, increased wetness gives narrower stem and branch leaves.

The two morphogradients with three samples, AF 9 and 10, do not give a clear indication of the trend of leaf B/L variation along the "wet-dry" ecogradient.

The "shade-exposure" morphogradients AF 8 and 11 are similar in that they both have relatively narrower branch and relatively broader stem leaves in the "shaded" compared to the "exposed" samples. The position of the additional plots of "shaded" samples referred to above also supports this. Some typical leaf shapes of morphogradients of *affine* are given in Fig. 18.

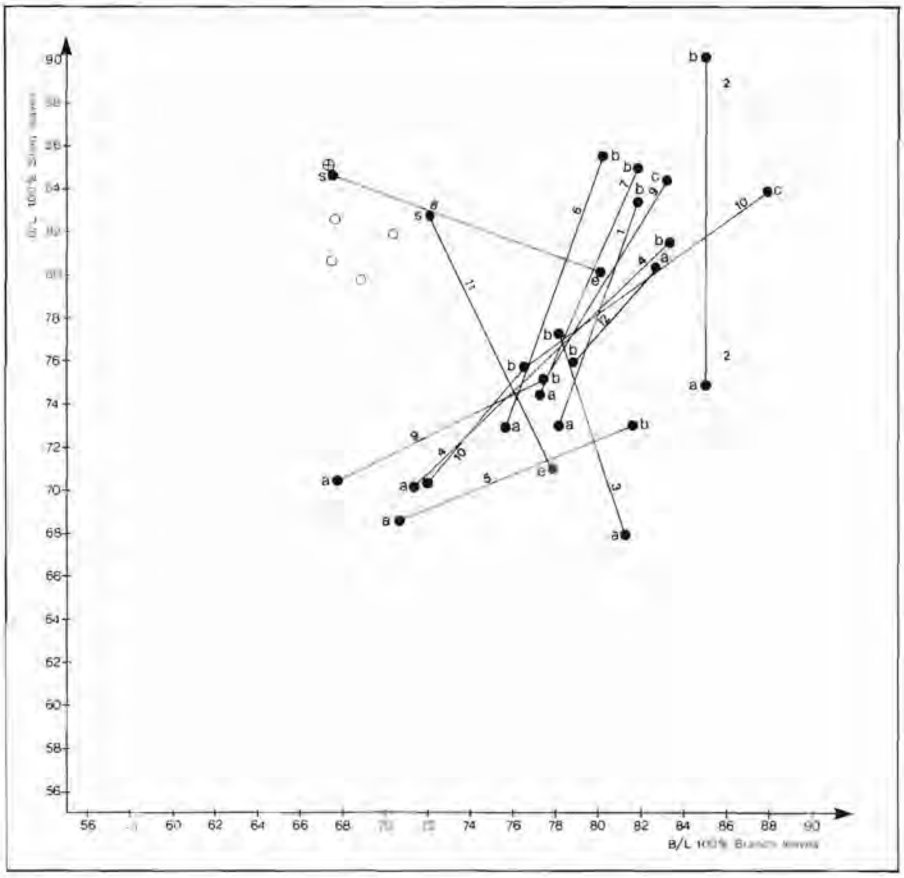


Fig. 14. Morphogradients of *Sphagnum imbricatum* ssp. *affine* with regard to leaf breadth/length (B/L) ratios. The lines connect plots representing samples from the same morphogradients; a = the driest-growing samples, b or c = the wettest-growing samples; e = exposed samples, s = shaded samples. Open circles indicate shade-growing fen samples from the same mire as morphogradient 8; the crossed circle indicates a sample from a moist type of Bazzanio-Pinetum forest at the same locality as morphogradient 11. See the text for the localities of the individual morphogradients and methods.

L values

No general trend is obvious in the "wet-dry" morphogradients (Fig. 15). In several of them the leaf lengths group so close to each other with their ranges overlapping to such a degree that no significant differences can be discerned (Table 4); this is especially the case with the branch leaves.

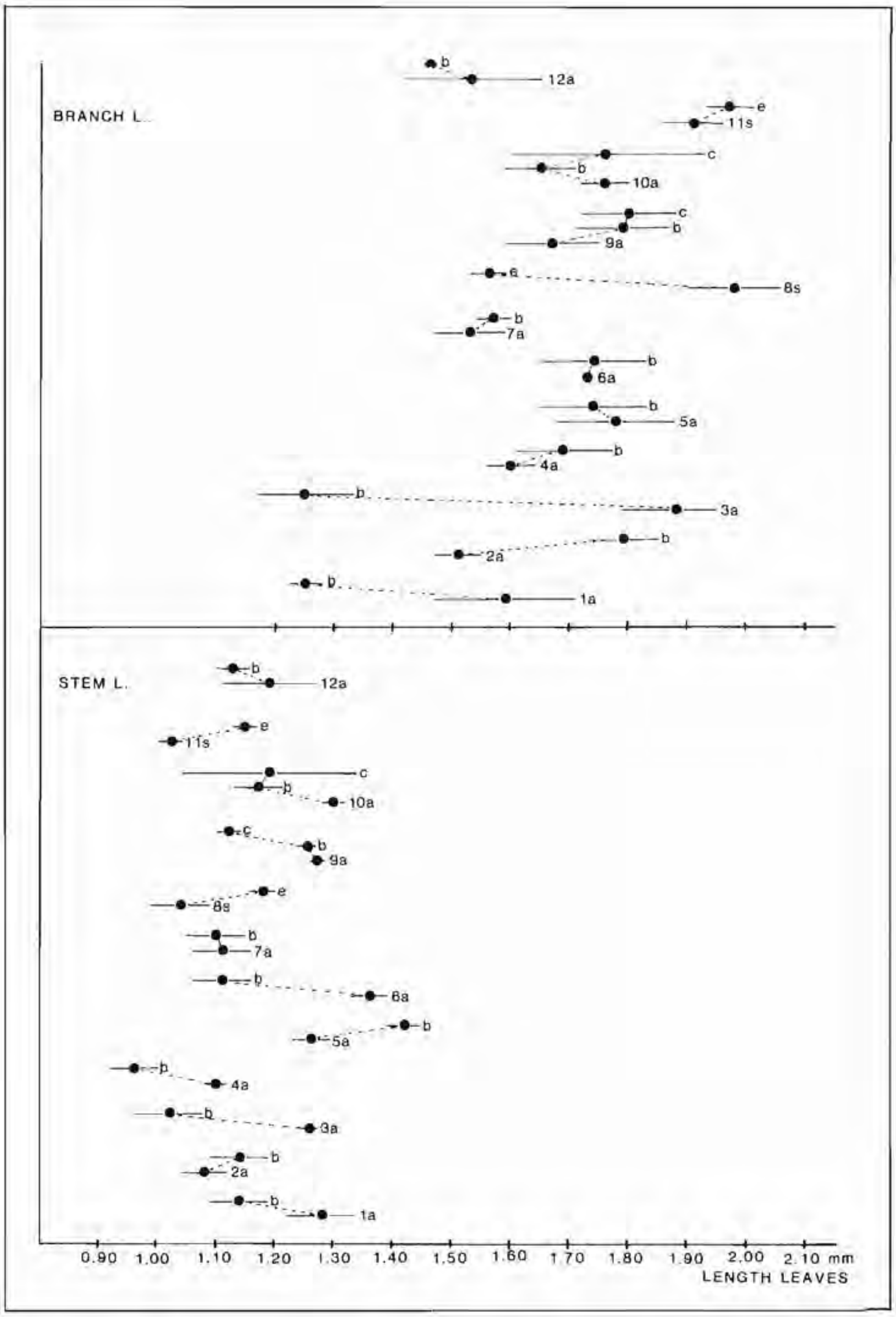


Fig. 15. Morphogradients of *Sphagnum imbricatum* ssp. *affine* with regard to leaf lengths. Material is the same as in Fig. 14; the lines give the ± S.D. range. See the text for details.

Increasing wetness along the "wet-dry" ecogradient promotes significantly shorter stem leaves in the majority of the morphogradients, but at least in gradient AF 5 the wet-growing sample possesses longer stem leaves than the dry-growing sample. No corresponding trend is, however, visible when the branch leaves are considered. There is also no clear correlation between the stem and the branch leaves concerning the direction of the variation, but they vary their lengths in the same direction in morphogradients AF 1, 2, 3 and 12. The difference between the branch leaf lengths in gradients AF 1 and 3 is noticeably large, and is mainly caused by the unusually short leaves of the wetter-growing samples.

The leaf lengths of the ombrotrophic gradient AF 12 do not deviate significantly from the leaf lengths of the "wet-dry" minerotrophic gradients. Nor is there any other obvious morphovariational trend between the different minerotrophic gradients that can be clearly related to a trophic difference along the "poor-rich" ecogradient.

The two "shade-exposure" morphogradients, AF 8 and 11, show shorter stem leaves with increasing shade, but this is only significant in AF 8. The branch leaf plots behave concordantly in the two gradients.

A comparison of all the *affine* morphogradient plot values in relation to their relative positions along the "wet-dry" gradient (Fig. 16), does not add any further information concerning the variation in leaf lengths. However, the low-level lawn and the carpet samples mainly lack long stem leaves, and the carpet samples mainly lack short branch leaves.

B/L and L values compared

The general increase in the B/L values of the stem leaves with increasing wetness is mostly explained in terms of a shortening of the stem leaves (e.g. AF 3), or as a combined shortening and widening (Fig. 17). But in some cases (e.g. AF 2, AF 7) the B/L alteration is due almost entirely to a widening of the stem leaves. Gradient AF 5 deviates from the common

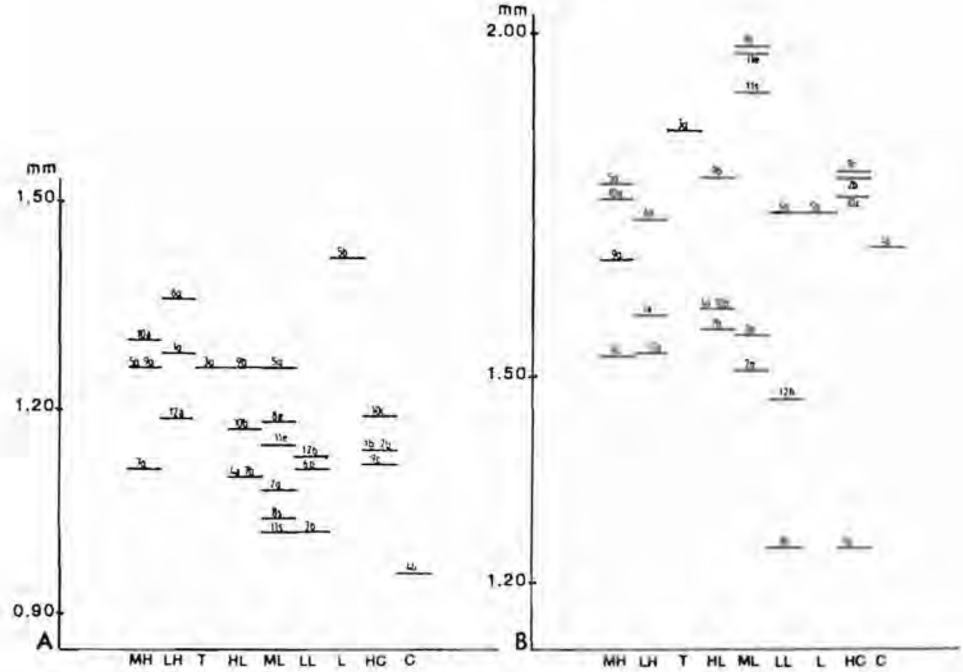


Fig. 16. Leaf lengths of the morphogradient samples of *Sphagnum imbricatum* ssp. *affine* in relation to their position along the "wet-dry" ecogradient. A: Stem leaves. B: Branch leaves. MH: Medium-level hummock; LH: low-level hummock; T: transitional between hummock and lawn; HL: high-level lawn; ML: medium-level lawn; LL: low-level lawn; L: unspecified lawn level; HC: high-level carpet; C: unspecified carpet level. Material is the same as in Figs. 14-15. See the text for details.

behaviour in that both length and especially, the breadth increase wit increasing wetness. In the ombrotrophic gradient (AF 12), the relatively narrower stem and branch leaves in the wetter growing sample (b) are apparently due to a more pronounced narrowing rather than a shortening of the leaves; but the length values do not differ significantly (Table 4).

The branch leaf variation is complex and less reliable than that of the stem leaves (Table 4). In the "wet-dry" ecogradient, increasing wetness causes a slight elongation combined with a more pronounced widening of the leaves in gradients AF 4, AF 6, AF 7 and AF 9. In the case of AF 5 and AF 10, increasing wetness mainly results in a widening of the leaves, whilst the higher B/L values in the wet-growing sample AF 1 is mainly due to a shortening of the leaves. In AF 3, the narrowing of the leaves is more pronounced than is the shortening, resulting in a lower B/L value in the wetter -growing sample.

The B/L variational pattern in the "shade-exposure" gradients AF 8 and AF 11, with higher B/L values for the stem leaves from the shaded samples, is mainly explained by a shortening of the leaves (AF 8), or by a combined shortening and widening (AF 11). The behaviour of the branch is leaves more complex.

Other morphological aspects

No obvious difference in the shape or size of the branch leaf hyalocysts, was observed during microscopical examination of the "wet-dry" morphogradient. This impression was confirmed by measurements made in the two samples of gradient AF 6 (the same procedure was used as for gradient AU 8, see above). The results were as follows (mean values ± S.D.): Sample AF 6a: B/L = 33.0 ± 5.6%; sample AF 6b: B/L = 32.8 ± 6.1%.

Corresponding measurements were not performed for the "shade-exposure" gradients, but no difference was seen in the cell structure between the extreme samples.

Increasing wetness and shade generally resulted in greener shoots in the individual gradients. As a rule this colour change was accompanied by the shoots becoming more slender and the branch fascicles, more widely spaced, and by a tendency for more squarrose branch leaves.

The number of pendent branches in each fascicle was 2 to 3 in the majority of the morphogradients, but in the wet-growing samples AF 9c and AF 10c, shoots with only 1 pendent branch in each fascicle were also common. Increasing wetness seems to promote a reduction in the number of pendent branches in *affine*, and not increasing dryness as one would expect if *affine* and *austinii* were particularly closely related to each other.

The characteristic stem cortical comb-lamellae were found in all the gradient samples, and no obvious difference in their distinctness was observed in samples belonging to one and the same gradient.

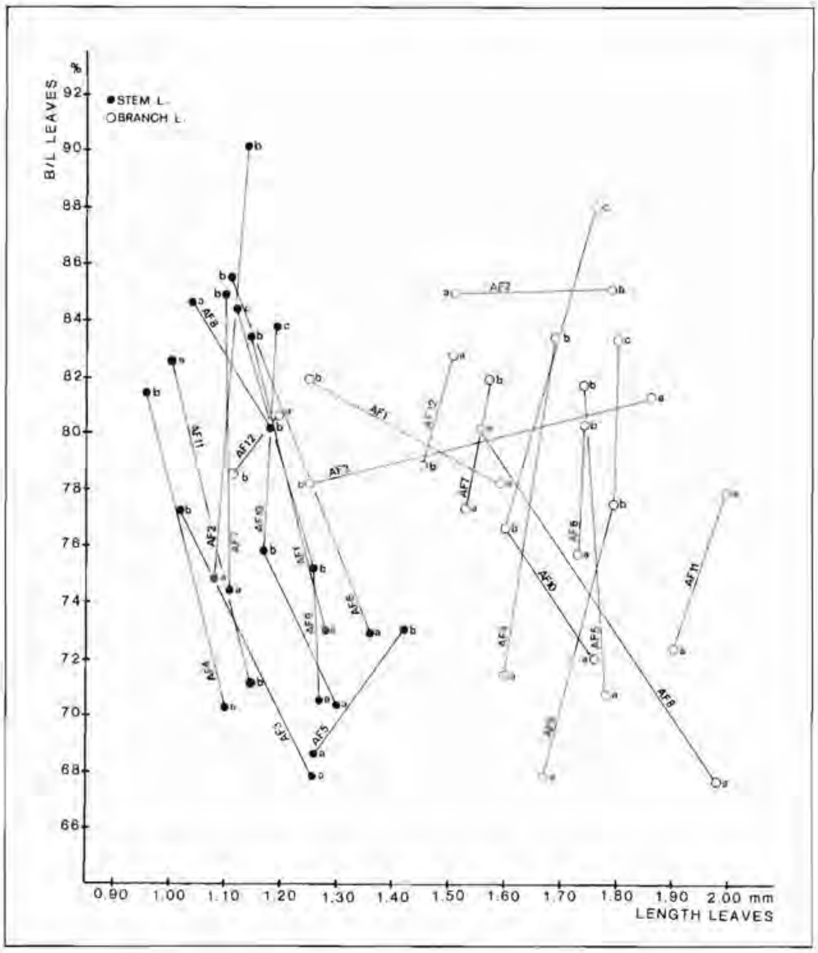


Fig. 17. Morphogradients of *Sphagnum imbricatum* ssp. *affine* with regard to leaf breadth/length (B/L) ratios and lengths. Material is the same as in Figs. 14-16. See the text for details.

A wide variation was found in the comb-lamellae of the branch leaves, but the structures were never totally lacking. Table 5, and the other microscopical examinations performed, show that increasing wetness generally results in fewer and less distinct comb-lamellae in the branch leaves, and that they decrease in number from the upper to the basal part of the leaves. The two "shade-exposure" gradients investigated (AF 8, AF 11) also indicate that shade promotes less distinct and more basally situated comb-lamellae than in ecads growing in a more exposed position.

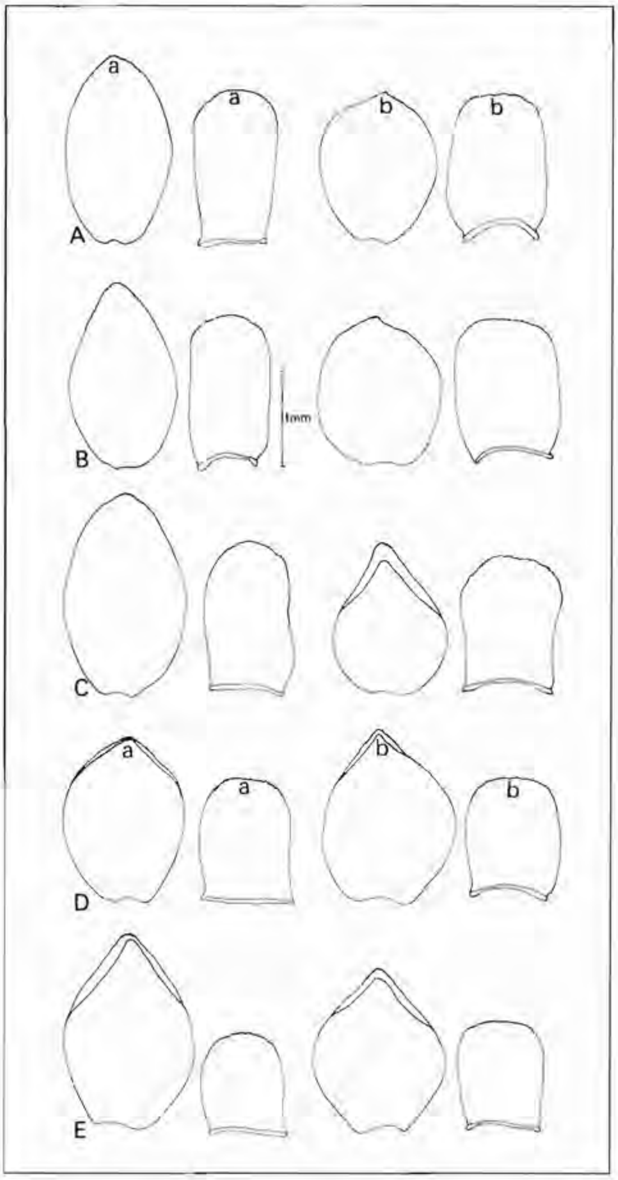


Fig. 18. Typical leaf shapes in selected morphogradient samples of *Sphagnum imbricatum* ssp. *austinii* (A-C) and ssp. *affine* (D-E). A: Morphogradient AU 4; B: morphogradient AU 1; C: morphogradient AU 8; D: morphogradient AF 6; E: morphogradient AF 8. In A-D,(a) corresponds to the driest and (b) to the wettest growing sample; in E,(a) corresponds to a shade-growing sample and (b) to an exposed growing sample. For details see the survey of the morphogradients in the text.

