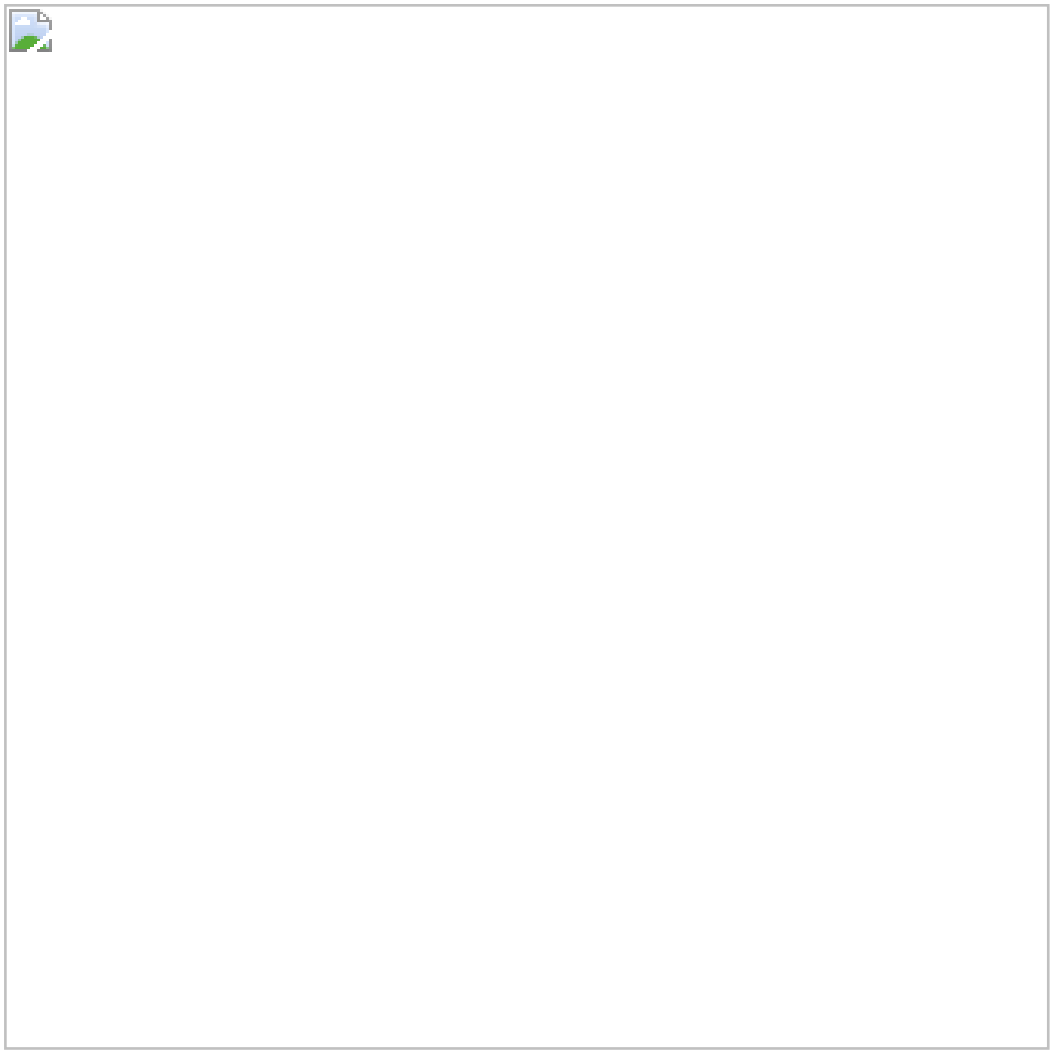

# Distribution, ecology, morphology and reproductive biology of Sphagnum majus in the south of its range (Hautes-Fagnes, Belgium)

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# Distribution, ecology, morphology and reproductive biology of *Sphagnum majus* in the south of its range (Hautes-Fagnes, Belgium)