The shape in transverse section, and the relative position of the branch leaf chlorocysts vary only moderately in the "wet-dry" morphogradients. As a rule the chlorocysts become somewhat more isosceles-triangular in the wet-growing samples, rather than more equilateral-triangular in the more dry-groving samples (Fig. 19A). This change was found to be accompanied by a movement of the apical end of the chlorocysts towards the convex surface of the leaves, but this partly seemed to result from the more common occurrence of sulcae rather than being directly related to drier-growing samples (the term *sulcus*, is defined in Flatberg 1984). The most pronounced difference in the shape of the chlorocysts was seen in the "shade-exposure" morphogradients (AF 8, AF 11). Here the chlorocysts in transverse section were trapezoidal-triangular to trapezoidal-rectangular and broadly exposed on the convex surface of the leaves in both the shade-growing samples (Fig. 19B).

The stem leaves were found to alter only very slightly in qualitative characteristics in the morphogradients. The number of septated hyalocysts, and the number of septae in each hyalocyst when present, remained fairly constant. Comb-lamellae of the kind met with in the stem leaves of *austinii* were not recorded.

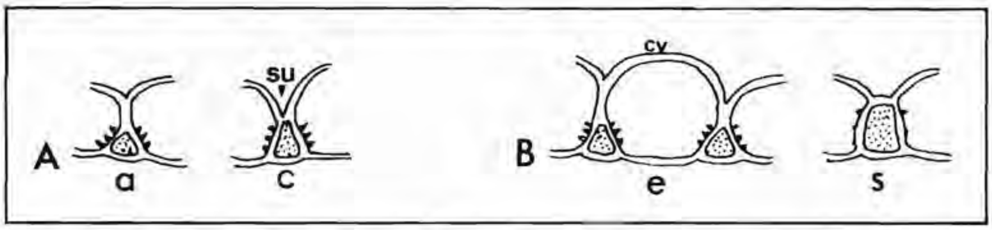


Fig. 19. The shape of the branch leaf chlorocysts in transverse section in morphogradients of *S. imbricatum* ssp. *affine*. A: The "wet-dry" morphogradient AF 9 (a = sample from medium-level hummock, c = sample from high-level carpet). B: The "shade-exposure" morphogradient AF 8 from a medium-level lawn. (e = exposed -growing sample, s = shade-growing sample). su = chlorocyst sulcus. cv = convex surface.

Table 5. Distribution and distinctness of comb-lamellae in the branch leaves of *Sphagnum imbricatum* ssp. *affine* in 12 morphogradients from Norway. The gradients AF 1-7, AF 9-10, and AF 12 mainly reflect the "wet-dry" ecogradient (a = driest sample, b or c = wettest sample), whilst AF 8 and 11 reflect the "shade-exposure" ecogradient (a = shade sample, b = exposure sample).

	Comb-lamellae distinct in the leaf:			
Morpho-gradient	only at the base	up to about the basal 1/3	up to about 1/2	up to about 2/3 or more
AF 1a				x
b			x	
AF 2a				x
b	x			
AF 3a			x	
b		x		
AF 4a			x	
b	x			
AF 5a				x
b			x	
AF 6a				x
b				x
AF 7a				x
b			x	
AF 8s	x			
e			x	
AF 9a				x
b				x
c			x	
AF 10a				x
b			x	
c			x	
AF 11s		x		
e				x
AF 12a				x
b				x

E. The cultivation experiment

Material and methods: Fifty shoots of *austinii* from a medium-level bog hummock were used for the experiment. The material was from the following locality: Sør-Trøndelag, Klæbu, Lysklettmyra, ca. 160 m, NR 74,21; the locality is the same as that used for the transplantation experiment (see p. 22). Only the capitula were used, and these were removed from their shoots at the start of the experiment. Ten capitula were used in each of the five experiments performed.

A cultivation box of hard plastic constructed for the purpose was used for the experiment. It was 50 cm long, 13 cm wide and 15 cm deep, and was divided into five compartments of equal size. A movable glass plate was used to cover the top of the box. The box was placed on a bedding of black plastic.

Six closely arranged 40 W Osram illumination tubes installed in reflectors were used as light source; three had light-colour values of 20, three of 22. The tubes were placed 45 cm above the surface of the capitula in the compartments, and measurements showed that these were therefore exposed to a light intensity of about 5000 lux. Sixteen hours daylight and eight hours darkness were employed during the cultivation.

Five kinds of experiment were performed: (1) The "inundation" experiment. (2) The "bog" experiment. (3) The "poor fen" experiment. (4) The "intermediate fen" experiment. (5) The "rich fen" experiment.

At the start of the cultivation, ten capitula of *austinii* were placed close together on the bottom of each compartment, but in the inundation experiment the capitula were soon floating freely in the compartment.

In the inundation experiment (1), the capitula were permanently grown in distilled water, the water being replaced once a week using 100 ml each time.

In experiments (2) to (5) (see above), the shoots were cultivated with the help of 2 ml of a nutrient solution administered once a week with a pipette. The four nutrient solutions used consisted of a common standard, basic solution, to which different amounts of $CaCl_2 . 2H_2O$ were added to give concentrations of Ca corresponding to 0.70, 2.1, 6.3 and 18.9 mg/l, respectively. These values of Ca correspond to those recorded from natural mire waters in respectively, bogs, poor fens, intermediate fens and moderately rich fens in Fennoscandia (see e.g. Witting 1947, 1948, 1949; Malmer 1962a, b; Tolonen & Hosiaisluoma 1978). The basic solution (made up occording to a formula given by Brehm 1970) consisted of 40 mg $NaH_2PO_4.H_2O$, 20 mg $MgSO_4.7\ H_2O$, 8 mg KNO_3, 20 mg NH_4NO_3, 0.81 mg $FeCl_3.6\ H_2O$ dissolved in 1000 ml of distilled water and supplemented with 1 ml of an AZ-solution to supply trace elements. The pH was adjusted in the four solutions to lie at 4.0 in the bog experiment, 4.5 in the poor fen experiment, 5.4 in the intermediate fen experiment, and 6.2 in the rich fen experiment.

To avoid desiccation effects, and induce "rainy periods", the capitula in compartments (2) to (5) were sprayed once a week with a small and equal amount of distilled water, midway time between the times the nutrient solutions were added. This ensured that, the capitula remained constantly and moderately moist during the cultivation period. The glass plate was removed for about two hours after the the nutrients were added. The temperature was measured in a control compartment, and varied during the cultivation period from about +10 to +18°C. The cultivation period lasted for eight months (Jan. 7 to Aug. 8, 1980). At its termination, the five best-developed shoots in each compartment except number 5 (see below) were selected. Stem and branch leaves were removed and examined quantitatively and qualitatively using the same procedures as previously. Caution was exercised to select leaves only from the uppermost part of the shoots. Five shoots of *austinii* from the original collection, served as a reference. The shoots (and capitula) in all the compartments except for the "rich fen" compartment, looked healthy at the end of the experiment. The only difference in appearance visible on the capitula was a change to a more greenish colour. This occurred in all the compartments and may be due to light deficiency as the light intensity used during the experiment did not match the light conditions under which *austinii* usually grows. However, the change in colour may equally well be a result of a lack of induced chilling periods during the experiment. As demonstrated by Rudolph (1963) and Rudolph et al. (1977), an induced chilling period of a few days is necessary to promote the development of sphagno-rubin in the relative *S. magellanicum*. Although not proved, the same may be true for promoting a brown colouration. The capitula grown under "rich fen" conditions were clearly hindered in their growth. Some elongation of the branches of the capitula could be recognized after about two months, but afterwards the capitula were overgrown by algae and fungi. At the end of the cultivation period, the capitula were apparently not alive. The inhibited growth may be due to the high concentration of Ca, or result from the high chloride content in the solution used. The extensive growth of algae and fungi may also have had a destructive effect, but this was probably a secondary effect. As scarcely any new leaves were developed in the "rich fen" compartment that experiment had to be excluded from the measurements.

The growth rate of the shoots in the "bog", "poor fen" and the "intermediate fen" compartment was about equal, and the total elongation of the shoots was ca. 15 - 25 mm, indicating a rather slow growth rate.

The capitula of *austinii* which were grown inundated in distilled water also turned green, and had developed ca. 30 -35 mm long shoots by the end of the cultivation period. Some of the shoots had developed lateral innovations, a feature commonly found in several *Sphagna* induced to grow permanently or semipermanently inundated.

B/L values

Two striking features are visible in the leaf B/L scattergram (Fig. 20). Firstly, the "bog" plot groups close to the plot representing the original hummock material of *austinii* used in the experiment. Secondly, the "poor fen", "intermediate fen" and the "inundated" plots are distinctly removed from those two plots, but reciprocally group in the same area. In practice, this implies that the shoots of the "bog" experiment have maintained their leaf shapes nearly unaltered during the cultivation period, whilst the shoots of the "poor fen", "intermediate fen" and the "inundated" experiments have changed their leaf shapes to become relatively broader than at the start of the cultivation.

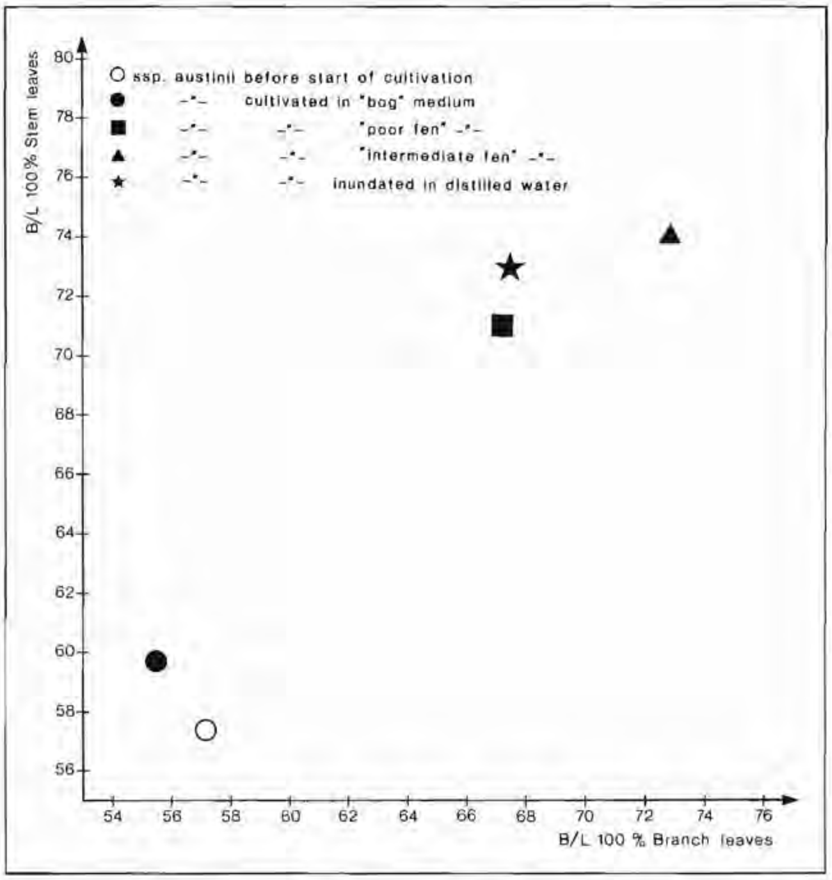


Fig. 20. The behaviour of *Sphagnum imbricatum* ssp. *austinii* with regard to leaf breadth/length (B/L) ratios, and as a result of cultivations performed under controlled and varying environments. Se the text for material and methods.

L values

The shortest leaves are found in the "intermediate fen" and the "inundation" samples, which both plot with significantly (Table 6) shorter leaves than they do in the original (basic) material of *austinii* (Fig. 21). However, only the branch leaves of the two samples differ significantly from that of the "bog" and the "poor fen" cultivations. Otherwise, the most striking features are the short stem leaves of the "bog" sample as compared with the original (basic) sample, and the very long branch leaves of the "poor fen" sample.

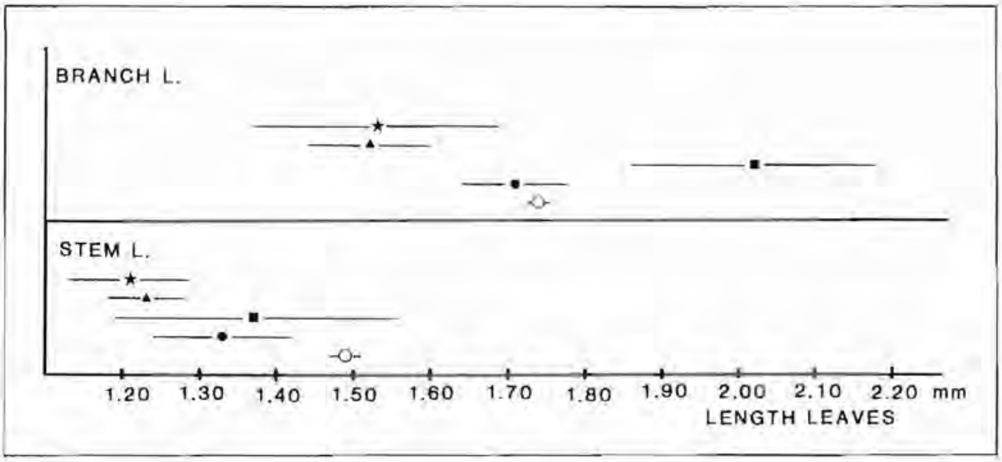


Fig. 21. The behaviour of *Sphagnum imbricatum* ssp. *austinii* with regard to leaf lengths, and as a result of cultivations performed under controlled and varying environments. Material and symbols as in Fig. 20, the lines give the ± S.D. range.

Qualitative aspects

The number of pendent branches in each fascicle remained constant in the shoots from each of the cultivations. In the branch leaves, scattered pores in the upper and mid median parts of the concave surface were found in some leaves from the "bog" experiment; such pores were usually present in branch leaves from the original collection of *austinii*, but were very rare in the other cultivations. Distinct comb-lamellae were found in the basal half of the branch leaves from the "bog" experiment sample. In the "poor fen" and the "intermediate fen" shoots, comb-lamellae were only just distinct and as a rule only at the base of the leaves. Comb-lamellae were not observed in the

Table 6. Statistical significance of differences between leaf lengths in the cultivation experiment of *S. imbricatum* ssp. *austinii*. b = branch leaves, s = stem leaves. ***: p<0.001; **: p<0.01; *: p<0.05; -: p>0.05 (not significant).

	2		3		4		5	
	b	s	b	s	b	s	b	s
1. Basic material	-	*	**	-	**	***	*	***
2. "Bog" cultivation			**	-	*	-	*	-
3. "Poor fen" cultivation					***	-	**	-
4. "Intermediate fen" cultivation							-	-
5. "Inundation" cultivation								

branch leaves from the "inundation" shoots. Likewise, comb-lamellae were numerous and distinct only in the stem leaves from the "bog" shoots. In the shoots from the "poor fen" and the "intermediate fen" cultivations, comb-lamellae were always seen to be present, but were often few and indistinct. No lamellae were observed in shoots from the "inundation" experiment.

A distinct hemi-isophyllose tendency was seen in the shape of the stem leaves from the "fen" compartments, and from the "inundation" compartment. Those stem leaves also partly resembled the branch leaves in that they had numerous pores on the convex surface. However, stem leaves with approximately straight sides predominated, mostly carrying resorbed hyalocyst membranes on the convex surface. In the "bog" shoots, the stem leaves also mostly had resorbed hyalocyst membranes, although leaves with a mixture of large membrane gaps and irregular pores also occurred.

F. Sexual leaf dimorphism

Sexual leaf dimorphism seems to be common in many dioecious *Sphagna*: i.e. the leaves are different in shape and size in female and male shoots.

One mixed stand of male and female shoots of *affine* was investigated in order to elucidate the behaviour of this taxon. The locality for the mixed-stand collection was: Sør-Trøndelag. Orkdal. W of Husdalsvatnet, ca. 180-185 m, NR

42,26. September 2, 1981. An intermediate and topogenous fen lawn constituted the collecting habitat.

Stem and branch leaves from each of 33 female and 33 male shoots growing intimately mixed in the field, were removed and measured with regard to the B/L and L parameters. The procedure was as previously outlined, and the mean B/L and L values were calculated for all the shoots (Fig. 22). An attempt was made to ovoid leaves from antheridial branches.

Both the stem and the branch leaves were found to be longer in the female than in the male shoots. A t-test performed showed the differences to be highly significant ($t = 4.43$ and $p<0.1\%$ for the stem leaves; $t = 7.16$ and $p<0.1\%$ for the branch leaves).

The B/L ratios were found not to differ significantly (stem leaves: B/L female shoots = 73.0%; male shoots = 73.8 %; branch leaves: B/L female shoots = 75.3%; male shoots = 74.1 %; all the figures are mean values). No difference was seen in morphological details between shoots of the two sexes. Several mixed stands must be investigated to show how far the differences found are of general validity.

As I have found no mixture of male and female shoots of *austinii*, the intersexual behaviour concerning the leaf shape and size is so far unknown in this taxon.

It is difficult to distinguish between male and female shoots of *affine* and especially *austinii* during most of the vegetative season. However, in the late autumn, the short, stout, dark antheridial branches in the capitula of the male shoots contrast with the divergent branches in the capitula of the female shoots, although not markedly so in *austinii*. In older parts of the male shoots, the antheridial branches from preceding years are often difficult to distinguish (especially in *austinii*), although they may also be fairly distinct. According to my experience, both *affine* and *austinii* are several times more abundant with female than with male shoots in Norway.

Although care was taken when selecting shoots for the morphogradient studies, a few male shoots, may have been inadvertently included. Likewise, some of the herbarium specimen shoots are likely to be male, because I was not wholly aware of the phenomenon of sexual leaf dimorphism in *Sphagnum* when those

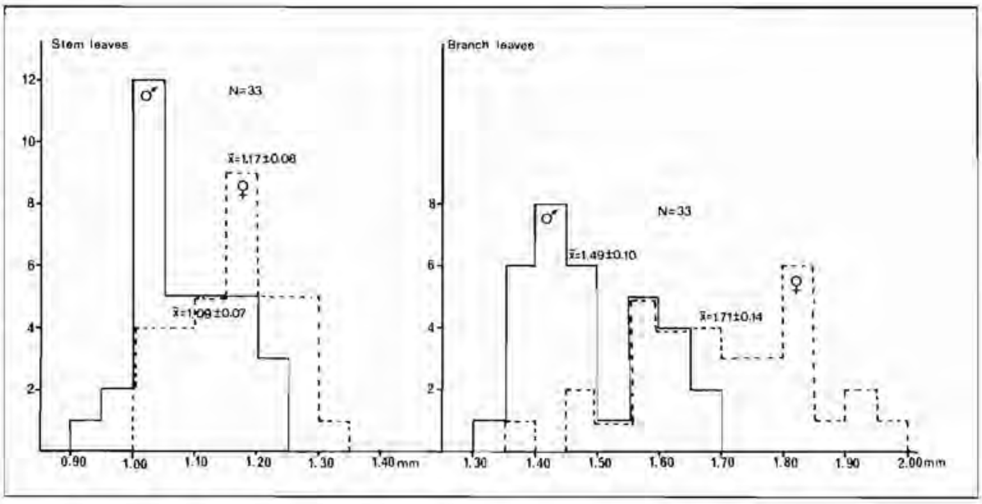


Fig. 22. Frequency histograms of the distribution of leaf lengths in a mixed stand of male and female shoots of *Sphagnum imbricatum* ssp. *affine*. See the text for material and methods.

shoots were selected for measurement (Figs. 5, 6). But the good conformity between the leaf lengths of the Norwegian herbarium material of *affine* (Fig. 6), and the female shoots of the mixed stand (Fig. 22), indicates that few male shoots are included in the herbarium material of *affine*. Apart from those, the studies and experiments referred to concern only female shoots.

G. Discussion

The mixed stand study establishes that *austinii* and *affine* can easily be distinguished from each other by the sum of their qualitative and quantitative characteristics when they grow in intimate association in the field under the same ecological environment.

With regard to the leaf B/L values (Fig. 7), the A and the B plots of *austinii* - the most dry-growing samples - group within or close to the ombrotrophic hummock "morphoarea" as defined by the morphogradients of *austinii* (Fig. 12). But the B/L plot of sample B is also located close to the minerotrophic hummock gradient plots AU 5a (from the same mire as the mixed stand analysis) and AU 6a. The position of the *austinii* plot C may at first glance seem surprising since the B/L values are even higher than in the associated *affine* sample, and considerably higher than in the other two *austinii* plots. This plot is, however, located very close to the minerotrophic, medium-level lawn plot determined by the gradient sample AU 6b (Fig. 12), i.e. within the gradient "morphoarea" where ombrotrophic hollow and corresponding minerotrophic samples of *austinii* group.

The ability that a minerotrophic and relatively wet-growing ecad of *austinii* to possess relatively broader leaves than those of *affine* in the same environments whilst considerably narrower at drier and/or poorer conditions, is also evident when the morphogradient analyses of *austinii* (Fig. 12) and *affine* (Fig. 14) are compared. Sometimes *austinii* even has relatively broader leaves than *affine* under the same habitat conditions. The mixed-stand investigation thereby confirms the results of the morphogradient studies, namely that *austinii* reacts much more strong to an alteration along the "wet-dry" ecogradient than *affine* does when the leaf B/L ratio is considered. The two taxa differ greatly in their B/L values at the hummock level, but are mainly similar at lower levels. This seems to be maintained even when *austinii* is growing under minerotrophic conditions. As sample C in the mixed stand was situated at an intermediate level between hummock and lawn it is also evident that the leaf B/L ratio in *austinii* changes fairly abruptly at about that level. Compared with the morphogradient plots of *affine* which represent a similar ecology to the *affine* samples in the mixed stand study, the latter samples group at slightly lower values, but the deviation is insignificant (Figs. 7, 14).

The morphogradient and cultivation studies of *austinii* show that the leaf B/L ratio along the "wet-dry" and the "poor-rich" ecogradients mainly changes in the same direction. The morphological behaviour of *affine* along those two ecogradients appears much more complex when the B/L ratio is considered. In the minerotrophic morphogradients of *affine*, increasing wetness always results in a higher B/L value for the stem leaves (Fig. 14), and as a rule also for the branch leaves. But the behaviour of the ombrotrophic morphogradient AF 12 is quite the contrary, i.e. the effect of the "wet-dry" and the "poor-rich" ecogradients seemingly influences the leaf B/L ratio in opposite directions in *affine*. The high B/L values obtained for *affine* in the transplantation experiment (Fig. 10) support this. On the basis of the response seen in the morphogradients of *affine* to the "wet-dry" ecogradient (Fig. 14), the hummock transplants may be expected to gradually develop relatively narrower leaves than those of the low-level fen lawn sample which constitutes the starting point. However, the contrary occurred; the transplantation experiment in the ombrotrophic hummock resulted in gradually higher leaf B/L values, and after three years, the leaf B/L values of *affine* were as high as those at the majority of the wet-growing, minerotrophic samples of the *affine* morphogradients (Fig. 14). A similar behaviour is also indicated by the comparatively high B/L values for the *affine* plot representing the sample from the extremely poor fen hummock at the same mire site as that which provided the mixed stand (Fig. 7).

It therefore seems as if the effect of the "wet-dry" ecogradient is mainly greater than that of the "poor-rich" ecogradient at the "richer" (transitional poor and intermediate minerotrophic) levels of the latter gradient, whereas the opposite is the case in the "poorer" (ombrotrophic and extremely poor minerotrophic) levels of the former gradient. Such a reaction pattern may simply reflect the adaptation of *affine* to grow under minerotrophic mire conditions. The gradually diminishing vitality of the *affine* shoots transplanted in the bog hummock also shows this. Indeed, the morphogradient AF 12 locality is the only place in Norway where I have found *affine* growing in bog vegetation.

Affine and *austinii* apparently also behave in a different manner in their response to the "shade-exposure" ecogradient (compare AF 8 and AF 11 with AU 5 and AU 13, Figs. 12, 14). In both taxa increased shade promotes a higher B/L value for the stem leaves. However, when the branch leaves are considered, the samples growing in the shade have a lower B/L value in *affine*, and a somewhat higher B/L value in *austinii*, than in the corresponding samples which are growing under more exposed conditions. But this statement has to be confirmed by additional "shade-exposure" morphogradients of *affine* and *austinii*.

When comparison is made between the morphogradient B/L scattergrams of *affine* and *austinii* (Figs. 12, 14) and the corresponding scattergram based on the herbarium specimens of the two taxa (Fig. 5), some interesting aspects emerge. If one assumes that the majority of the values in the herbarium scattergram are a fairly good reflection of the leaf B/L ratio characteristics of the habitats in which they were collected, one can, within certain limits extrapolate from the gradient scattergrams the kind of habitats from which the herbarium specimens originated, provided the main part of the leaf B/L variation is phenotypically induced by local ecogradients. This shows that the herbarium specimens of *austinii* chiefly derive from bog hummocks, as herbarium plots in positions corresponding to the wet-growing or minerotrophic gradient plots occur very rarely. I believe this behaviour reflects the positions in the field where *austinii* is most easily recognized and thereby collected, namely on arched bog hummocks. In the more wet-growing habitats, the colour and habit of *austinii* become more anonymous, and the plants can then be easily confused with, for example *S. papillosum*. But the herbarium scattergram of *austinii* also of course reflects the most common habitat of the taxon in Norway.

In the case of *affine*, the herbarium and the morphogradient plot groupings are more in accordance with each other. But the scarcity and partial lack of herbarium plots in the morphogradient plot area corresponding to the most wet-growing ecads, is conspicuous. Likewise, there is a noticeable lack of herbarium plots of *affine* in that part of the morphogradient B/L scattergram which is occupied by plots reflecting ecads growing in the shade. Those differences are not especially surprising as the lawn and low-level hummock ecads of *affine* are the most common ones in the field, and at the same time they possess shoots which are sufficiently brown enough to fit the description of *S. imbricatum* usually given in handbooks of *Sphagnum*. The wet- and shade-growing ecads of *affine* have predominantly greenish shoots, and thus may very easily be mistaken for *S. papillosum*, *S. palustre*, *S. centrale*, and even *S. magellanicum* in the field.

However, the most surprising difference in distribution between the herbarium specimen plots and the morphogradient plots of *affine* (Figs. 5, 14) lies in the abundance of stem leaf herbarium plots in the B/L range of about 58-67 %; morphogradient plots of *affine* are absent in this part of the B/L scattergram. Judging from the variational trend observed along the different ecogradients of *affine*, I am inclined to believe that the herbarium specimens of *affine* which provide the low B/L values (Fig. 5) mostly originate from more high-level hummocks than are included in the *affine* morphogradients, and that these are at the same time fairly rich in nutrients. This is a less common habitat for *affine* in Norway but is more in agreement with the habitat usually cited for *S. imbricatum* in the literature.

It may be concluded from the above comparisons that the Norwegian herbarium specimens of *affine* and *austinii* included in the present study do not give a reliable picture of the habitat amplitude met with as regards the leaf B/L ratios of the two taxa. In the case of *austinii*, the B/L scattergram (Fig. 5) is a fairly good reflection of its most common habitat in Norway, ombrotrophic hummocks. But in the case of *affine*, there is evidently an overrepresentation of specimens collected from fairly high-level minerotrophic hummocks as compared with its habitat preference in the field, viz. minerotrophic lawns and low-level hummocks.

If leaf B/L "morphoareas" are to be defined for the two taxa with regard to the Norwegian material studied and with the intention of covering their usual habitats, the typical leaf "morphoarea" for *austinii* can be looked on as the B/L values of about 52-64(66) % for the stem leaves, and 54-66(68) % for the branch leaves. The corresponding "morphoarea" values for *affine* are approximately 66-84 % and 70-86 %, respectively. However, *affine* and *austinii* are in reality less readily distinguishable on the basis of the leaf B/L parameter than the herbarium scattergram (Fig. 5) implies. This is emphasized when their entire habitat ranges are considered. One advantage of the morphogradient analyses is that they provide a rational way of explaining much of the variational pattern found in the herbarium scattergram. However, a regional morphological variation may be included in the herbarium scattergram which is not picked out by the morphogradient studies, as the herbarium material includes a larger spectrum of the ranges in distribution of the two taxa in Norway.

The quantitative results of the cultivation experiment should be treated with caution with respect to comparison with naturally-growing *austinii*. But, as moisture and illumination were constant factors, the relative position of the B/L and L values of the individual cultivations, must be assumed to be related to the different trophic levels employed in the experiment (except for the "inundation" experiment). Furthermore, the cultivation experiment suggests that the Ca factor in some way influences the leaf morphology of *austinii*. However, as it is impossible to change only the cation concentrations in nutrients employed in cultivation experiments, the chloride content in this particular case may also have had some sort of effect.

A striking feature of the cultivation experiment was that the "poor fen" sample had considerably longer branch leaves than the "bog" and especially the "intermediate fen" samples. Likewise, *austinii* had by far the longest branch leaves in the mixed-stand sample B, even thrugh this was collected at an intermediate position between samples A and C along the "wet-dry" ecogradient.

As was shown in the *austinii* morphogradient studies (Fig. 13), increasing wetness along the "wet-dry" ecogradient consistently led to shorter leaves in all the gradients, except for the branch leaves of the two exclusively minerotrophic gradients AU 5 and 6. There, the most wet-growing samples possessed the longest leaves on average and therefore seem to be more affected by the "poor-rich" than the "wet-dry" ecogradient. However, non of the differences are statistically significant (Table 4). Nevertheless, the three examples referred to do indicate the presence of a common trend, namely that *austinii* seems to develop its longest branch leaves along the "poor-rich" gradient in habitats which approximately correspond to a transitional poor fen richness, and that shorter leaves are found in bog and especially intermediate fen habitats. Although no observations were made at the mixed stand locality which led to sample B being placed in an intermediate position between samples A and C along the "poor-rich" ecogradient, it is not inconceivable that such was the case, and that this level was lying somewhere in the richer part of the poor fen spectrum. The distinctly shorter branch leaves of the extremely poor minerotrophic, low-level lawn sample AU 4b as compared with the ombrotrophic hummock sample AU 4a, should then be the result of the stronger effect of the "wet-dry" ecogradient relative to the "poor-rich" ecogradient. The stem leaf lengths of *austinii* seem to be less affected by the "poor-rich" ecogradient than the branch leaves (cf. Figs. 8, 21).

The distinctly shorter stem leaves in the "bog" sample compared with the original bog hummock sample of *austinii* in the cultivation experiment (Fig. 21) can be explained in several ways. Firstly, the cultivated shoots were kept more constantly wet than will be the case in a field hummock of the kind from which *austinii* was collected. Secondly, the light intensity used during the cultivation period, is likely to be somewhat lower on average than at the exposed hummock from which *austinii* was collected. A shading effect like that seen in the morphogradient AU 11 (Fig. 13) may therefore be present. The effect of both these factors, i.e. increased wetness and increased shade, is shorter stem leaves. However, other factors may also have some influence.

The *affine* studies do not give an unambiguous explanation of how the "wet-dry" and the "poor-rich" ecogradients affect the leaf lengths. The picture is also complicated by the often uncorrelated alteration of the branch and stem leaves (cf. the morphogradients, Fig. 15). In the case of the stem leaves, the poorest (compare the *affine* hummock plot A and the *affine* plot from the extremely poor fen hummock in Fig. 8, with the alteration of *affine* in the transplantation experiment, Fig. 11) and the wettest habitats (compare the ombrotrophic morphogradient AF 12, with the majority of the other morphogradients, Figs. 15, 16) apparently promote the shortest stem leaves. If this holds true, the contradictory case where stem leaf lengths increase with increaseding wetness, as found in the *affine* mixed-stand study (Fig. 8) and in morphogradients AF 2 and 5 (only AF 5 shows a significant difference, Table 4), can be explained in terms of a simultaneous alteration along the "poor-rich" ecogradient in the direction of a richer habitat (which was not clearly indicated by the species composition), where the effect of the "poor-rich" ecogradient is greater than the effect of the "wet-dry" ecogradient.

The widespread contradictory behaviour as regards the alteration of the branch leaf lengths compared with the stem leaves (Fig. 15), may reflect a greater sensitivity on the part of the former to alterations along the "poor-rich" ecogradient (see Fig. 8). The same trend was also seen in *austinii* (AU 5, AU 6, Fig. 13; see also plot B, Fig. 8). A comparison of *affine* and *austinii* in the mixed stands (Fig. 8), also shows that the "wet-dry" ecogradient begins to take effect earlier in *austinii* (when moving towards a wetter habitat) than the "poor-rich" ecogradient; this holds good for both the branch and the stem leaves (compare the A and C plots in the two taxa).

It could be suggested that the longer stem leaves in the drier than in the wetter-growing ecads of *affine* and *austinii* (at the same nutrient status) are the result of an etiolation effect. Increasing wetness leads to a less crowded habit with more distant branch fascicles permiting more light to reach the stem leaves than in the densely crowded hummock shoots of *affine* and especially *austinii*. The decreasing length of the stem leaves in the "shade-exposure" morphogradients of both *affine* and *austinii* with an increasing shading effect is, however, opposed to this hypothesis.

For the effect of the different ecogradients upon the cell structure see the description of the morphogradients (p. 38, 48).

How reliable are the results of the cultivation and the transplantation experiments performed? It may argued that periods involving 8 months of cultivation, and 2-3 years of transplantation, are too short to change one *Sphagnum* ecad into another, especially in a slow-growing taxon like *S. imbricatum*. There is some evidence (see e.g. Longton 1979: 361) that the morphological behaviour of bryophytes may partly be determined by the environmental conditions acting at the moment when the primordia of the shoot apices are formed. That view is to some degree also supported by the experiments performed by Agnew (1958) on British *Sphagna* in Sect. *Cuspidata*. This implies (in theory at least) that only leaves developed from primordia initiated in the new environment, should be interpreted. That developmental point is not easy to ascertain in practice, and can also be expected to vary from species to species, depending among other things on individual growth rate capacities. In any case, a transplantation period of nearly 3 years is very likely to have produced leaves which are the result of primordia initiated in the new environment.

DISTRIBUTION AND ECOLOGY

The detailed distribution maps are mainly based on revised material preserved in the herbaria of BG, H, O, S, TRH and TROM, with the addition of my own specimens and the personal specimens of A. Moen (Trondheim), A. Skogen (Bergen) and K.-D. Vorren (Tromsø). No specimen information derived from the literature is included in the detailed maps, nor any specimens with uncertain localization data. The climatic data used in the geographical discussions are mainly taken from Fægri (1960), Sjörs (1965), Bruun (1967), Bruun & Håland (1970), Hultén (1971), Abrahamsen et al. (1977), Laaksonen (1979) and DNMI (1982).

A. Ssp. *austinii*

The Norwegian distribution is shown in Fig. 23, the Fennoscandian distribution being outlined on the inset map.

In Norway austinii is seen to be strikingly restricted to a fairly narrow strip bordering the Atlantic Ocean. The northernmost localities known in Norway are situated in the archipelago of Lofoten and Vesterålen, at about 69°09'N latitude (Vorren 1979a). Only a few records have been made on the southern and southeastern coast, and the taxon is apparently absent (or at least rare) in the Olsofjord area of southeastern Norway. The occurrences in the extreme southeastern part of Østfold county - close to the Swedish border - are related to an area of distribution in the adjacent part of Sweden, mainly in the provinces of Västergötland, Småland and the northern part of Skåne. In addition, there is an interesting observation from Eidsskog, Hedmark county (Herb. TRH), this being the northernmost known locality in southeastern Norway.

Except for a few collections made in the interior parts of Rogaland county (see Moen 1975) and adjacent parts of Hordaland county in southwestern Norway where the taxon ascends to an altitude of about 600 m a.s.l., the majority of records are from strictly lowland areas under 300 m a.s.l. It should also be emphasized that all but a few of the known localities are sites within 20 km of the nearest shores of the Atlantic Ocean.

Austinii is a typical mire species in Norway, and mostly prefers bog hummocks situated on the open expanse of ombrotrophic mires. However, it is often also found growing in bog communities of a submarginal character with scattered *Pinus* (Fig. 24). On certain kinds of "atlantic bogs" which are in the erosional phase (see later), it is sometimes mostly confined to the submarginal part of the mires. However, *austinii* is not an exclusively ombrotrophic taxon as it is also occasionally found in fen hummocks of an oligotrophic to mesotrophic character, although in such cases it usually occurs in close connection with adjacent bog occurrences on the same mire. There seems, however, to be a tendency for it to occupy somewhat more minerotrophic sites towards the peripheries of its distribution in Norway, especially in the north (Vorren 1979a:9, 37).

As a rule the shoots of *austinii* are aggregated together in very compact and dense cushions with an even and firm external surface (Fig. 25). The cushions vary from fairly small fragments scattered as low-level patches on hummock surfaces, to large cushions building up high-level hummocks. Although *austinii* no doubt prefers a relatively high-level position on the hummocks, the cushions only rarely arch over the uppermost and very exposed summits. They more commonly occupy various positions on the rims where they are probably better protected from desiccating winds. Usually the cushions are situated well above the ground water level and its fluctations, and therefore also well above the indicative lower *Calluna* limit. However, occasionally the cushions descend continuously to reach upper hollow levels (mainly lawns), and may then be associated with, for example, *S. papillosum*. In hummocks with steep rims caused by erosion *austinii* cushions as a whole can settle slowly and eventually come to stand adjacent to mud-bottom hollows. Usually that kind of

Fig. 23. Distribution of *Sphagnum imbricatum* ssp. *austinii* in Norway as based on herbarium material. The inset map outlines the Fennoscandian distribution.

Fig. 24. The marginal part of an eroded "atlantic bog" in a *Pinus*-forested area in West Norway. In the foreground hollow vegetation, in the middle distance hummocks in which *Sphagnum imbricatum* ssp. *austinii* and *Racomitrium lanuginosum* predominate in the bottom layer. In the background a damp *Pinus sylvestris* forest. Locality: Hordaland. Osterøy, Herlandsnesjane. August 28, 1971 KIF.

cushion disintegrates during the movement, and occasionally disintegrated remnants of destroyed cushions can be observed behaving as lawn fragments surrounded by naked, eroded peat. These fragments seem healthy, and may function as starting points for regeneration of new, elevated cushions of *austinii*.