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*Sphagnum majus* (Russ.) C. Jens. is a rare dioecious peat moss in its southern range, and in particular, in southern Belgium (Wallonia). Based on original field observations and revision of herbarium material, the distribution of this species in Wallonia is revised and updated. Although it is the most common of the two subspecies, *S. majus* subsp. *norvegicum* is reported from Belgium for the first time.The two subspecies are easily differentiated in the field based on macroscopic features, but high levels of variability of microscopic features were observed between the two subspecies in some populations. *Sphagnum majus* has a very specific niche and is nearly restricted to lithalsas, which are threatened ecological environments in the context of global climatic warming. In Wallonia, male plants of *Sphagnum majus* subsp. *norvegicum* are more common than in northern Europe. Capsule production was, however, observed at only one location.

Keywords: conservation, Cuspidata, ecology, norvegicum, Sphagnum, Sphagnum majus

*Sphagnum majus* (Russ.) C. Jens. is an allopolyploid dioecious peat moss that belongs to subgenus *Cuspidata* (Cronberg 1991, Såstad et al. 2000, Shaw et al. 2010). Macroscopically, *Sphagnum majus* is characterized by inconspicious apical bud, green to dark brown capitulum and fascicules of four hardly differentiated branches (Daniels and Eddy 1985). Microscopically, the abaxial surface of branch leaf hyalocysts possesses numerous pores (usually between 8 and 17, Fig. 1C, 2D) while the adaxial surface is usually aporose or possesses few commissural imperfect pores (Crum 1984, Hill 2004, Fig. 1D). Abaxial surface of antheridial bracts has few perfect pores and many commisural pseudopores (Flatberg 1987, Fig. 1E). Heavy staining is usually necessary to see the unringed pores of *S. majus* (Hill 2004). Chlorocysts are exposed on both surfaces but with wider exposure on abaxial surface (Hill 2004, Fig. 1C–D).

*Sphagnum majus* is common in the boreal and subarctic zones of Europe, northern Asia and eastern North America but rare in western North America (Daniels and Eddy 1985, Laine et al. 2018). *S. majus* is a rare peat moss in southwestern Europe and is not reported from Ireland, Portugal, Andorra and Grand-Duchy of Luxembourg (Sénéca and Söderström 2009, Hodgetts 2015). The southern limit of distribution of *S. majus* is located in Spain and is attributed to subsp. *norvegicum* (Munoz and Aldasoro 1995, Guerra and Cros 2007). In United Kingdom, *S. majus* is mainly known from several locations in northern Scotland (Sénéca and Söderström 2009, National Biodiversity Network 2019). In France, this peat moss is known from several locations in the Vosges mountains (Frahm and Bick 2013, Mahévas et al. 2016). Moreover, scattered records are reported from several departments: Ardennes, Cantal, Corrèze, Finistère, Isère, Loire, Lozère, Puy-de-Dôme and Savoie (Gauthier and Pujos 1994, Hugonnot 2007, De Beer 2017, Legland and Garraud 2018, CNBMC 2020). In the Netherlands, *S. majus* is a rare species mainly known from the northern area of the country (Siebel et al. 2012, VerspreidingsAtlas 2019).

*Sphagnum majus* includes two subspecies, subsp. *majus* and subsp. *norvegicum* Flatb. The distribution area of the two subspecies is still imperfectly known. Both subspecies are reported from Europe and North America (Flatberg 1987, McQueen and Andrus 2007). In Europe, subsp. *norvegicum* is a lowland taxon. This subspecies has a mainly western distribution and is reported from Norway, Sweden, Finland, Denmark, United Kingdom, France, Spain, Czech Republic, Slovenia and Lithuania (Flatberg 1987, Munoz and Aldasoro 1995, Sénéca and Söderström 2009, Hodgetts 2015, CNBMC 2020). Subspecies *majus* is mainly confined to minerotrophic mires and is an upland to subalpine taxon. This subspecies has a north–eastern distribution and is reported from Norway, Sweden, Denmark, France, the Netherlands, Germany, Austria, Slovenia, Poland, Romania, Estonia, Latvia, Lithuania, Ukrain, Belarus and Russia (Flatberg 1987, Sénéca and Söderström 2009, Hodgetts 2015).