Among European Sphagna, *austinii* is the taxon that ascends to the highest levels in the bog hummocks. Only *S. fuscum*, the common substituting species of bog hummocks in more eastern, northern and subalpine mires of Norway, may reach and surpass the high-level position of *austinii*. As a rule, therefore, only very few *Sphagna* or other mosses are recorded inter-

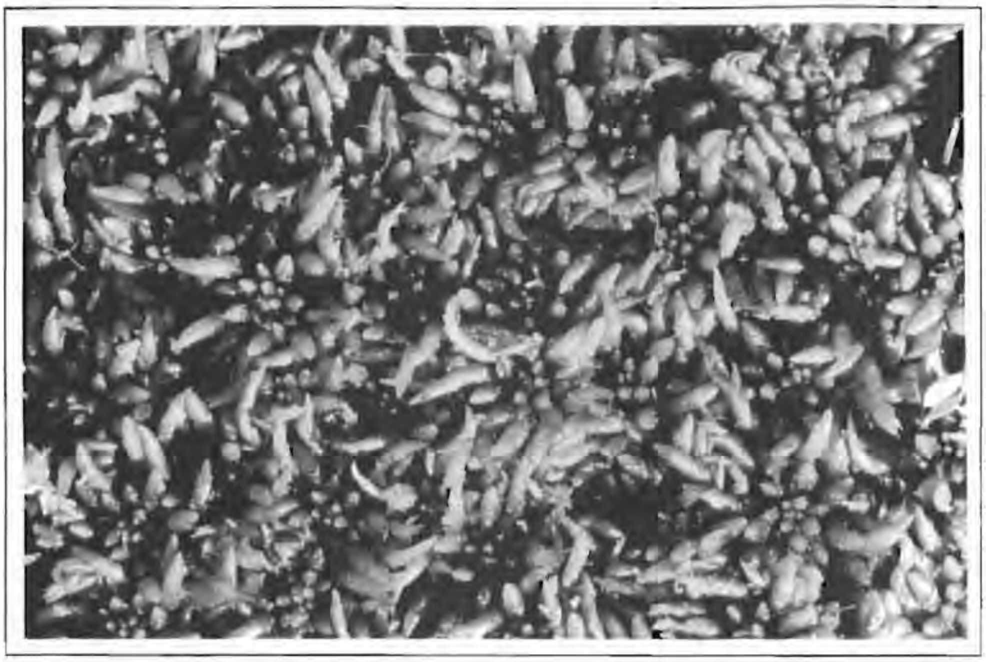


Fig. 25. Habit of *Sphagnum imbricatum* ssp. *austinii* growing in a bog hummock cushion. Note the compact external structure of the shoots, and the narrowly pointing and often somewhat curved divergent branches with tightly imbricate branch leaves. Locality: Sør-Trøndelag. Klæbu, Lysklettmyra. August 4, 1975 KIF.

mingled within the *austinii* cushions or growing adjacent to *austinii*. *S. rubellum* is the *Sphagnum* most commonly associated with *austinii*, and to some extent it overlaps the lower borders of the cushions. *Racomitrium lanuginosum* very often codominates in the bottom layer, but the two taxa usually grow side by side in individual cushions or mats without a pronounced overlap, and with *Racomitrium* in the highest levels. Hepatics are rare in expansive and relatively low-level cushions of *austinii*, but in high-level, compact, slow-growing or stagnant cushions, such hepatics as *Odontoschisma sphagni*, *Cepalozia* spp., *Lepidozia setacea*, *Riccardia latifrons* and *Mylia anomala* are usually interplaited. Lichens of the subgenus *Cladinae*, which form an important constituent of the bottom layer of the bog hummocks of many eastern and northern bogs in Norway, usually only occur sparsely; among them *Cladonia portentosa* is a common species. Cushions which are partly colonized or overgrown by algae and microlichens (like *Lecidea granulosa*) in the apices of the cushion cupolas of *austinii*, are common, and these undoubtedly function as starting points for an accentuated erosion of stagnant cushions.

The density and composition of the field layer varies somewhat depending on the relative position of the cushions, their age and their structure. In exposed positions with very compact cushions, vasculars are often totally absent except for a few scattered individuals of, for example, *Calluna* and/or *Eriophorum vaginatum*. At intermediate and lower levels, *Calluna* as a rule increases in frequency, but the field layer is often still sparse.

Table 7 (sqs. 1-9) gives a phytosociological survey of some typical *austinii* bog hummock sites in western Norway. Skogen (1969:95) and Vorren (1979a:9, b:35) give additional information on the sociological behaviour of *austinii* in Norway (their *S. imbricatum*). Quite similar communities are described from southwestern Sweden by Osvald (1923:137-139) and Malmer (1962a:267-268, 282, 291). The most commonly associated taxa in Fennoscandia seem to be: *Andromeda polifolia, Calluna vulgaris, Empetrum hermaphroditum* (in northern parts), *E. nigrum* (in western and southern parts), *Erica tetralix* (partly), *Eriophorum vaginatum, Drosera rotundifolia, Rubus chamaemorus, Sphagnum fuscum* (mostly in southeastern and northern localities), *Racomitrium lanuginosum, S. rubellum, Cephalozia* spp., *Lepidozia setacea, Mylia anomala, Cladonia portentosa* (partly). It is a characteristic feature that *Sphagnum fuscum* is lacking in *austinii* communities along the western coast of Norway south of the mouth of Trondheimsfjord. I have, however, found *S. fuscum* associated with *austinii* even in the most extreme coastal areas of West Norway, on the Lindås peninsula in Hordaland county.

The Scandinavian communities containing *austinii* mostly can be classified as belonging to the association Erico-Sphagnetum magellanici (Osvald 1923) Moore 1968, which has as characteristic and differential species *Erica tetralix, Narthecium ossifragum, Odontoschisma sphagni, Sphagnum imbricatum* (see

Dierssen 1982). This association constitutes part of the alliance Oxycocco-Ericion tetralicis (Nord. 1936) Tx. 1937 emend. Moore 1968, which is arranged in the order Erico-Sphagnetalia Schwick. 1940 emend. Br.-Bl. 1949. Erico-Sphagnetum magellanici, however, does not only include ombrotrophic atlantic bog and blanket bog communities, but also some types of sloping fen communities of temperate affinity from which *austinii* is absent but where *affine* commonly occurs. I consider it inadvisable to ingnore the "fen plant limit" when constructing and delimiting this mire association.

Some of the *austinii* communities situated at the northern and southeastern outskirts of the distribution of *austinii* in Scandinavia also exhibit a very close affinity to the association Empetro (hermaphroditi)-Sphagnetum fusci Du Rietz 1921, within the alliance Oxycocco-Empetrion hermaphroditi Nordh. 1936. In some cases, *austinii* is the sole differential taxon.

With respect to mire community complexes (in the sense of Dierssen & Dierssen 1978), *austinii* belongs to the Erio-Sphagnetum-Sphagno-Rhynchosporetum albae complex (p. 109). This community complex is found along the Norwegian coast from the Trøndelag region in the north to the county of Vestfold in the southeast. It avoids the Oslofjord area, but occurs again further southeast in Østfold county.

Austinii in Norway is mainly confined to mire complexes that can be called collectively "atlantic bogs" (sensu Moen 1973). This term embraces various hydrotopographical and physiognomical types of bog complexes, but excludes "blanket bogs" (s.str.) ("mountain blanket bogs", see Overbeck 1975:184). "Atlantic bogs" are distributed in a comparatively broad strip along the atlantic coast of Norway from about Kristiansand (Vest-Agder county) in the south to about Andøya (Nordland county) in the north (Moen 1973).

Floristically, the areas with "atlantic bogs" are characterized by the occurrence of a number of humid-demanding atlantic taxa like *Erica tetralix*, *Scirpus cespitosus* ssp. *germanicus*, *Juncus squarrosus* and *Sphagnum strictum*, which constitute the floristic province of *Erica tetralix*. "Atlantic bogs" occur in a narrow coastal strip which geographically corresponds approximately to the distribution of atlantic, ericaceous heaths. These are largely represented by "ridge raised bogs" ("ridge raised mires" sensu Moore & Bellamy 1974: 28), but also include some mires with close affinity to "lowland (coastal) blanket bogs" which have their main occurrence in western parts of the British Isles (Overbeck 1975:183). Further inland, in the forested areas, and more generally along the coast towards the north, an atlantic variety of more or less domed bogs predominates, often characterized by the mire features having a very reticulate pattern.

The "atlantic bogs", however, occupy only a western and lowland section of the floristic province of *Erica tetralix*, mostly corresponding to the distribution of *Scirpus cespitosus* ssp. *germanicus* of the above-mentioned taxa. It should, however, be emphasized that *austinii* is not strictly confined to "atlantic bog" complexes. It is also found in, for example, the eccentrically-domed bogs in southeastern Norway (Østfold county) (Moen 1970) and the Trøndelag area east of Trondheimsfjord. In southwestern Sweden it is also reported from "plateau domed bogs", but still in the *Erica* province (Aletsee 1967, Overbeck 1975: 174). In a vegetational context, the broad strip occupied by "atlantic bogs" is heterogenous, and consists of different vegetational sections and regions which pass through the Boreo-Nemoral and southern Boreal Zones of Norway. A near-shore main section cuts through the Boreo-Nemoral Zone of West Norway and continues, with decreasing frequency, northwards to Nordland where the bogs occur patchily through the southern Boreal Zone, including the archipelago of Lofoten and Vesterålen. But "atlantic bogs" are also common in the main section of the adjacent forested parts of the Boreo-Nemoral Zone of the southwestern and western coast, north to Nordland.

The "atlantic bogs" themselves are floristically and phytosociologically heterogenous in Norway, mainly as a reflection of chanching climatic and/or anthropogenic influences. They can be grouped in several vegetational subsections, although they are still not entirely clarified. Vorren (1979:a, b), and Eurola & Vorren (1980) outline, the characteristics and distribution of some of these subsections for Central and North Norway, and in these *austinii* is a constituent of the bog hummock vegetation.

Along the western coast of Norway, *austinii* has attained a present-day optimum, both in frequency and quantity, in the forested (mainly *Pinus sylvestris*) areas which usually are somewhat removed from the outer coast, but which in some places also extend out to the extreme coast, as on the islands of Bømlo and Stord in Hordaland county. The more or less raised bogs which often prevail in the forested areas, can physiognomically be characterized as "stagnant" or "erosional" complexes with an asymmetric and reticulate dissected pattern of mosaic mire features on their cupolas. The mire features include large, irregular and often very high-level hummocks (frequently occupied by small *Pinus*) surrounded by hollows (or extreme-oligotrophic "pseudohollows" with dispersed fragments of lawns, carpets and naked peat mud-bottoms (see Fig. 24). The marginal parts are usually dissected by erosional gullies acting as drainage pathways out of these mires. This kind of "atlantic bog" is fairly undisturbed by human activities in Norway, except for peat-cuttings which occur to a varying extent, largely depending on the distance to the nearest settlement. The type of "atlantic bog" outlined therefore mainly represents a climatically-determined climax in atlantic bog development. Nowadays, these bogs seem to be mostly in a stagnant or erosional phase. My observations suggest that the *austinii* cushions today reach an optimum, as regards extent, in the "stagnant complexes" along the western coast of Norway. The cushions occur more patchily in "erosional complexes", and seem to decrease in number at the expense of *Racomitrium lanuginosum*. This may be partly due to the erosional break-up and collapse of the compact *austinii* cushions, but I assume it is mostly due to the general lowering of the water table that occurs in connection with an erosional phase, and which commonly creates deeply penetrating gullies that effectively drain surplus water away from the bog cupolas. In hummock sites, where the atmospheric microhumidity is high, where the mean subsoil water level is permanently lowered for some reason, *R. lanuginosum* will undoubtedly in due course replace *austinii*. Along the western coast of Norway I have often observed cushions of *austinii* partly or almost completely overgrown by *Racomitrium*. The increase of *Racomitrium* when bogs in very humid areas dry out is also reported from the British Isles (Burnett 1964:

453). It seems that *R. lanuginosum* endures an exposed position and desiccation periods better than *austinii*, and probably this species is also practically independent of the level of the underlying water table. But like *austinii* it is a taxon which is weakly competitive having a linear growth capacity of about 5-15 mm per year according to Tallis (1964:417). However, *Racomitrium* under well-defined environmental circumstances is able to elongate its shoots distinctly over the surface of the *austinii* cushion. It furthermore seems that *Cladonia portentosa* in a successional stage prior to a *Racomitrium* takeover, sometimes effectively overgrows and kills *austinii* cushions, especially when a field layer of *Calluna* is present.

Austinii is considerably less abundant and frequent in the bogs of the woodless, extreme coastal parts of western Norway, than in the forested areas mentioned above. In this heathland region the "atlantic bogs" are characterized by a different physiognomy and relief (see Fig. 26). The microrelief much more undulating the hummocks are more low-level and less distinctly delimited from the underlying and often obscure hollows. Erosional features are less common, but as a rule some drainage gullies can be recognized. The field layer is dense, with *Calluna*, *Erica tetralix*, *Eriophorum vaginatum*, *Scirpus cespitosus* and sometimes *Narthecium* as important dominants, the relative composition often reflecting the degree of anthropogenic influence. The bottom layer is often sparsely developed, and *Sphagna* only exceptionally dominate over larger areas. The "fen plant limit" is often difficult to recognize, and this kind of "atlantic bog" often takes the form of extreme-oligotrophic "pseudobogs" with a varying content of euminerobionts. Partly at least, these "pseudobogs" represent regenerate phases after former very extensive peat-cutting activity.

The physiognomical and partly also the floristic difference between the two main types of "atlantic bogs" outlined above, namely the very reticulate raised type with distinct mire features and the "ridge raised bogs" (including "lowland blanket bogs"), undoubtedly are caused by a primarily different anthropogenic influence, but climatical parameters like strong winds may at present contribute to maintaining of the differences. The woodless, heathland region along the western coast of Norway has been intensively influenced up to the present day

Fig. 26. An "atlantic bog" in the outer, coastal heath region of West Norway, strongly influenced by anthropogenic activities. In the background plantation stands of *Pinus*. *Sphagnum imbricatum* ssp. *austinii* only occurs in a scattered fashion in this kind of "atlantic bog". Locality: Hordaland. Austerheim/Lindås, Storemyr at Mongstad (viewed towards SE). August 4, 1971 KIF.

by anthropogenic activities such as early deforestation, regular burnings, grazing by domestic animals, mowings, and peat-cuttings to obtain solid fuel. One or more of these activities has lasted for a considerable time, see e.g. Kaland (1974), Vorren (1979c). That kind of "atlantic bog" may therefore be termed an anthropogenically determined vegetational climax. According to Pearsall (1956), Birks & Birks (1974:611) and Birks et al. (1976:114) cushions of *S. imbricatum* are most sensitive to fires. I would also like to stress the importance of the trampling effect of grazing animals on the *austinii* cushions. Trampling breaks up the firm surface of the cushions easily promoting disintegration, which decreases the water-retaining capacity of the *austinii* cushions. The strong winds that prevail on the exposed coast are also likely to prevent to some degree the development of elevated *austinii* cushions, partly by physical damage, partly by increased evapotranspiration. This will more easily promote desiccation effects on the capitulum region of the cushions. The dense field layer, which is a common characteristic of these bogs, may also inhibit the building-up of *austinii* cushions, as the taxon undoubtedly has a low ability to compete, and according to Schumacher (1958) may also be sensitive to shade.

Austinii usually does not occur in the typical "blanket bogs" (s.str.) which are usually situated in higher-lying areas along the western coast of Norway than the "atlantic bogs". But like the "ridge raised bogs", the "blanket bogs" (s.str.) of this kind, are (or have been) heavily influenced by grazing, trampling and regular burnings, which have created an even surface with a dense field layer mostly unfitted for a general cushion rise of *Sphagna*. *Austinii* is so far unrecorded from the climatically determined "blanket bogs" (s.str.) in Trøndelag.

To summarize, I think it is essential to point out that *austinii* is a constant constituent of "atlantic bogs" throughout their distributional area in Norway, even though it is sometimes uncommon. Of the exclusively mire taxa, *austinii* is therefore floristically one of the best characterizers for the distribution of "atlantic bogs" in Norway, despite its occasional occurrences outside the "atlantic bog" area. As far as I have ascertained, no other mire vasculars, bryophytes or lichens coincide in their distribution with *austinii*. However, some of its common associates in the bog hummocks along the western coast, such as *Odontoschisma sphagni*, *Hypnum jutlandicum* and *Cladonia portentosa*, may have a similar distribution, but this requires confirmation. But these taxa are also common in *Calluna*-dominated coastal heath vegetation in addition to bog hummocks, and therefore should be classified as facultative mire taxa. Of the facultative mire vasculars commonly found growing in coastal hummocks, *Erica tetralix* shows approximately the same horizontal trend in its distribution as *austinii*, although broader in extension. Contrary to *austinii*, it also ascends up to pre- and subalpine altitudes throughout most of its distributional area (Fægri 1960). The same applies to *Sphagnum strictum*, which is now and then also found growing in hummocks of "atlantic bogs" in a narrow section along the southwestern coast (Flatberg 1976a). It is, however, the coastal heath taxon *Scirpus cespitosus* ssp. *germanicus* - only occasionally found in mire vegetation in Norway - that shows the closest similarity in horizontal and vertical distribution to *austinii* among the vasculars (Hultén 1971, Flatberg 1976b, Fremstad & Skogen 1978). As claimed by the last two authors (p. 39), ssp. *germanicus* is mainly restricted to lowland localities in Norway, but it reaches an altitude of about 860 m a.s.l. in the southeastern part of Hordaland county, i.e. in an area situated fairly close to the highest occurrences reported for *austinii* in Norway.

The distribution of *austinii* in relation to climatic variables can be summarized as follows:

1) The distributional area shows a close conformity with areas delimited by a maritime and temperate Köppen C-macroclimate (see e.g. Abrahamsen et al. 1977:33-34, 37-38), which is characterized by relatively mild winters (mean of coldest month exceeds about $-3^{\circ}C$), cool summers, lack of a regular dry season, and a high precipitation frequency.
2) It largely avoids areas with a precipitation frequency below 150 days each year, expressed as the number of days with a precipitation ≥ 0.1 mm (Fægri 1960).
3) It only occasionally ascends into upland and subalpine areas with precipitation maxima along the western coast, and is often also recorded growing in areas with a relatively low mean annual precipitation (between 750 and 1000 mm).

The relative and absolute positions of individual *Sphagna* along the ecogradients within one and the same mire site, and at corresponding sites in different regions and zones, and which *Sphagna* are present at the different sites, is in my opinion mainly a question of the relative growth rate capacity and the relative ability to avoid and/or tolerate desiccation. The growth-rate capacity of a particular *Sphagnum* at a certain microsite is determined by the sum of interacting factors such as:

1) Internal factors, which define the upper limit of growth rate at certain levels of an external influence (assimilation rate, respiration effect, cation exchange capacity etc.); 2) climatic

micro- and macrovariables (temperature, humidity, precipitation etc.); 3) the position of the mats/cushions relative to different trophic levels; 4) the degree of exposure (solar radiation, wind velocity), which influences the temperature of the surface layer of the capitula, the evapotranspiration and the atmospheric humidity of the immediate surroundings; 5) the water retention capacity; 6) the capillary ability to suck in water; 7) the ability to withstand evaporation loss.

Parameters 5, 6 and 7 depend on the surface structure, the density and compactness of the mats/cushions, and the proportion of internal and external capillary spaces which are present in the individual shoots (see e.g. Overbeck & Happach 1956), and which again to a large degree depends on the growth rate of the shoots, and thus to some extent creates a circular effect.

The cation-exchange capacity deserves comment as it may be important as an underlying factor in *Sphagnum* successions. Clymo (1963), Craige & Maass (1966) and Spearing (1972) have demonstrated that the cation exchange capacity in *Sphagna* is closely correlated to the content of polyuronic acid, and that hummock taxa have a higher content of that particular acid than hollow taxa. Pakarinen (1978) demonstrated a higher concentration of Ca in shoots of *S. fuscum* than in shoots of the hollow species *S. balticum* and *S. majus* collected at the same site; the difference is likely to reflect a different content of polyuronic acid.

The above considerations imply that each *Sphagnum* has a certain potential habitat range (potential econiche) where growth can be maintained, and an optimum habitat as regards growth rate, both of which will vary according to the peculiarities of the different sites. But in my experience it is the interaction and the growth competition with other *Sphagna* that very largely determine what part of the habitat range will be exposed - if any - at the different sites, and this need not necessarily be the optimum part of the range as far as concerns the growth rate is concerned (actual econiche).

The optimum microhabitats for growth rates in bog hummock and lawn *Sphagna* - as far as they are investigated - are situated in the wetter parts of their habitat amplitude (see e.g. Overbeck & Happach 1956, Clymo 1970, Pedersen 1975).

However, this is not tantamount to saying that this is the area best fitted for survival. A high growth rate also involves a more lax structure of the shoots and mats, and this increases the surface area for evapotranspiration and decreases the water retaining capacity and the effectiveness of capillary action. Such an alteration in structure therefore makes the shoots less able to withstand drought.

No investigations have so far been performed to exactly determine the growth rate capacity of *austinii* in its natural habitats, or under different induced environments. But as indicated by Green (1968) and Clymo (1970:18), and by my own cultivation experiments, growth is slow, probably slower than in most other European mire *Sphagna*, except for *S. fuscum*, *S. capillifolium* and possibly *S. rubellum* (see e.g. Overbeck & Happach 1956, Moore & Bellamy 1974:95). With the help of transplantation and cultivation experiments Green (1968: 55) found that aquatic ecads of *S. imbricatum* elongated their shoots considerably faster in wet than in dry habitats, but also that *S. imbricatum* had a markedly lower growth rate than *S. papillosum* under identical and fairly wet conditions. He also reported (op.cit.) that transplants grown intermixed with *S. recurvum* in a minerotrophic lawn community, were rapidly overgrown by the latter. (The material of *S. imbricatum* referred to is no longer available, but according to information given by Green (pers. comm. 1982) it must have belonged to ssp. *austinii*).

The general absence of *austinii* from bog hollows and fen sites can therefore be explained in terms of a low growth rate capacity compared with other competing *Sphagna*, like *S. papillosum*, *S. magellanicum*, *S. rubellum*, *S. recurvum* (s.lat.), and even *affine*. My own experiments and observations in the field have also ascertained that *austinii* is easily capable of growing in both wet (even inundated) and minerotrophic conditions. A slow growth rate, and thus a low ability to compete with other *Sphagna*, is therefore, in my opinion, an important factor in delimiting the present-day habitat niche of *austinii* in Boreal and Boreo-Nemoral peatlands.

Fairly high-level hummocks (primarily ombrotrophic ones) may be the only peat habitat in which *austinii* can effectively compete with - and also oust - other *Sphagna*. However, *Sphagna* growing in a hummock level will be vulnerable to desiccation effects. A prerequisite for survival of *Sphagna* with a high water-retaining capacity in such a habitat is likely to be either: 1) They are resistant to desiccation damage brought about by long-lasting droughts and thus can make moderate (or even slight) demands on the atmospheric humidity of the close surroundings and can also tolerate considerable oscillations in the subsoil water table; or 2) they are moderately or weakly resistant to long-lasting droughts, and thus require that the immediate atmospheric surroundings have a high and fairly constant humidity and/or a high frequency of precipitation; in addition they are sensitive to marked oscillations of the subsoil water table. My observations may indicate that *S. fuscum* and *austinii* are examples of the two kinds of *Sphagna*, respectively, but experiments are needed to confirm this.

The ability to take up water by capillary action and the water-retaining capacity of *austinii* are high, judging from the experiments made by Green (1968). The very dense and compact external structure of the cushions (Fig. 25), the very tight internal arrangement of the individual shoots and fascicles, the strongly concave and cucullate branch leaves closely and imbricately arranged, and the internal cell structure of the comb-lamellae in the leaf hyalocysts (Fig. 3), make *austinii* extremely well adapted to high-level hummock positions, provided that the immediate atmospheric surroundings have sufficient humidity and/or precipitation frequency. The amount of precipitation as such is scarcely especially decisive, due partly to the high ability of the cushions to store water falling in situ (or deposited as dewfall), and partly because of their high ability to raise water by capillary action from the underlying water table and retain that water. A high frequency of precipitation is undoubtedly of greater importance for *austinii* than the precipitation amount. Firstly, a high precipitation frequency keeps the cushions more or less constantly moist in the capitulum region. Secondly, an evenly distributed precipitation influences the hydrology of the mire sites in such a way as to prevent pronounced oscillations of the subsoil water level as compared with mire sites situated in more continental regions.

Probably, therefore, *austinii* in its most high-level positions is very sensitive to a lowering of the water table, and especially to long-lasting water-table low levels, which reduce the accessibility of capillary updrawn water to the capitulum region of the shoots. The reduced frequency and abundance of *austinii* observed in some highly eroded bogs as compared with less eroded, stagnant bogs in western Norway, may be brought about by a general lowering of the subsoil water table in the former complexes. That also helps to explain the declining frequency of *austinii* along the southeastern coast of Norway and its apparent absence from the neighbourhood of Oslofjorden, as both the humidity and the precipitation frequency are lower in these areas compared with areas where *austinii* is common. Its rarity along the southernmost parts of Norway (mostly the district of Jæren) is, however, at least as likely to be the result of the comprehensive destruction of mires by ditching and cultivation.

The local spatial and regional distribution of *austinii* in Norway may therefore be due to 1) its low growth rate capacity (low ability to compete with other *Sphagna*), 2) its high water-retaining capacity and its ability to effectively suck water by capillary action from the subsoil water table, and 3) the need for certain minimum levels of atmospheric humidity and frequency of precipitation.

However, the hygric and hydric parameters outlined, can hardly be the sole variables delimiting the distribution of *austinii* in Norway, as the taxon is absent from the maritime (and at least as humid) upland and subalpine areas along the western coast, except for the few occurrences in the interior parts of Rogaland and Hordaland counties previously referred to. The lowland affinity elsewhere along the western coast can only reflect the lack of suitable bog habitats at more elevated altitudes, due to the generally steep slopes of the mountains along most of the western coast. The distribution of the common habitat, i.e. the "atlantic bogs" themselves, is a lowland phenomenon, and results from thermic, hygric, hydric and geomorphological parameters.

Although the majority of the known *austinii* localities are confined to areas with a mean January temperature exceeding -2 to -3°C, I consider this conformity to be mainly of secondary importance, as Boreal *Sphagna* in my experience endure low winter temperatures very well. *Austinii*, indeed, is also exposed to very severe winter temperatures in arctic areas along the northern coast of Alaska (Flatberg 1984).

The absence of *austinii* from the coastally removed, but very humid and mire-rich areas of interior Trøndelag (altitudes 300-700 m a.s.l.) is somewhat surprising. These areas contain a number of hygric-demanding, peatland taxa such as *Erica tetralix, Sphagnum molle, S. strictum*. Apparently suitable ombrotrophic sites are common. Frequency and amount of precipitation, and humidity, should not be minimum factors, and the length of the growing season is about the same as in the Lofoten-Vesterålen archipelago where *austinii* occurs at its northern limit. Most of the areas mentioned in inner Trøndelag do, however, fall outside the influence of a maritime Köppen C-macroclimate, mainly due to relatively low winter temperatures. In what way a thick and long-lasting snowcover affects the structure of the cushions af *austinii* is unknown.

As previously mentioned the distribution of *Sphagnum fuscum* and *austinii* overlaps only to a moderate degree, and the taxa are mainly ecosubstituting in "atlantic" and "continental" bog hummocks, respectively. However, as mentioned, *S. fuscum* more commonly accompanies to *austinii* in outlying areas for the latter in Scandinavia (see also Malmer 1962:282, Vorren 1979a:9, b:35). At the easternmost locality known in Sør-Trøndelag county (Sq. 1, Table 7), *austinii* is restricted to three small hummock cushions; *Sphagnum fuscum* codominates with *austinii* in the bottom layer of one of the hummocks. The remainder out of the bog-expanse hummocks on this eccentrically-domed bog are occupied by *S. fuscum*, some *Racomitrium lanuginosum* (in the more elevated positions) and the macrolichens *Cladonia stellaris, C. arbuscula* and *C. rangiferina* in somewhat depressed levels, and *S. rubellum* in the lower levels bordering the hollows.

As *S. fuscum* and *austinii* occupy nearly identical niches as regards the mud-bottom - hummock vegetational gradient, it is reasonable to assume that only small alterations in the climatical parameters would decide which of them will predominate or be autocratic. If the growth interrelationship of *S. fuscum* and *austinii* with regard to different and varying climatical parameters was classified, it would probably provide important information helping to solve the distributional behaviour of *austinii* not only at present, but also in the past.

Another possible hypothesis (originally suggested by Green 1968) to explain the absence of *austinii* from the ocean-removed, but nevertheless very humid areas, is that *austinii* has a certain minimum demand for some chemical nutrients. This can be satisfied in bog sites situated close to the Atlantic Ocean by supply of sea salts carried by the strong onshore winds and the precipitation, but not in bogs further removed from the Atlantic Ocean. It is well known that several mire taxa have an "ombrotrophic ecoarea" in western Europe (Aletsee 1967). In Norway *S. papillosum* has a broad, coastal "ombrotrophic ecoarea", whereas *S. subnitens*, *S. strictum* and possibly *S. auriculatum* have a narrow "ombrotrophic ecoarea" confined to the extreme western coast. All those, and other taxa known to have an "ombrotrophic ecoarea" are, however, facultative bog taxa possessing a main, exclusively minerotrophic, ecoarea in addition to the ombrotrophic one. If the same applies to *austinii*, this taxon is mainly confined to its ombrotrophic ecoarea in Europe at the present time. That would be somewhat surprising, but the hypothesis should be further investigated and tested.

B. Ssp. *affine*

The Norwegian distribution is shown in Fig. 27, the Fennoscandian distribution being outlined on the inset map. A subatlantic distribution pattern is obvious, the distribution deviating in several ways from that of *austinii* (Fig. 23). The main occurrences are situated within the Boreo-Nemoral Zone, but Boreal occurrences are also common, e.g. in southeastern Norway and in Sweden north of "limes norrlandicus".

In Norway, it is recorded north to Meløy in Nordland county at lat. 66° 43' N (Vorren 1972:9). The localities known along the northern part of the west coast are, however, very scattered. In southeastern Norway it has been collected north to Våler in Hedmark county, and in Oppland county north to Gjøvik west of lake Mjøsa (Flatberg 1971:46-47). It has been recorded to an altitude of about 600 m a.s.l. in Oppland (Flatberg 1971:54-55), to about 400 m a.s.l. in Buskerud (Torbergsen 1980:50), and about 500 m in Telemark (Flatberg 1971), and in all these areas it reaches the upland coniferous subregion. Along the western coast of Norway it has been collected up to about 700 m a.s.l. in Hordaland county, and locally extends up into subalpine areas.

In Sweden *affine* is common in the western parts of the country north to Dalarna (Eriksson 1963:477), and has even been collected in northwestern parts of Jämtland (Handölsåns deltaland, 30. VII. 1946, Silfversparre, herb. S). The record of *S. imbricatum* from a prealpine mire site at about 500 m a.s.l. in northwestern Jämtland by Sjörs (1943:82, 1946:74) also very likely refers to *affine*. Along the coast of the Gulf of Bothnia it reaches Hälsingland, and unlikely *austinii*, it is also found in the southernmost parts of Finland (Auer 1937:19, Isoviita 1970:158; several specimens seen at herb. H). A general distributional feature is that the altitudinal amplitude narrows significantly towards sealevel, northwards along the western coast of Norway. It reaches the Boreo-Nemoral lowland area bordering Trondheimsfjord in the Trøndelag region, but is not recorded from the very humid, Boreal pre- and subalpine areas east of there.

Although it is not clearly visible from the distribution map (Fig. 27), the frequency of *affine* is low in the coastal heathland region bordering the west coast of Norway compared with the forested areas further inland.

In Norway (and probably elsewhere in Europe) *affine* has to be classified as an exclusively minerotrophic mire taxon. However, I have once in an "atlantic bog" mire situated on the Lindås peninsula, in Hordaland county, collected *affine* in a hummock community from which exclusively fen plant indicators were otherwise totally absent (see morphogradient AF 12).

Along the mud-bottom - hummock vegetational gradient, the main occurrence of *affine* is within lawn communities which are characterized by a soft bottom cover of *Sphagna* and by a fairly dense field layer. However, it also commonly occupies adjacent high-level carpets and the lower part of ericaceous hummocks. When present, it usually makes up extensive mats.

Fig. 27. Distribution of *Sphagnum imbricatum* ssp. *affine* in Norway as based on herbarium material. The inset map outlines the Fennoscandian distribution.

These are loosely arranged, possess a broken surface (contrary to *austinii*), and the shoots are more lax and have less imbricately-arranged branch leaves than in *austinii* (Fig. 29). Along the poor-rich vegetational gradient it prefers poor to intermediate fens, with a preference for the richer part of the poor fens (transitional poor fens). Some regional variation also seems to exist with regard to the latter gradient. In the southern and mainly Boreo-Nemoral parts of Scandinavia it has a fairly wide range along the poor-rich vegetational gradient, and extends from poor fens via transitional poor fens to intermediate fens (see Osvald 1923:209, Malmer 1962a:250, 252-253, 278-280, 284-285, Fransson 1972:122-123, 129). In the numerous wind-protected, slightly soligenous mires and mire sites of the Boreo-Nemoral and Boreal Zones situated north, northwest and west of Oslofjord in southeastern Norway (see Fig. 28), *affine* occurs most commonly in intermediate minerotrophic communities, and has as common associates in the bottom layer other *Sphagna* like *S. pulchrum, S. flexuosum, S. papillosum*, and sometimes also *S. subfulvum, S. subnitens, S. angermanicum*, and *S. warnstorfii* (Flatberg 1971:19, 22, 26-27, 34-35, 37-38, 43-44, 46, 55). The same also mostly applies to the western coast of Norway, where it undoubtedly prefers intermediate fens or transitional poor fens (Sqs. 10-14, 16-21, Table 7; Vorren 1972:8; Håland 1979:9), although it is found in poorer habitats as well (see above).

Along the mire margin-expanse vegetational gradient, *affine* prefers mire margin communities. But in fen sites with a distinct slope and movement of the subsoil water, it also commonly extends into expanse communities. Its most common habitat in the Boreal Zone is slightly soligenous fens situated in the bottom of small valleys and dips surrounded by forested hills. It mostly occurs along the margins of mire brooks and small mire lakes, in microsites which are influenced by periodical inundations (see also Sjörs 1946:74, Eriksson 1963:477, Vorren 1972:8). At the upper margin of soligenous fens where subsoil water is pressed out on to the surface it is now and then found growing in communities which are transitional to damp mineral soil heath and forest communities. In the humid parts of coastal Hordaland

Fig. 28. A slightly soligenous valley fen in the Boreo-Nemoral Zone of southern Norway. *Sphagnum imbricatum* ssp. *affine* is common in lawns and high-level carpets of poor to intermediate character. The mire is surrounded by ridges dominated by *Picea abies* with an element of *Fagus sylvatica*. Between the mire and the forested ridges, a narrow zone with *Betula pubescens* and scattered *Alnus glutinosa* occurs. Locality: Vestfold. Brunlanes, Storemyr SE of Tyskhus. August 5, 1970 KIF.

it is sometimes also found in connection with damp mesotrophic *Pinus sylvestris* forests. Likewise, in the coastal treeless, heathland region of West Norway it is sometimes found in connection with very small streams along with a vegetation that is transitional between mesotrophic fen and moist heath, and in such localities it may grow wholly exposed to the strong winds which often prevail there.

Judging from information given by Malmer (1962a), and my own experience from southeastern Norway, lagg fens and fen soaks are the common habitats in the Boreo-Nemoral Zone of

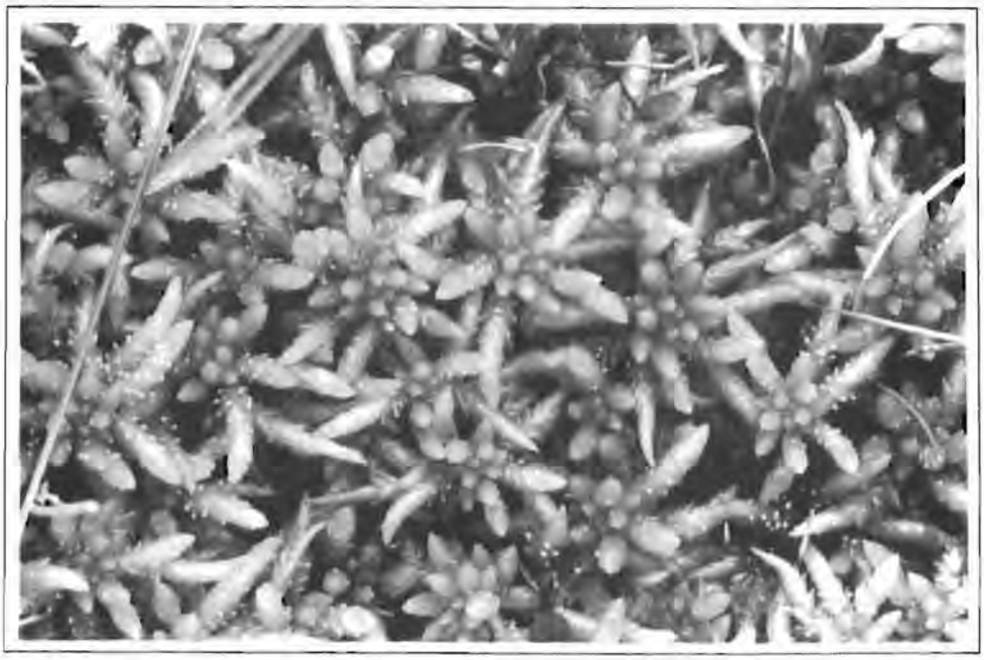


Fig. 29. Habit of *Sphagnum imbricatum* ssp. *affine* growing in a fen lawn community of intermediate character. Notice the loose arrangement of the shoots, and the fairly blunt tapering divergent branches with leaves that are somewhat recurved and dried-up at their apices. Locality: Møre & Romsdal. Rauma, E of Stenså. July 3, 1980 KIF.

Scandinavia in addition to small valley fens and fen soaks. The synedria squares presented (Table 7), mainly give an impression of the floristic composition in typical habitats of *affine* along the western coast of Norway. The presence of some exclusively minerotrophic *Carex* species and herbs is the most pronounced difference from the *austinii* synedria in the same table. The absence of hepatics and the limited importance of *Calluna*, are also striking features. The information given by Sjörs (1948), Fransson (1958, 1972) and Malmer (1962a), and the squares of Table 7, show that *Carex lasiocarpa* is an important species of *affine* communities in Scandinavia. The high frequency of *C. lasiocarpa* is indicative, as this species prefers sites where the water table is sloping somewhat and where it shows no profound fluctuations during the vegetative period (Malmer 1962a: 182-183). On the other hand, *C. lasiocarpa* has a wide range in minerotrophic mire vegetation (Gorham 1952), and it is indifferent with respect to the "mire margin-expanse" gradient. Of herbs, *Drosera rotundifolia*, *Menyanthes trifoliata* and *Potentilla erecta* seem to be the most common of the associated taxa. Along the western coast, the combination of *Carex dioica* and *C. pauciflora* is often typical for *affine* communities (Table 7).

The Fennoscandian communities which contain *affine* apparently fall into different syntaxa, which divide into at least the classes Oxycocco-Sphagnetea Br.-Bl. & Tx. 1943, and Scheuchzerio-Caricetea nigrae (Nordh. 1936)Tx. 1937. As pointed out earlier, *affine* often enters into oceanic/suboceanic fen communities which constitute a part of Erico-Sphagnetum magellanici. This is especially the case with fen lawn and hummock sites containing *affine*. However, some fen carpet types of *affine* communities with, for example, *Sphagnum fallax*, *Rhynchospora alba* and *Carex limosa*, and with *Menyanthes trifoliata* and *Carex lasiocarpa* as dominant field species (see e.g. Malmer 1962:278, Fransson 1972:122), undoubtedly conform closely to some alliances within *Scheuchzerietalia palustris* Nordh. 1936, especially the alliance Caricion lasiocarpae Osvald 1923 emend. Dierssen 1978. Some of the communities where *affine* is found growing along the coast of West Norway also group close to Ericetum tetralicis and moist varieties of the forest syntaxon Bazzanio-Pinetum K.-L.

The peculiarities of *affine* sites and the different ecological parameters acting there can be mentioned:

1) The growing habitats are characterized by a fairly stable subsoil water table.
2) The majority of occurrences are on fens with an apparently oxygen-rich subsoil water.
3) The habitats are as a rule situated in fen sites which are protected against wind (valley fens, lagg fens etc.).
4) *Affine* is usually absent from areas in Fennoscandia with an annual precipitation under 650-700 mm and in Norway with an annual precipitation frequency under 150 days (expressed as the number of days with a precipitation $\geq$0.1 mm).