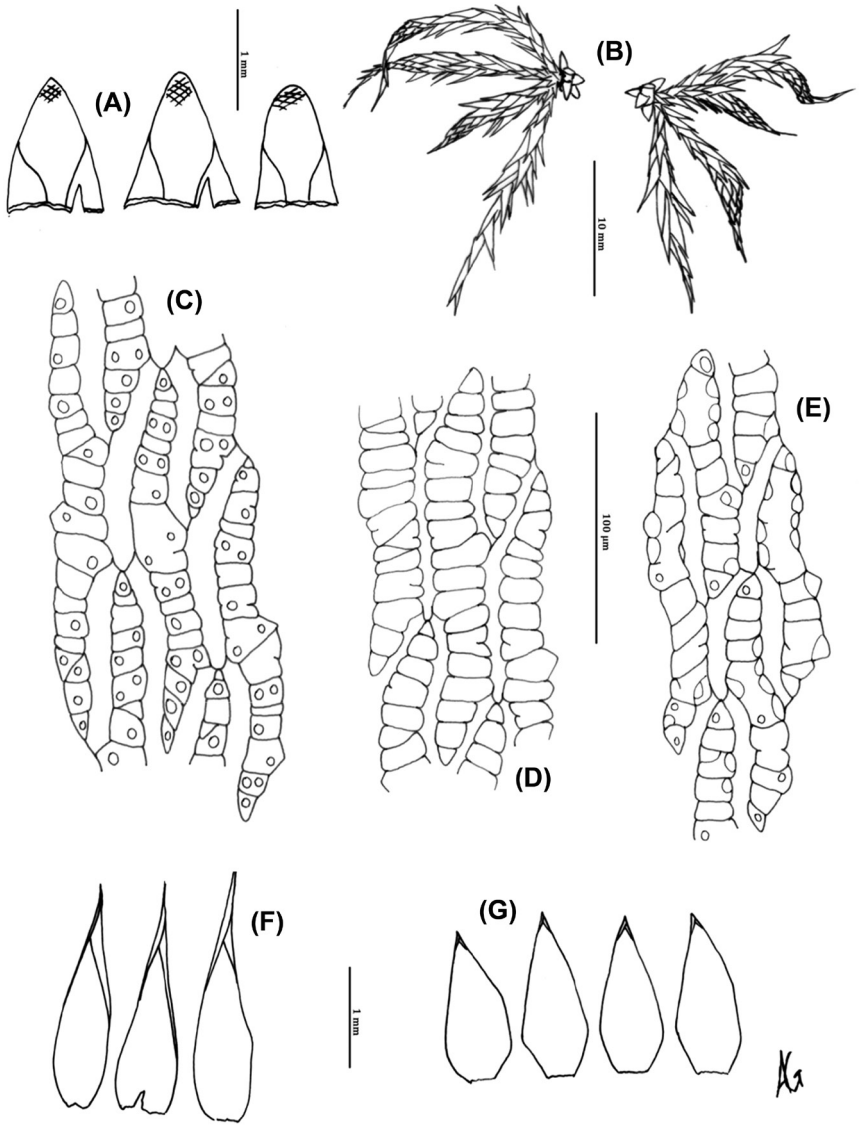


Figure 1. *Sphagnum majus* subsp. *majus*, male plants from oligotrophic mire. (A) Stem leaves. (B) Branche fascicules with three antheridial branches. (C) Abaxial surface of leaf from sterile divergent branche. (D) Adaxial surface of leaf from sterile divergent branche. (E) Abaxial surface of antheridial bract. (F) Leaves from middle part of sterile divergent branches. (G) Antheridial bracts. (Konnerzvenn, herb. Graulich no. SMAJUS43/19, 26 X 2019, dupl. TRH.)