Table 7. Selected synedria square analyses of *Sphagnum imbricatum* ssp. *austinii* (sqs. 1-9) and ssp. *affine* (sqs. 10-21) from Norway, showing typical aspects of their sociology. Degree of cover according to the Hult-Sernander scale. Square size 0.25 m^2.

Square No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Andromeda polifolia	1	1	1	1	-	-	-	-	-	-	1	2	1	1	1	1	2	3	1	-	-
Betula nana	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Calluna vulgaris	3	3	4	4	4	5	5	1	3	-	-	1	-	2	-	-	-	-	4	2	2
Empetrum nigrum	-	2	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Erica tetralix	-	1	1	-	-	1	1	-	1	-	-	-	1	2	-	-	-	-	-	1	-
Myrica gale	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-
Oxycoccus microcarpus	-	-	-	-	1	-	-	2	-	-	2	2	-	1	1	-	-	1	1	-	-
O. quadripetalus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-
Pinus sylvestris (juv.)	1	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	1	-
Comarum palustre	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Drosera rotundifolia	1	1	-	1	1	1	-	-	1	1	1	1	1	-	1	1	1	-	-	-	-
Equisetum fluviatile	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-
Menyanthes trifoliata	-	-	-	-	-	-	-	-	-	1	-	-	1	-	1	-	-	2	-	-	-
Narthecium ossifragum	-	-	1	-	1	2	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Potentilla erecta	-	-	-	-	-	-	-	-	-	-	1	1	-	3	-	2	1	-	1	1	-
Rubus chamaemorus	1	-	1	-	1	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-
Succisa pratensis	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Viola palustris	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-
Agrostis canina	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	1
Carex chordorrhiza	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
C. dioica	-	-	-	-	-	-	-	-	-	-	2	1	1	1	-	4	4	1	-	-	1
C. echinata	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	1	-	-	1	-
C. lasiocarpa	-	-	-	-	-	-	-	-	-	2	-	1	2	-	-	1	1	1	-	-	-
C. limosa	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
C. panicea	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	1	1
C. pauciflora	-	-	-	-	-	-	-	-	-	-	1	1	-	2	-	2	2	1	-	-	-
C. rostrata	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-
Eriophorum angustifolium	-	-	-	-	-	-	-	-	-	-	-	1	-	1	1	1	1	1	-	-	2
E. vaginatum	1	3	1	2	1	1	2	3	2	-	1	1	-	1	2	-	-	1	1	2	-
Juncus filiformis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Molinia caerulea	-	-	-	-	-	-	-	-	-	-	-	1	-	2	4	1	1	1	2	1	1
Scirpus cespitosus ssp. cespitosus	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1
Aulacomnium palustre	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Calliergon stramineum	-	-	-	-	-	-	-	-	-	1	1	1	-	-	-	1	1	2	1	1	2
Dicranum leioneuron	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Drepanocladus badius	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Hypnum jutlandicum	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Pleurozium schreberi	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pohlia nutans/sphagnic.	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Polytrichum alpestre	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Racomitrium lanuginosum	-	-	-	-	-	-	1	2	1	-	-	-	-	-	-	-	-	-	-	-	-
Sphagnum compactum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
S. fallax	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	1
S. flexuosum	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	1	-	-	-
S. imbr. ssp. affine	-	-	-	-	-	-	-	-	-	5	5	5	5	5	3	5	5	5	5	5	5
S. imbr. ssp. austinii	5	5	5	5	5	5	5	5	5	-	-	-	-	-	-	-	-	-	-	-	-
S. inundatum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
S. jensenii	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-
S. magellanicum	-	-	1	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
S. molle	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-	-	-	-	-
S. palustre	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-
S. papillosum	-	-	1	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	4	-	3
S. pulchrum	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	1	-	-	-
S. rubellum	3	-	3	2	3	3	3	1	3	-	1	2	-	-	-	-	1	1	-	1	-
S. subfulvum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-
S. subnitens	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	2	-	-	-	-
S. tenellum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Calypogeia sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Cephalozia spp.	1	1	-	1	1	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Lepidozia setacea	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mylia anomala	-	1	-	1	1	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Odontoschisma sphagni	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Riccardia latifrons	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cladonia portentosa	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-
C. uncialis	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
C. sp.	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Localities for the analyses: Sq. 1: ST: Klæbu, Lysklettmyra, ca. 150 m, NR 74,21, Aug. 19 1980. Sq. 2: ST: Snillfjord. E of Slåttavik, ca. 30 m, NR 10,42, July 7 1980. Sq 3: ST: Hitra. W of Sandstad, ca. 60 m, NR 03,44, Sept. 25 1980. Sq 4: ST: Hitra. At Middammen, ca. 50 m, MR 78,46, Sept. 26 1980. Sq. 5: MR: Rauma. NW of Soggesætra, ca. 30 m, MQ 31,31, July 3 1980. Sq 6: Ho: Lindås. SW of Ringås, ca. 30 m, KN 96-97, 37-38, Aug. 26 1971. Sqs. 7-9: Same as sq 6, but April 6 1982. Sq 10: Ho: Osterøy. NE of Vestrevatn, ca. 150 m, LN 11,19, Aug. 28 1971. Sqs. 11-12: MR: Rauma. E of Stenså, ca. 50 m, MQ 19,53, July 3 1980. Sq. 13: ST: Snillfjord. At Fossdalsvatn, ca. 110 m, NR 17,40, July 7 1980. Sq. 14: ST: Hitra. At Brattåstjønna, ca. 65 m, NR 03,33, Sept. 25 1980. Sq. 15: Bu: Hurum. N of Stikkvassklumpen, ca. 250 m, NM 86,11, Aug. 11 1970. Sqs. 16-17: ST: Orkdal. W of Husdalen, ca. 190 m, NR 431,265, Sept. 2 1981. Sq 18: ST: Orkdal. W of Husdalsvatnet, ca. 180-185 m, NR 42,26, Sept. 2 1981. Sqs. 19-20: Ho: Lindås. SW of Ringås, ca. 20-30 m, KN 96,38, April 5 1982. Sq. 21: Ho: Lindås. S of Mongstad, ca. 30 m, KN 84.47, April 6 1982.

5) It is common in the summer-warm but only moderately humid Boreo-Nemoral areas bordering Oslofjord in southeastern Norway.
6) Practically all the known localities of *affine* in Fennoscandia lie in areas with a mean July temperature exceeding about 14.0°C.
7) Some of the Boreal sites are situated in winter-cold areas with a mean January temperature between -5 and -10°C (e.g. west and east of lake Mjøsa in southeastern Norway.
8) It avoids the very humid Boreal areas of prealpine, eastern Trøndelag.

I believe that the regional and local distribution of *affine* in Norway mainly reflects areas with a relatively high summer temperature or a relatively favourable warmth sum during the vegetative period, and mire sites situated within areas having a fairly constant supply of nonstagnant subsoil water. Furthermore, it seems necessary that the water table should not have lenghty periods of low level. Precipitation and humidity (in the sense of precipitation in excess of evapotranspiration) probably are factors of more secondary importance for obtaining the necessary surplus of runoff water which is a prerequisite for the formation and maintenance of the kind of soligenous mire sites which *affine* prefers.

The abundance of *affine* in sheltered valley fens, along mire brooks and on peaty lake shores - especially in the Boreal Zone - probably also demonstrates some preference for a relatively high and constant atmospheric humidity in the close surroundings. During most of the growing season an ample supply of water will be no obstacle in *affine* sites, as a fairly stable water table is in close reach of the capitulum region. However, droughts involving a relatively low precipitation frequency and/or atmospheric macrohumidity, which will occur from time to time in more continental areas, can be critical. Thus I consider that *affine* is somewhat sensitive to desiccation effects. The water-retaining capacity and the desiccation tolerance is, however, unknown, but it may be thought to be moderate judging by the relatively loose surface structure of the mats and the fairly lax appearance of the individual shoots. The branch leaf apices of *affine* easily dry up due to their somewhat subsquarrose appearance (Fig. 29).

As mentioned earlier I have found *affine* growing in the heathland region of West Norway in highly exposed habitats. These areas are, however, characterized by high atmospheric humidity and a high frequency of precipitation throughout the year, and these conditions are likely to satisfy the demands for water supply in *affine*.

Lagg fens - a common habitat for *affine* in the Boreo-Nemoral Zone - are also sites possessing a favourable microhumid climate as they are usually areas with still air, and are often also protected against sunshine that promotes increased evapotranspiration.

Although there may be a slight risk of *affine* having been overlooked in the extensive, but thoroughly investigated area east of Trondheimsfjord in the Trøndelag region, it must anyway be very rare there. This area is rich in suitable soligenous fen sites, has a more than sufficient precipitation and atmospheric humidity, and several humid-demanding taxa are common there, so it is reasonable to assume that the warmth sum during the vegetative period must be a factor of some importance for the occurrence of *affine*. The predictable habitat niches for *affine* in this area are mainly occupied by *Sphagnum papillosum* and taxa within the *S. recurvum* complex. Since these taxa are among the most common associates of *affine* elsewhere in Fennoscandia it is unlikely that other *Sphagna* or bryophytes have ousted *affine* to account for its apparent absence there. The growth rate capacity of *affine* is unknown, but judging from the expansive communities in which it is usually found, it must be fairly high and comparable with, for example, *S. papillosum*.

The *affine* locality in western Jämtland is situated fairly close to the humid eastern upland forest and prealpine areas of Trøndelag. The two areas on the whole possess a similar climate, although, the summer temperature is generally somewhat more favourable in western Jämtland than in adjacent and corresponding parts of Trøndelag.

I consider that the warmth sum during the growing season is in some way responsible for the eastern and northern distributional limits along the western coast of Norway, and for the upper altitudinal limit more generally, whereas precipitation/humidity factors are responsible for the northern limits in southeastern Norway and adjacent parts of Sweden, and also for the northern limit along the Gulf of Bothnia and in Finland. The rarity of *affine* in many places on the extreme coast of western Central Norway (it is for example, extremely rare on the islands of Hitra and Smøla on the Trøndelag coast, and has not been found on the island of Frøya, see Fig. 27), is also strong support for the view that the summer temperature is of decisive importance for its distribution; the summer temperature is not especially favourable on those islands.

In its Fennoscandian distribution *affine* mainly behaves in a fashion intermediate to the vasculars *Myrica gale* and *Erica tetralix* (see Fægri 1960, Hultén 1971) as regards its horizontal distribution. Those two species are also commonly associated with *affine* in the field. But judging from the positions of the innermost localities of *Myrica* in southeastern Norway, and the prolonged northward extension in distribution of *Myrica* along the western coast of Norway and along the Gulf of Bothnia, the demands of *affine* to both atmospheric humidity and the summer temperature must be somewhat higher than of this species. *Erica*, on the contrary, may be looked on as having a greater requirement for atmospheric humidity and less for summer temperature than *affine*, judging, among other things by its total absence from the western part of the Oslofjord area and its abundance in the humid upland forest and subalpine parts of inner Trøndelag (Fægri 1960) where *affine* is absent.

The distribution of *affine* also shows some conformity with certain summer thermophilous, but only moderately humid-demanding and suboceanic mire taxa like *Drosera intermedia* (Hultén 1971, Skogen 1979:17), *Rhynchospora fusca* (Hultén 1971), and even the mire facultative taxon *Sieglingia decumbens* (Fægri 1960, Hultén 1971). These taxa also extend far northwards in southeastern Norway, but at the same time exhibit a pronounced coastal and lowland narrowing of their distributions towards the north along the western coast. It should also be emphasized that *Drosera intermedia* and *Rhynchospora fusca*, contrary to *Myrica* and *Erica* but in common with *affine*, have high-altitudinal occurrences in the mountains of Central and East Europe (e.g. in the Alps and the Carpathians, see Meusel et al. 1965). These two taxa, like *affine*, are also amphiatlantic in their distributions (Hultén 1958).

Affine has very much in common with *Sphagnum palustre* in its Fennoscandian distribution (Lid 1925:237, Nyholm 1954-1969:703, Isovitia 1970:158). Like *affine*, *S. palustre* is confined to lowland, coastal areas towards its northern limit along the western coast of Norway, and similarly also avoids the humid areas east of Trondheimsfjord in the Trøndelag region. *Sphagnum molle* (Nyholm 1954-1969:729, Isoviita 1970:161, Flatberg & Moen 1972:6) has a similar distribution to *affine*, but is apparently not so summer thermophilous, and perhaps also requires a higher atmospheric humidity. Detailed mapping of *S. inundatum* would probably also reveal a distributional pattern mainly like that of *affine*. I consider that *affine* in an ecogeographical sense is best classified as behaving intermediately between a suboceanic, primarily humid-demanding "*Erica tetralix* element", and a hydrophilous and summer thermophilous suboceanic element with only moderate demands for atmospheric macrohumidity, and which contains species like *Drosera intermedia*, *Rhynchospora fusca*, *R. alba*, *Lycopodium inundatum*, *Ophioglossum vulgatum*, and maybe also *Myrica gale*. Typical features of the distribution of all those taxa in Fennoscandia are that they reach the coastlines of the Gulf of Bothnia in both Sweden and Finland and that they are found north to at least the southern end of lake Mjøsa in southeastern Norway.

Although *affine* exhibits the same "Nemoral" trend in its Fennoscandian distribution as the above species, I believe it is somewhat more macrohumid-demanding than those. This difference may simply reflect the different methods used for intake and retention of water in a vascular and a *Sphagnum*. In Fig. 30 I have attempted to group *affine* relative to some other taxa with an atlantic affinity in their Fennoscandian distribution, using climatical parameters as the variables.

POSTGLACIAL HISTORY

Several stratigraphic palaeoecological investigations of mires and peats situated in northwestern Europe have demonstrated that S. *imbricatum* was more abundant in most postglacial periods than at the present day (see e.g. Godwin & Conway 1939, King & Morris 1956, Schumacher 1958, Tallis 1964, Green 1968, Dickson 1973). *Sphagnum imbricatum* has even been found to constitute a large, and in part dominant subfossil component in the lower peatlayers of many bog mires in the British Isles. In the coastal areas of northwestern Germany the taxon is extinct or nearly so in areas where it has grown previously (Schumacher 1958:335). The same trend is obviously not so pronounced in Scandinavia as elswhere northwestern Europe.

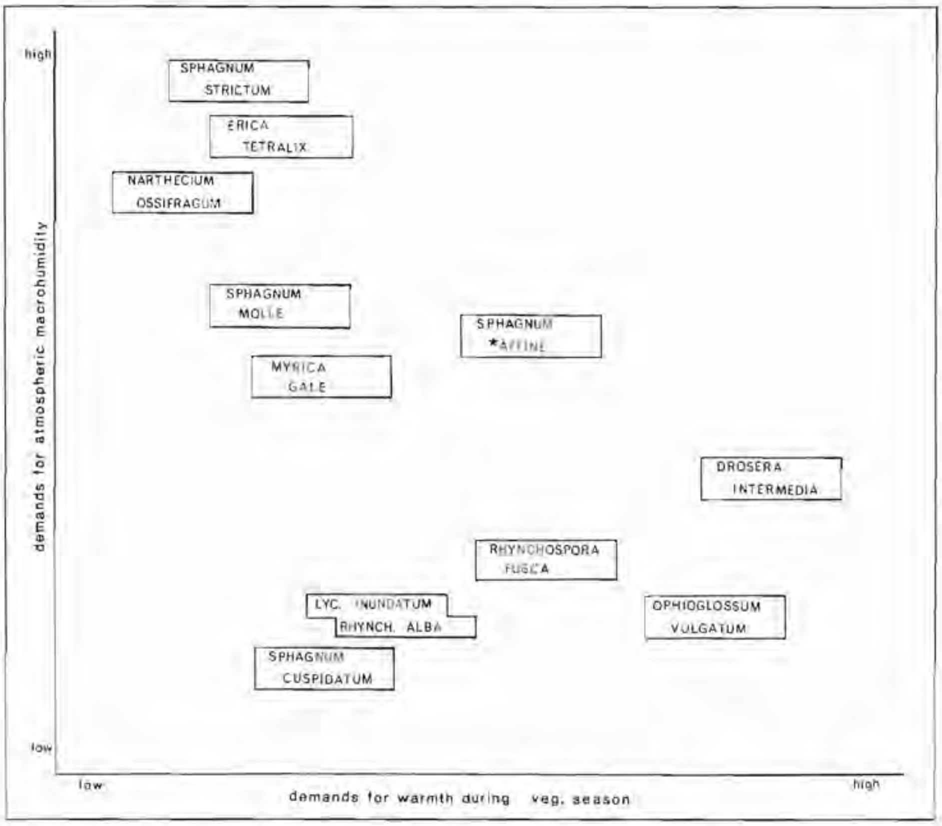


Fig. 30. Proposed position of *Sphagnum imbricatum* ssp. *affine* relative to some other subatlantic, wetland taxa in Fennoscandia, and as seen in relation to demands or preferences for two ecoclimatical factors.

Several theories have been put forward to explain the peculiar decrease and partial disappearance of *S. imbricatum* from many of the European peatlands. Godwin & Conway (1939) suggested a general decrease in the oceanity of the climate in recent times as the factor most responsible. King & Morrison (1956) and Lobley & Fitzgerald (1970) advocated lowering of the water table (mostly due to human activities), and the subsequent decreased ability of *S. imbricatum* to effectively compete with other *Sphagna* in drier facies, as the most reasonable factor. Pearsall (1956) and Pigott & Pigott (1963) also drew attention to the anthropogenic influence and proposed especially fire and grazing as factors destructive to a taxon like *S. imbricatum* (see also Birks & Birks 1974).

According to Tallis (1964), peat stratigraphy indicates the species to be very susceptible to a lowering of the water table. He therefore claimed that human exploitation was the main reason for its decline in many British peatlands. He even drew attention to atmospheric pollution as a recent factor of possible importance for the general decline of *Sphagna* in many British bogs. Green (1968) followed up an idea first put forward by Tallis (1961), that the abundance of *S. imbricatum* in many postglacial peats, could mainly be ascribed to the previous existence of semiaquatic ecads of the taxon, and that a lowering of the water table followed by a subsequent drying out of the mire surface for some reason gave rise to remnants that survived as solely hummock ecads.

A stratigraphic peat profile

In order to investigate the problem outlined above, with reference to Norway, a stratigraphic peat profile was performed at a mire locality where *austinii* is found growing abundantly on the surface at present.
The locality chosen was: Sør-Trøndelag Co., Trondheim. Høstadmyra, ca. 100 m, NR 56,31. The sampling was done on May 7, 1982.

Høstadmyra is a large and partly undisturbed, sligthly eccentric ombrotrophic mire complex. On the treeless expanse of the bog, hummocks and hollows alternate. The hummocks in this part of the bog are dominated by *Racomitrium lanuginosum and Cladonia* spp., but also contain *Sphagna* such as *S. fuscum, S. rubellum* (lower parts) and scattered patches of *austinii*. In the hollows *S. papillosum, S. magellanicum, S. rubellum, S. tenellum, S. balticum, S. majus* and *S. cuspidatum* are the dominant species.

Austinii occurs most abundantly in submarginal sites with more low-level *Calluna* hummocks where the hollows are not distinctly separated. *Racomitrium lanuginosum* and *Cladinae* play a less important role in such hummocks. Apart from *austinii, S. fuscum* is the most common *Sphagnum* and *Pleurozium* is also common. *Austinii* forms medium-level to sometimes fairly high-level, rust-brown cushions (see also morphogradient AU 13).

At Høstadmyra, *austinii* is situated close to its known eastern limit in the district. *Affine* is not found at Høstadmyra, or elswhere in the district at present.

The place selected for the profile was a medium-level ombrotrophic *Calluna* hummock with a small cushion of *austinii*, situated at the east side of the mire. The exact point of the profile was 20 cm outside the edge of the surface extent of the *austinii* cushion.

<u>Methods</u>: A Hiller peat sampler with a chamber length of 50 cm and a diameter of 2.5 cm was used. The standard distance between the samples was 10 cm. Each peat sample was taken from the central part of the core, and comprised a length of 1 cm on each side of the standard 10 cm marks. The samples were stored in small plastic bags with a flap, and were placed in a refrigerator until treated. In the laboratory, each sample was thoroughly washed with distilled water, and finally sieved. The sediments were examined with a dissection microscope, and a selection of the *Sphagnum* and other bryophyte leaves or parts of leaves that looked different were picked out and semipermanently mounted on slides. Special attention was paid to Sect. *Sphagnum* leaves, which are easily recognized even in a dissection microscope. Remnants of vasculars were ignored.

Bryophyte leaves and leaf fragments identified in in the peat samples:

(The number of leaves/leaf fragments refers to the number found in the slide preparations).

Sample 10 cm: A very few branch leaves of *austinii*; numerous shoot fragments and leaves of *S. fuscum*.

Sample 20 cm: The same as the preceding; in addition 5 stem leaves of *austinii*.

Sample 30 cm: Numerous shoot fragments and branch leaves of *austinii* and 2 stem leaves; scattered branch leaves and a few stem leaves of *S. fuscum*.

Sample 40 cm: The same as the preceding; 1 stem leaf of *austinii*.

Sample 50 cm: The same as the preceding; no stem leaves of *austinii*.

Sample 60 cm: The same as the three preceding; 1 stem leaf of *austinii*; no stem leaves of *S. fuscum*; 2 leaf fragments of *Dicranum leioneuron*.

Sample 70 cm: A few branch leaves of *austinii*; very few branch leaves of *S. fuscum*; 3 leaves/leaf fragments of *Dicranum leioneuron*; many leaves of *Pleurozium*.

Sample 80 cm: 1 branch leaf fragment of *austinii*; a few leaves of *Pleurozium*; a very few branch leaves of *S. fuscum*.

Sample 90 cm: 1 branch leaf of *austinii*; numerous branch leaves of and about 10 stem leaves *S. fuscum*; 1 branch leaf and 1 stem leaf of *S. balticum*; 1 leaf of *Pohlia nutans/sphagnicola*.

Sample 100 cm: 1 imperfect branch leaf of *austinii*; no other moss leaves.

Sample 110 cm: 2 branch fragments and scattered branch leaves of *austinii*; no other moss leaves.

Sample 120 cm: Numerous branch leaves of *austinii* and 1 stem leaf; very few branch leaves of *S.* cf. *fuscum*.

Sample 130 cm: Scattered branch leaves and 1 stem leaf of *austinii*; a very few branch leaves of *S.* cf. *fuscum*; 3 branch leaves of *S. tenellum*; upper half of 1 branch leaf of *S. majus*.

Sample 140 cm: Scattered branch leaves of *austinii*; scattered branch leaves of *S. fuscum*.

Sample 150 cm: Part of a branch, and scattered branch leaves of *austinii*; a few branch fragments and scattered branch leaves of *S. fuscum*; part of a *Cladinae* species.

Sample 160 cm: A few scattered branch leaves of *austinii*; part of a branch with leaves of *S. papillosum*; a few scattered branch leaves of *S. fuscum*.

Sample 170 cm: Scattered branch leaves and 1 stem leaf of *austinii*; numerous branch leaves of *S. rubellum*; a few branch leaves of *S. tenellum*; 1 branch leaf fragment of *S. majus*; 1 leaf of *Pleurozium*; a few leaves/leaf fragments of *Dicranum affine*.

Sample 180 cm: Part of 1 branch and scattered branch leaves of *austinii* and 1 stem leaf; scattered branch leaves of *S. fuscum* and *S. rubellum*, and 1 stem leaf of each.

Sample 190 cm: Scattered branch leaves of *austinii*; numerous branch leaves and 2 stem leaves of *S. fuscum*; scattered branch leaves and 1 stem leaf of *S. rubellum*; 1 shoot fragment of *Pleurozium*.

Sample 200 cm: Part of 1 branch, and scattered branch leaves of *austinii*; numerous branch leaves and 7 stem leaves of *S. rubellum*.

Sample 210 cm: Scattered branch leaves and 1 stem leaf of *austinii*; numerous branch leaves and 4 stem leaves of *S. rubellum*; scattered branch leaves of *S. fuscum*; a few leaves of *Drepanocladus fluitans* (coll); 1 leaf of each of *Calliergon sarmentosum*, *Pleurozium* and *Pohlia nutans/sphagnicola*.

Sample 220 cm: 2 branch leaves of *austinii*; numerous branch leaves of *S. fuscum*; scattered branch leaves and 1 stem leaf of *S.* cf. *capillifolium*; 1 branch leaf of *S.* cf. *angustifolium*; 2 shoot fragments of *Pohlia nutans/sphagnicola*.

Sample 230 cm: A few scattered branch leaves and 5 stem leaves of *austinii*; a few branch leaves and 1 stem leaf of *S. balticum*; 1 entire and 1 imperfect branch leaf of *S. strictum*; 1 leaf of each of *Aulacomnium palustre* and *Pohlia nutans/sphagnicola*.

Sample 240 cm: Scattered branch leaves of *austinii* and *S. fuscum*; numerous leaves of *Pleurozium*; 1 leaf of each of *Aulacomnium palustre* and *Racomitrium lanuginosum*; a few leaves of *Pohlia nutans/sphagnicola*.

Sample 250 cm: 3 branch leaves of *austinii*; a few scattered branch leaves of Section *Acutifolia*, including 1 leaf of *S.* cf. *warnstorfii*; a few leaves of each of *Calliergon stramineum*, *Hylocomium splendens* and *Pleurozium*.

Sample 260 cm: Numerous branch leaves of *austinii*; scattered branch leaves of Section *Acutifolia* (*S.* cf. *subnitens*); 1 shoot fragment of *Cladinae* sp.

Sample 270 cm: Scattered branch leaves and 2 stem leaves of *austinii*; several branch leaves of Section *Acutifolia* (*S.* cf. *subnitens*); 2 branch leaves of *S.* cf. *warnstorfii*; 6 leaves of *Hylocomium splendens*; 1 leaf fragment of *Dicranum* sp.

Sample 280 cm: Scattered branch leaves and 1 stem leaf of *austinii*; 1 branch leaf of Section *Acutifolia* (*S.* cf. *subnitens*); 1 branch leaf of *S.* cf. *warnstorfii*.

The bottom sample of the core at a depth of 280 cm partly consisted of clay; otherwise the samples consisted of peat.

Leaves of *S. imbricatum* were present in all the samples in the profile, but in the 80, 90 and 100 cm samples only one branch leaf/fragment of a branch leaf was found in each of the samples. Few leaves too were recorded in the 220 and 250 cm samples. Stem leaves were found in the 20, 30, 40, 60, 120, 130, 170, 180, 210, 270 and 280 cm samples, as a rule one leaf in each sample. It should, however, be emphasized that stem leaves are difficult to spot with a dissection microscope, so some may have been overlooked. Stem pieces of *S. imbricatum* were seen only in the 20, 30 and 40 cm samples, whereas parts of branches occurred more commonly.

All of the *S. imbricatum* leaves seen proved to belong to ssp. *austinii*, and little variation was seen in microscopical details. In the branch leaves, comb-lamellae occurred abundantly throughout, and the shape of the hyalocysts was also typical *austinii* (Fig. 31). In most cases, hyalocyst pores were also found on the median concave surface of the branch leaves.

All the stem leaves seen had characteristic hyalocyst comb-lamellae, and the hyalocysts in the marginal upper half regions were at the most 1-septated (Fig. 31).

The extreme rarity of other Section *Sphagnum* species is somewhat surprising as only *S. papillosum* was observed, and only in one sample. At present both *S. magellanicum* and *S. papillosum* are common on Høstadmyra. However, *S. papillosum* largely avoids the marginal and submarginal parts of the mire.

Sphagnum cf. *warnstorfii* in the 250, 270 and 280 cm samples is very likely that species, but as similar small ringed pores can also occur on the convex surface in the upper third of the branch leaves of *S. russowii* I will not definitely state the identity of the few leaves found.

The two branch leaves of *S. strictum* (one of them imperfect) in the 270 cm sample deserve comment. To my knowledge, this is the first subfossil report of this oceanic species. It is especially interesting that it was located in a peat layer which indicates a bog hummock as the growing habitat. At present, *S. strictum* is absent from Høstadmyra and the surroundings, but it is found in prealpine, moist heath vegetation at Gråkallen some 5 km east of the mire. *Sphagnum strictum* is the most humid-demanding of the Norwegian species in the genus, and is at present only found growing in ombrotrophic hummocks in a narrow zone bordering the coast of West Norway; i.e. its bog hummock occurrence in Norway is a highly oceanic phenomenon. In West Norway I have only twice found *S. strictum* growing in close association with *austinii* in bog hummock vegetation, namely at Ringås on the Lindås peninsula, and at Herlandsnesjane on Osterøy, both in Hordaland county (for precise locations, see Flatberg 1976:67, 99). The past occurrence at Høstadmyra indicates the presence of a more oceanic climate there previously.

The only indisputable leaf records of bryophyte taxa which in present day mire vegetation indicates minerotrophy, are

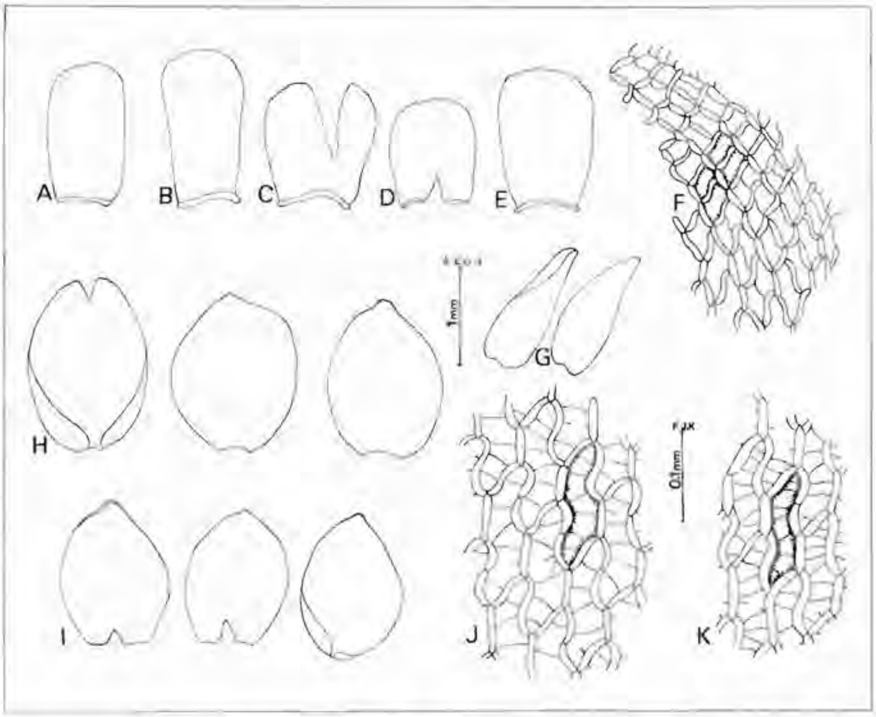


Fig. 31. Subfossil leaves and cell structure of *Sphagnum imbricatum* ssp. *austinii* from a peat profile (see Fig. 32). A-E: Stem leaves from samples at different depths. A: 40 cm; B: 130 cm; C: 210 cm; D: 270 cm; E: 280 cm. F: Subapical margin of a stem leaf from the sample at 270 cm depth. G: Narrow branch leaves of the kind excluded from the measurements. H-I: Branch leaves from the profile. H: 270 cm depth; I: 280 cm depth. J-K: Cell structure at the mid-median part of the concave surface of branch leaves. J: 270 cm depth; K: 280 cm depth. For locality see Fig. 32.

those of *Calliergon sarmentosum* in the 210 cm sample and of *Sphagnum* Section *Subsecunda* in the 280 cm sample. However, if the suggested leaves of *S. subnitens* and *S. warnstorfii* are taken into consideration, minerotrophy is also indicated for the 250, 260 and 270 cm levels, although *S. subnitens* (as previously mentioned) may at present be found scattered in ombrotrophic mire vegetation in the most oceanic and western parts of Norway.

Leaves of taxa which indicate lawn and carpet vegetation were found in the 130 (*Sphagnum tenellum*, *S. majus*), 160 (*S. papillosum*), 170 (*S. tenellum*, *S. majus*), 210 (*Calliergon sarmentosum*, *Drepanocladus fluitans*) and 260 (*S. tenellum*) cm samples. In present-day bog vegetation at Høstadmyra, *S. baltic-*

um and *S. rubellum* prefer hollow vegetation, but also occur in low-level hummock vegetation. Their presence in the 90, 230 (*S. balticum*), and 170 to 210 cm (*S. rubellum*) samples, may therefore indicate an element of vegetation that at least was of a low-level hummock kind, if not lower. It should, however, be emphasized that a peat sample 2 cm in length in the lower half of the profile at least, is likely to include several decades of vegetational development, i.e. more than one stage of succession can be involved in a particular sample. In most of the samples, one or several of the following hummock indicators were present: *Aulacomnium palustre, Cladinae* sp(p). *Hylocomium splendens, Pleurozium schreberi, Pohlia nutans/sphagnicola, Racomitrium lanuginosum* and especially *Sphagnum fuscum*.

Measurements (Fig. 32): The breadth to length ratio (B/L) of the intact (or nearly so) stem and branch leaves of *austinii* found on each slide was measured. With one exception, all kinds of leaves found were included in the measurements (see later). The mean B/L values were calculated for each slide. The surface B/L value of *austinii* (Fig. 32) is the same as that of the morphogradient sample AU 13e (Fig. 12).

Discussion: A complicating factor when attempts are made to compare these figures with the leaf B/L ratios of *austinii* presented previously (see especially Fig. 12) is that we do not know whether the subfossil leaves derive from divergent or pendent branches, and from what part of the branches. The branch leaves from the outer half of the pendent branches and from the exact tip of the divergent branches are very narrow and their shape make them easily recognizable (Fig. 31G). That kind of leaf which proved to be extremely rare in the profile samples, was left out of consideration when making the measurements.

In order to determine the B/L ratios of the branch leaves in present-day bog hummock *austinii* material, three pendent and three divergent branches were removed from fascicles of three shoots. The shoots were taken from the *austinii* cushion beside the profile sampling point. Leaves were removed from the base, middle and outer end of the divergent branches, and from the basal half of the pendent branches. Fifteen leaves of each of the four kinds were selected for B/L ratio measurements. The mean B/L values (%) obtained were: 59.3 ± 5.1 for leaves from the pendent branches, 69.1 ± 8.6, 63.3 ± 4.4 and 50.4 ± 4.4, respectively for leaves from the base, middle and outer end of the divergent branches. The mean for all of the sixty leaves was 61.5 ± 8.3%, i.e. there is close agreement between this and the mean B/L value for the middle part of the divergent branches (63.3 ± 4.4%).

To make an additional test of this apparent agreement the profile sample at 30 cm depth, which was very rich in *austinii* branch leaves, was examined in more detail. This sample is undoubtedly from a bog hummock level, indicated among other things by the abundant presence of *Sphagnum fuscum* leaves, and the B/L values of the two stem leaves found. Fifty-five branch leaves where detached from their branches, and the B/L ratio of all of them (except for the very narrow leaves referred to above) was determined, the mean value being 60.8 ± 9.4% (Fig. 32). This value is in good accordance with both the 60-leaves mean B/L value (61.5 ± 8.3%), and the surface sample B/L value (60.1 ± 1.3%, Fig. 32) which only took into account leaves from the middle part of divergent branches. However, the B/L values of both the 55- and the 60-leaves samples show a considerable scatter. In the latter case this undoubtedly is a result of leaves from different parts of the branches being included, and this is also likely to be the explanation in the 55-leaves sample. There are therefore some grounds for claiming that the B/L values obtained in the peat-profile samples of *austinii* (Fig. 32) are comparable to those found in for example, the morphogradient studies of *austinii*, provided that only profile samples numbering ten or more leaves are considered, and when trends are sought.

The stem leaves are usually less variable in shape than the branch leaves of *austinii*, and fewer leaves will be suffient to indicate the common B/L behaviour, although the B/L values of only one or two stem leaves will not give a reliable picture. All the seven uppermost samples from the profile (Fig. 32) are very likely to include the bog hummock ecad of *austinii*, as the low B/L values of the branch leaves (partly also the stem leaves) are in good accordance both with the surface sample of *austinii* and the bog hummock B/L plots of the morphogradient study (Fig. 12). For this reason, and provided the same morphological response of *austinii* to the "wet-dry" ecogradient was in existence in the past, one can with a reasonable degree of certainty also say that the 110, 140, 150, 160, 190, 230 and 240

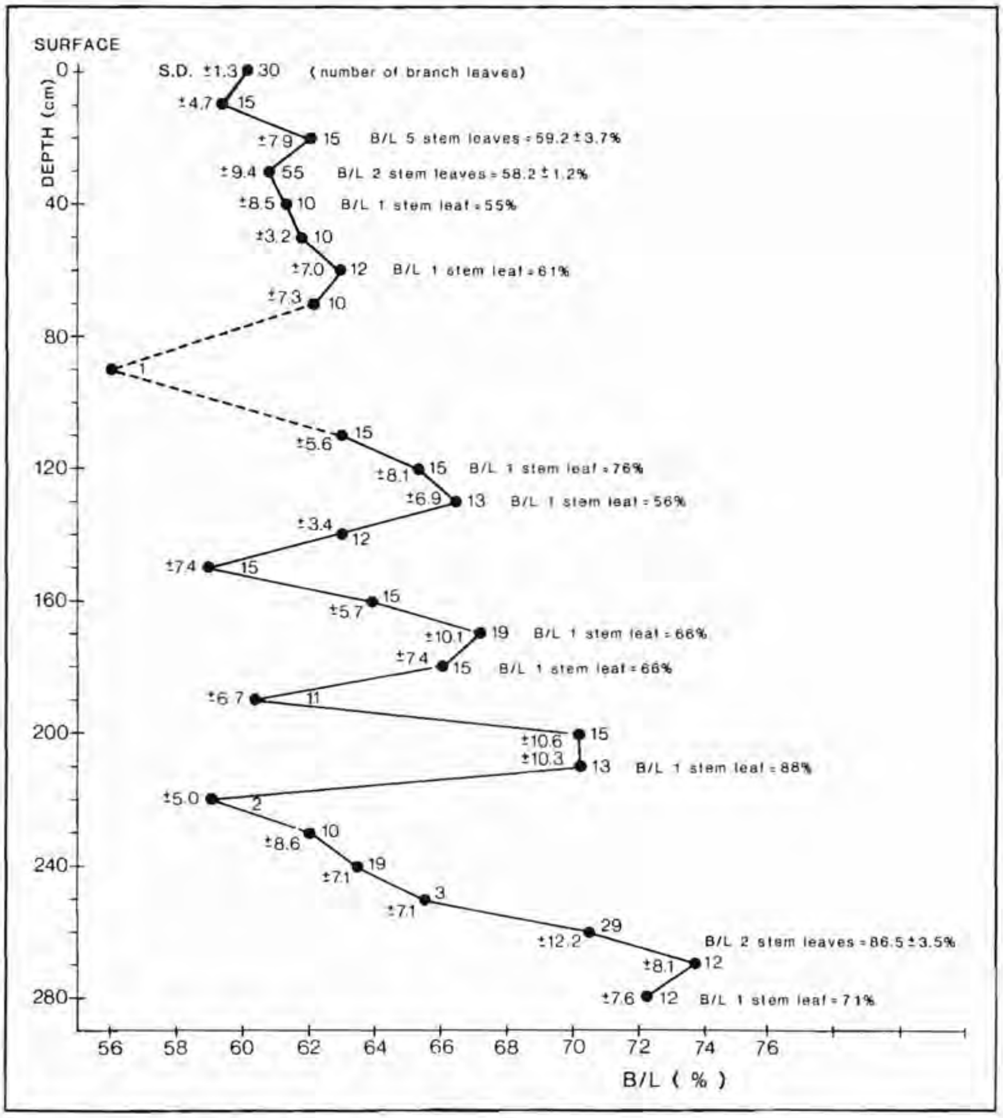


Fig. 32. Peat profile showing the breadth/length (B/L) ratio of subfossil branch leaves of *Sphagnum imbricatum* ssp. *austinii*. Locality: Sør-Trøndelag. Trondheim, Høstadmyra, May 7, 1982 KIF. See the text for methods.

cm samples are dominated by *austinii* branch leaves of a bog hummock origin. The 90 and 220 cm samples are left out of consideration. This also corresponds well with the remains of other mosses found in those samples as no really good hollow indicators were present.