The aim of this study is to report the morphological distinction between the two subspecies of *S. majus* and document their ecology and reproductive biology in southern Belgium.

## Material and methods

The distribution of *Sphagnum majus* in Wallonia was investigated based on field work and a revision of herbarium specimens of *S. cuspidatum* and *S. fallax*, with which it could have been confused, from BR and LG, and of one specimen collected by D. De Beer (no. 5967). Fieldword was conducted in the Hautes-Fagnes nature reserve located in the highlands of eastern Belgium. New localities were recorded according to the IFBL system (Atlas de la Flore de Wallonie 2020), which uses a 1 km$^2$ grid and wherein each 1 km$^2$ pixel is identified with a code of one letter and five numbers.

For stem leaf measurement, the leaves were removed from the part of stem below the capitulum. The breath over length (B/L) ratio was calculated from n leaves ($5 < n < 19$) for each stem, avoiding aberrant leaves (Appendix 1). A calibrated optical microscope was used for the leaf measurements. A saturated hydroalcoolic solution of crystal violet was used for staining to visualize the pores.

## Results and discussion

In Belgium, *Sphagnum majus* is a rare peat moss only known from ten locations in Flanders (De Beer 2017) and from Malchamps bogs (IFBL G8.31.12) in Wallonia (Sotiaux and Vanderpoorten 2015). The species was also reported from the minerotrophic fens of Landbruch (IFBL L7.56.32) (De Beer 2017), but re-identification in the course of the present work indicates that this collection (herb.

Table 1. Specimens examined.

Herbarium samples

F8.55.22, Waimes, Brackvenn, 10 VII 1978, «dans un pingo», leg. R. Schumacker, herb. LG no. 780710/05

G8, Membach, Fagne de la Soor, 03 XI 1957, «Bord de la Fagne de la Soor (Vallée de la Helle, Hautes-Fagnes)», leg. J. Lambinon, herb. LG no. nil

G8.14, Waimes, Fagne de Polleur, VIII 1936, leg. Delarge, herb. BR 5040068132386

G8.14.11, Baelen, Fagne des Deux-Séries, alt 620 m, 04 VII 1973, «butte tourbeuse à *Carex limosa* et *Phragmites communis*, entre les touffes de *Molinia* et *Carex*...», leg. P. De Zuttere, herb. LG no. B0172

G8.24.22, Waimes, Fagne Wallonne, 23 IX 1979, leg. P. De Bock, herb. BR 5040363408469

G8.31, Spa, Fagne de Malchamps, 06 VIII 1967, «tapis de sphaignes d'un vivier», leg. J. Lambinon, herb. LG 67/B/576 (with sporophytes!)

G8.31, Spa, Fagne de Malchamps, 06 VIII 1967, «flottant dans l'eau libre au milieu d'un vivier», leg. J. Lambinon, herb. LG 67/B/577

New records

F8.46.13, Eupen, Allgemeines Venn, 570 m a.s.l., 16 VI 2019, 50°59′53.13″N, 6°18′32.63″E, several mats of subsp. *norvegicum* in a closed ditch evolving towards bog, somewhat shaded oligotrophic location, herb. Graulich no. SMAJUS35/19 dupl. TRH

F8.46.14, Eupen, Steinley, 570 m a.s.l., 16 VI 2019, 50°60′29.96″N, 6°20′73.36″E, several small patches of subsp. *norvegicum* in a ditch along Steinley fen with *Sphagnum auriculatum*, open oligotrophic location, herb. Graulich no. SMAJUS37/19

F8.46.32, Eupen, Konnerzvenn, 595 m a.s.l., 01 VI 2019, 50°58′60.53″N, 6°19′93.60″E, subsp. *majus* and subsp. *norvegicum* in large mats in a damaged lithalsa by a draining track with *S. cuspidatum*, *S. fallax* and *Eriophorum angustifolium*, open oligotrophic location, herb. Graulich no. SMAJUS27/19maj and SMAJUS27/19norv