The morphogradient study of *austinii* (Fig. 12) indicates that the bog hummock ecad is not likely to produce branch and stem leaves with a B/L ratio which has a mean value exceeding 65%. In Fig. 32, the peaks in the profile line with the highest branch leaf B/L values all exceed 65%, although not by much in the 120 and 170 cm samples. However, both those samples contain the lawn and carpet indicators *Sphagnum tenellum* and especially *S. majus*. When the mean B/L values of these two samples are compared with the B/L plots in Fig. 12, they show greatest conformity with AU 2b, 3b, and 7b among the "ombrotrophic-exposed" plots, which corresponds to a level along the mud-bottom - hummock vegetational gradient ranging from medium-level lawn to transitional between lawn and hummock. The high peak B/L values of the 200 and 210 cm samples are accompanied by the lawn and carpet indicators *Calliergon sarmentosum* (indicates also minerotrophy) and *Drepanocladus fluitans* of the 210 cm sample, although hummock indicators such as *Pleurozium* and *Sphagnum fuscum* are also present. However, the element of these taxa does not necessarily imply that *austinii* was growing in intimate association with them in the same community, for reasons previously mentioned.

The highest B/L values for branch leaves of *austinii* are found in the 260, 270 and 280 cm samples, i.e. in the bottom-layer samples of the profile. But when these values are compared with the wet-growing ecad plots in Fig. 12, they are found to fall short of the branch leaf B/L values usual in those. In as much as minerotrophic species are present (Section *Subsecunda*, and probably *S. subnitens* and *S warnstorfii*), in addition to the hummock indicators *Hylocomium splendens* (the 270 cm sample) and a *Cladinae* sp. (the 260 cm sample), a low-level minerotrophic hummock community is indicated. The two stem leaves of the 270 cm sample have an unusually high B/L value, as has also the 210 cm sample; the values are higher than any of the morphogradient plot values (Fig. 12).

The age of the bottom layer sample of the profile at a depth of 280 cm is unknown. In a peat profile investigated at Høstadmyra by K. Vik Knudsen in connection with a palaeoecological study (Vik Knudsen 1969, Pl. 1), the Atlantic period was recorded at a similar depth.

A comparison between the B/L values of the samples from the upper 1/3 and lower 2/3 of the profile (Fig. 32) gives some reason for claiming that *austinii* was more commonly growing in hollow vegetation in the past than at present or during at least part of the last few hundred years. But it should be made clear that the typical bog hummock ecad also occurred at Høstadmyra in the more remote postglacial past, as indicated both by the B/L profile line (Fig. 32) and by the species composition of the individual samples.

Postglacial synopsis. The stratigraphic investigation performed at Høstadmyra gives some support for the view that the postglacial wet-growing ecads of *S. imbricatum* mentioned by Green (1968) could refer to *austinii* (the subfossil material referred to by him is, however, no longer available; B.H. Green pers. comm. 1982). However, if this is the case, I find it unlikely that a lowering of the water table should lead to a disappearance from the hollows and not from the hummocks. I consider it more reasonable that *austinii* was ousted from the hollows by other *Sphagna*, such as *S. papillosum*. In the few cases where *austinii* is found growing in hollow vegetation at present, it is precisely in places where competition from other *Sphagna* is small. On the other hand, it shows no sign of failure to thrive under the influence of a fairly high water table. But the past postglacial abundance, the subsequent decrease, and the present rarity and partial extinction of *S. imbricatum* from many bog mires in northwestern Europe can also be explained as follows: *affine* was the main "*imbricatum*" constituent of carpets, lawns and low hummocks in the minerotrophic facies during the early peat development, but vanished or transferred to fen soaks or other minerotrophic sites when the mire surfaces become predominantly ombrotrophic. This can also explain some statements made by Green (1968), namely (1) that *S. imbricatum* in the past produced extensive mats ("lawns") under high water table conditions, (2) that the subfossil plants of *S. imbricatum* commonly had a more lax form of growth than the hummock ecads at present, (3) subfossil remnants of *S. imbricatum* are abundant in peats of a distinctly eutrophic character. These features fit very well some of the present ecological and morphological behaviours of *affine* in northwestern Europe. King & Morrison (1956:107) reported *S. palustre* (among other *Sphagna*) as commonly occurring along with *S. imbricatum* in Subatlantic peats. As *S. palustre* (at least at present) is an exclusively fen species in Europe, and partly prefers the same habitat as *affine*, this is further support for the above assumption. The measurements of leaves from Subatlantic peats made by Tallis (1961:384), furthermore indicate the existence of *affine*.

The transition from a minerotrophic to an ombrotrophic dominance in the surface layer of the mires had therefore to be succeeded by a corresponding decrease in the exclusively fen taxon *affine*, if it was initially growing there.

It should also be emphasized that a great many of the fens that today would be suitable for the growth of *affine* are cultivated or otherwise destroyed by human exploitation in vast areas of northwestern Europe. The common distribution in Norway of *affine* as compared with, for example in the British Isles, is mainly I think, due to a still common presence of undisturbed or only partially disturbed fens in the lowlands.

In the present state of knowledge concerning the postglacial history of *S. imbricatum* in Europe little can so far be said about the past distribution of *affine* and *austinii*. As the two European taxa of *S. imbricatum* can be distinguished on leaf characteristics with a high degree of certainty, it should not be difficult to estimate the quantitative and qualitative relationships between the two taxa in successive peat deposits and at different mire sites.

However, *austinii* undoubtedly became less frequent in many bog mires of western Europe during the last part of the Subatlantic. This is most likely to be chiefly the result of human interference in the form of burnings, grazing animals (trampling effects), extensive peat-cuttings, and in the last century also as a result of ditching for agricultural and forestry purposes. Only a detailed examination of *S. imbricatum* leaves in postglacial peat deposits in mire sites that preferably contain both *austinii* and *affine* at present, can reveal the postglacial history and the reciprocal development of the two taxa in northwestern Europe.

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REFERENCES

Abrahamsen, J., Dahl, E., Jakobsen, N.K., Kalliola, R., Påhlsson L., & Wilborg L. 1977. Naturgeografisk inndeling av Norden. *NUB 1977*,34:1-30.

Agnew, S. 1958. *A study in the experimental taxonomy of some British Sphagna (Section Cuspidata), with observations on their ecology.* Ph. D. thesis, Univ. of Wales.

Aletsee, L. 1967. Begriffliche und floristische Grundlagen zu einer Pflanzengeographischen Analyse der europäischen Regenwassermoorstandorte. *Beitr. Biol. Pflanzen* 43:117-283.

Andrus, R.E. 1974. *The Sphagna of New York State.* Ph. D. Thesis, State University of New York, College of Environmental Science and Forestry, Syracuse, New York.

Arnell, S. 1956. *Illustrated moss flora of Fennoscandia I. Hepaticae.* Lund.

Auer, A.V. 1937. Tietoja *Sphagnum*-lajien levinnelsydestä ja kasvupaikkojen luonteesta varsinais-suomessa. *Ann. Bot. Soc. Zool. Bot. fenn. Vanamo* 9:1-121.

Birks, H.J.B. & Birks, H.H. 1974. Studies on the bryophyte flora and vegetation of Isle of Skye. I. Flora. *J. Bryol.* 8:19-64.

Birks, H.J.B., Ratcliffe, D.A. & Goode, D.A. 1976. Distribution maps of bryophytes in Britain and Ireland. *Sphagnum imbricatum* Hornsch. ex Russ. *J. Bryol.* 9:114.

Brehm, K. 1970. Kationenaustausch bei Hochmoor-*Sphagnen*: Die Wirkungen von an den Austauscher gebundene Kationen in Kulturversuchen. *Beitr. Biol. Pfl.* 47:91-116.

Bruun, I. 1967. *Standard normals 1931-60 of the air temperature in Norway.* Det norske meteorologiske institutt, Oslo.

Bruun, I. and Håland, L. 1970. *Climatological summaries of Norway. Standard normals 1931-60 of number of days with various weather phenomena.* Det norske meteorologiske institutt, Oslo.

Burnett, J.H. 1964. *The vegetation of Scotland.* Edinburgh.

Clymo, R.S. 1963. Ion exchange in *Sphagnum* and its relation to bog ecology. *Ann. Bot.* (*London*) 27:309-324.

Clymo, R.S. 1970. The growth of *Sphagnum*: methods of measurement. *J. Ecol.* 58:13-49.

Craigie, J.S. & Maass, W.S.G. 1966. The cation-exchange in *Sphagnum* spp. *Ann. Bot.* (*London*) 30:153-154.

Dickson, J.H. 1973. *Bryophytes of the Pleistocene. The British records and its chorological and ecological implications.* Cambridge University Press, London.

Dierssen, K. 1982. *Die wichtigsten Pflanzengesellschaften der Moore NW-Europas.* Conservatoire et Jardin botaniques, Geneve.

Dierssen, K. & Dierssen, B. 1978. The distribution of communities and community complexes of oligotrophic mire sites in western Scandinavia. *Coll. Phytosoc.* 9: 95-119.

Det Norske Meteorologiske Institutt (DNMI), 1982. *Nedbørsnormaler* (*1931-60*).

Eddy, A. 1977. *Sphagnales* of tropical Asia. *Bull. Br. Mus. nat. Hist.* (*Bot.*) 5:359-445.

Eriksson, P.A. 1963. Några *Sphagnum*-lokaler från Västerdalarna. *Svensk bot. Tidskr.* 57:487-488.

Eurola, S. & Vorren, K.-D. 1980. Mire zones and sections in North Fennoscandia. *Aquilo Ser. Bot.* 17:39-56.

Flatberg, K.I. 1971. *Myrundersøkelser i fylkene Vestfold, Buskerud, Telemark og Oppland sommeren 1970. Rapport i forbindelse med Naturvernrådets landsplan for myrreservater og IBP-CT-Telmas myrundersøkelser i Norge.* K. norske Vidensk. Selsk. Mus. Trondheim. (Mimeographed paper).

- 1976a. Myrundersøkelser i Sogn og Fjordane og Hordaland i forbindelse med den norske myrreservatplanen. *K. norske Vidensk. Selsk. Mus. Rapp. Bot. Ser.* 1976,8: 1-112.

- 1976b. Plantefunn fra Lofoten. *Blyttia* 34:23-45.

- 1984. A taxonomical revision of the *Sphagnum imbricatum* complex. *K. norske Vidensk. Selsk. Skr. 1984*,3: 1-80.

Flatberg, K.I. & Moen, A. 1972. *Sphagnum angermanicum* og *S. molle* i Norge. *K. norske Vidensk. Selsk. Skr.* 3: 1-15.

Fransson, S. 1958. Stutekärret på Glahöjden i sydvästra Värmland. *Sv. Bot. Tidskr.* 52:112-132.

- 1972. Myrvegetation i sydvästra Värmland. *Acta Phytogeogr. Suec.* 57:1-133.

Fremstad, E. & Skogen, A. 1978. *Tricophorum caespitosum* ssp. *germanicum* i Norge. Blyttia 36:135-144.

Fægri, K. 1960. Maps of distribution of Norwegian plants I. The coast plants. *Univ. Bergen Skr.* 26:1-134.

Godwin, H. & Conway, V.M. 1939. The ecology of a raised bog near Tregaron, Cardiganshire. *J. Ecol.* 27:313-359.

Gorham, E. 1952. Variation in some chemical conditions along the borders of a *Carex lasiocarpa* fen community. *Oikos* 2:217-240.

Green, B.H. 1968. Factors influencing the spatial and temporal distribution of *Sphagnum imbricatum* Hornsch. ex. Russ. in the British Isles. *J. Ecol.* 56:47-58.

Hultén, E. 1971. *Atlas över växternas utbredning i Norden.* Stockholm.

Håland, B. 1979. Småull, *Eriophorum gracile*, på Jæren. *Blyttia* 37:7-10.

Isoviita, P. 1966. Studies on *Sphagnum* L. I. Nomenclatural revision of the European taxa. *Ann. Bot. Fenn.* 3: 199-264.

- 1970. Studies on *Sphagnum* L. II. Synopsis of the distribution in Finland and adjacent parts of Norway and the U.S.S.R. *Ann. Bot. Fenn.* 7:157-162.

Kaland, P.E. 1974. Ble lyngheiene skapt av fimbulvinter eller menneskeverk. *Forskningsnytt* 19:7-14.

King, A.L.K. & Morrison, M.E.S. 1956. *Sphagnum imbricatum* Hornsch. ex. Russ. *Irish Nat. Journ* 12:105-107.

Krog, H., Østhagen, H. & Tønsberg, T. 1980. *Lavflora. Norske busk- og bladlav.* Oslo.

Laaksonen, K. 1979. Areal distribution of monthly mean temperatures in Fennoscandia (1921-1950). *Fennia* 157:89-124.

Lane, D.M. & Dubois, S. 1981. Water analysis of habitats of *Sphagnum* in the Coastal Plain of North and South Carolina. *Bryologist* 84:408-413.

Lid, J. 1925. An account of the *Cymbifolia* group of the Sphagna of Norway. *Nyt Mag. Naturv.* 63:224-259.

- 1974. *Norsk og svensk flora, 4. ed.* Oslo.

Lobley, E.M. & Fitzgerald, J.W. 1970. A revision of the genus *Sphagnum* L. in a flora of the north-east of Ireland. *Irish Nat. Journ.* 16:357-365.

Longton, R.E. 1979. Studies on growth, reproduction and population ecology in relation to microclimate in the bipolar moss *Polytrichum alpestre*. *Bryologist* 82: 325-367.

Malmer, N. 1962a. Studies on mire vegetation in the Archaean Area of southwestern Götaland. I. Vegetation and habitat conditions on the Åkhult mire. *Opera Bot.* 7,1:1-322.

\- 1962b. Studies on mire vegetation in the Archaean Area of southwestern Götaland. II. Distribution and seasonal variation in elementary constituents on some mire sites. *Opera Bot.* 7,2:1-67.

\- 1966. *De svenska Sphagnum-arternas systematik och ekologi.* 3. ed. by M. Sonesson. Lund. (Mimeographed paper).

Meusel, K., Jäger, E. & Weinert, E. 1965. *Vergleichende Chorologie der zentraleuropäischen Flora.* Jena.

Moen, A. 1970. *Myrundersøkelser i Østfold, Akershus, Oslo og Hedmark. Rapport i forbindelse med Naturvernrådets landsplan for myrreservater og IBP-CT-Telmas myrundersøkelser i Norge.* K. norske Vidensk. Selsk. Mus. Trondheim. (Mimeographed paper).

\- 1973. Landsplan for myrreservater i Norge. *Norsk Geogr. Tidsskr.* 27:173-193.

\- 1975. Myrundersøkelser i Rogaland. Rapport i forbindelse med den norske myrreservatplanen. *K. norske Vidensk. Selsk. Mus. Rapp. Bot. Ser.* 1975,3:1-127.

Moore, P.D. & Bellamy, D.J. 1974. *Peatlands.* London.

Nyholm, E. 1954-1969. *Illustrated moss flora of Fennoscandia II. Musci.* Lund.

Osvald, H. 1923. Die Vegetation des Hochmoores Komosse. *Sv. Växtsoc. Sällsk. Handl.* 1:1-422.

Overbeck, F. 1975. *Botanisch-geologische Moorkunde.* Neumünster.

Overbeck, F. & Happach, H. 1956. Über das Wachstum und den Wasserhaushalt einiger Hochmoorsphagnen. *Flora* 144: 335-402.

Pakarinen, P. 1978. Production and nutrient ecology of three *Sphagnum* species in southern Finnish raised bogs. *Ann. Bot. Fenn.* 15:15-26.

Pearsall, W.H. 1956. Two blanket bogs in Sutherland. *J. Ecol.* 44:493-516.

Pedersen, A. 1975. Growth measurements of five *Sphagnum* species in South Norway. *Norw. J. Bot.* 22:277-284.

Pigott, C.D. & Pigott, M.E. 1963. Late-glacial and Post-glacial deposits at Malham, Yorkshire. *New Phytol.* 62:317-334.

Rudolph, H. 1963. Die Kultur von Hochmoor- *Sphagnum* unter definierten Bediengungen. *Beitr. Biol. Pfl.* 39: 153-157.

Rudolph, H., Kabsch, U. & Schmidt-Stohn, G. 1977. Änderungen des Chloroplastopigment-Spiegels bei *Sphagnum magellanicum* in Verlauf der Synthese von Sphagnorubin und anderer membranochromer Pigmente. *Z Planzenphysiol.* 82:197-116.

Schumacher, A. 1958. Über westdeutsche Standorte von *Sphagnum imbricatum* (Hornsch.) Russ. *Abh. naturv. Ver. Bremen* 35:335-350.

Sjörs, H. 1943. Några myrtyper vid Mjölkvattnet. *Sv. Natur* 1943:81-88.

- 1946. Myrvegetationen i Övre Långanområdet i Jämtland. *Ark. Bot.* 33 A(6):1-96.

- 1948. Myrvegetationen i Bergslagen. *Acta phytogeogr. Suec.* 21:1-299.

- 1965. Features of land and climate. *Acta phytogeogr. Suec.* 50:1-12.

Skogen, A. 1969. Trekk av noen oceaniske myrers vegetasjon og utvikling. *IHD* 1:88-95.

- 1979. Dikesoldugg, *Drosera intermedia*, i Norge. Blyttia 37:15-20.

Spearing, A.M. 1972. Cation-exchange capacity and galacturonic acid content of several species of *Sphagnum* in Sandy Ridge bog, central New York State. *Bryologist* 75:154-158.

Tallis, J.H. 1961. Some observations on *Sphagnum imbricatum*. *Trans. Br. bryol. Soc.* 4:384-385.

Tallis, J.H. 1964. Growth studies in *Rhacomitrium lanuginosum*. *Bryologist* 67:417-422.

Tolonen, K. & Hosiaisluoma, V. 1978. Chemical properties of surface water in Finnish ombrotrophic mire complexes with special reference to algal growth. *Ann. Bot. Fennici* 15:55-72.

Torbergsen, E.M. 1980. Myrundersøkelser i Buskerud i forbindelse med den norske myrreservatplanen. *K. norske Vidensk. Selsk. Mus. Rapp. Bot. Ser.* 1980,3:1-104.

Vik Knudsen, K. 1969. *Postglacial vegetasjons- og klimahistorie i Trondheimsområdet. Utarbeidelse av normaldiagram.* Cand.real. thesis, University of Trondheim.

Vorren K.-D. 1972. Namdalens Sphagnumflora. *K. norske Vidensk. Selsk. Mus. Miscellanea* 6:1-41.

\- 1979a. Myrinventeringer i Nordland, Troms og Finnmark, sommeren 1976, i forbindelse med den norske myrreservatplanen. *Tromura Nat. Ser.* 3:1-116.

\- 1979b. Die Moorvegetation in Namdalen, Mittel-Norwegen. Eine Untersuchung mit besonderer Berücksichtigung des ozeanischen Gradienten der südborealen Hochmoorvegetation. *Tromura Nat. Ser.* 8:1-102.

\- 1979c. Anthropogenic influence on the natural vegetation in coastal North Norway, during the Holocene. Development of farming and pastures. *Norw. Arch. Review* 12:1-21.

Witting, M. 1947. Katjonbestämningar i myrvatten. *Bot. Not.* 1947:287-304.

\- 1948. Preliminärt meddelande om fortsatta katjonbestemningar i myrvatten sommaren 1947. *Sv. Bot. Tidskr.* 42:116-132.

\- 1949. Kalciumhalten i några nordsvenska myrvatten. *Sv. Bot. Tidskr.* 43:715-739.