F8.46.34, Eupen, Konnerzvenn, 585 m a.s.l., 07 IV 2019, 50°58′43.01″N, 6°19′27.54″E, subsp. *norvegicum* in mats in a lithalsa, open ombrotrophic location, herb. Graulich no. SMAJUS10/19

F8.56.13, Waimes, Brackvenn sud, 610 m a.s.l., 24 II 2019, 50°56′71.59″N, 6°17′95.48″E, subsp. *majus* and subsp. *norvegicum* in large mats in lithalsa with *Eriophorum angustifolium* and *Lycopodiella inundata*, open ombrotrophic location, herb. Graulich no. SMAJUS03/19maj and SMAJUS03/19norv

F8.56.13, Waimes, Brackvenn sud, 610 m a.s.l., 16 VI 2019, 50°64′54.2″N, 6°17′70.72″E, subsp. *norvegicum* in large mats in a lithalsa with *Eriophorum angustifolium*, *Carex rostrata*, *Sphagnum cuspidatum* and *Sphagnum fallax*, open ombrotrophic location, herb. Graulich no. SMAJUS38/19 dupl. TRH

G7.47.24, Stoumont, Fagne de Pansîre, 550 m a.s.l., 12 V 2019, 50°42′81.22″N, 5°82′24.64″E, probably subsp. *norvegicum* (this population is large but suffers of recurrent droughts), in large mat with *Cyperaceae* in a lithalsa, open ombrotrophic location, herb. Graulich no. SMAJUS19/19

G8.14.32, Waimes, Fagne Wallonne, 650 m a.s.l., 31 III 2019, 50°52′05.68″N, 6°07′70.01″E, subsp. *norvegicum*, small population submerged near a *Sphagnum papillosum* hummock in stagnation zone of a ditch, also on bare peat along the ditch, open oligotrophic location, herb. Graulich no. SMAJUS07/19 and 08/19

G8.15.42, Bütgenbach, Schwarzbach, 555 m a.s.l., 23 VI 2020, 50°51′57.31″N, 6°16′54.78″E, subsp. *majus* and subsp. *norvegicum*, several carpets in a fen dominated by *Sphagnum affine*, open oligotrophic location, herb. Graulich no. SMAJUS01/20maj and SMAJUS01/20norv

G8.31.12, Spa, Fagne de Malchamps, 570 m a.s.l., 09 VI 2019, 50°46′38.98″N, 5°91′82.82″E, large mat of mixed male and female plants of subsp. *norvegicum* in a lithalsa, associated with *Eriophorum angustifolium* and *Carex rostrata*, open ombrotrophic location, herb. Graulich no. SMAJUS31/19 and 32/19 dupl. TRH

G8.31.21, Spa, Fagne de Malchamps, 570 m a.s.l., 19 V 2019, 50°46′38.16″N, 5°91′79.91″E, subsp. *norvegicum* in a lithalsa with *Sphagnum cuspidatum*, *Sphagnum fallax* and *Warnstorfia fluitans*, open ombrotrophic location, herb. Graulich no. SMAJUS22/19

D. De Beer no. 5967) is in fact *S. fallax* (H. Klinggr.) H. Klinggr. According to the presented observations, *Sphagnum majus* was largely overlooked in southern Belgium (Table 1) even if its distribution area is very limited in this territory. Thus in Wallonia, *Sphagnum majus* is only known from an area restricted to the highest crest of Belgium between Stoumont and Roetgen (Fig. 3). This crest is included in the Hautes-Fagnes nature reserve. Moreover this crest is known to possess a large number of lithalsas dating back to the last glaciation. Typically, an ombrotrophic mire is located in the central depression of these lithalsas and these bogs are suitable habitats for numerous uncommon species in Belgium. Nearly all observations of large mats of *S. majus* were made in ombrotrophic mires occupying lithalsas. *Sphagnum majus* is extremely hydrophilous and is confined to the wettest parts of open, ombrotrophic to slightly minerotrophic mires (Fig. 4A). In ombrotrophic mires, *Sphagnum majus* usually grows with *Carex rostrata* in an association known as *Caricetum rostratae sphagnetosum fallacis* (Gauthier and Pujos 1994). In the studied populations, *Carex rostrata* Stokes is present at Malchamps and at Brackvenn but *Eriophorum angustifolium* Honck. is much more abundant in these bogs. *Sphagnum fallax* and *S. cuspidatum* Ehrh. ex Hoffm. are the more frequently associated peat mosses to *S. majus* in these bogs (Fig. 4A). In these ombrotrophic mires, *S. majus* is the dominant species and forms large and nearly monospecific mats. The occurence of small patches of *S. majus* in ditches (Table 1: G8.14.32 and F8.46.14) is probably the result of vegetative multiplication from upstream stands located in a restricted area of the Hautes-Fagnes nature reserve. Several lithalsas are also present in a small area between Les Tailles and Bihain (IFBL H7.46 and H7.47). In the attempt to find *S. majus*, I prospected several lithalsas in this area but the species was found in none of them. Indeed, these lithalsas are nearly silted and dominated by *S. papillosum* Lindb., *S. capillifolium* (Ehrh.) Hedw. and *S. fallax*. This habitat is too dry for *S. majus*. Nevertheless I observed *S. cuspidatum* in these lithalsas but only in very small populations.

In the mixed stands both subspecies are easily separated macroscopically due to differences in color, shape of capitula and vigor (Fig. 4B). The distinguishing features between these both subpecies are described in Flatberg (1987). Due to its pale capitulum, subsp. *norvegicum* could be confused with *Sphagnum cuspidatum* in the field. Nevertheless *S. cuspidatum* is less robust and has a more crowded capitulum in ombrotrophic conditions (Flatberg 1987). Microscopically the differenciation between both subspecies is less obvious (Fig. 1, 2). The breadth/lenght (B/L) ratio of stem leaf is

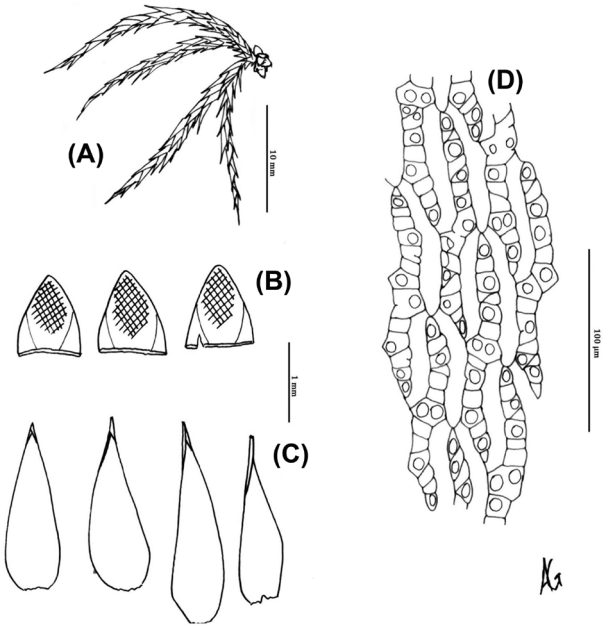


Figure 2. *Sphagnum majus* subsp. *norvegicum*, male plants from ombrotrophic mire. (A) Sterile branche fascicule. (B) Stem leaves. (C) Leaves from middle part of sterile divergent branches. (D) Abaxial surface of leaf from sterile divergent branche. (Brackvenn, herb. Graulich no. SMAJUS44/19, 26 X 2019, dupl. TRH.)

clearly the most useful feature to distingish both subspecies. In all sampled populations, subsp. *norvegicum* possess a B/L ratio of stem leaf comprises between 0.72 and 0.92, whereas subsp. *majus* has a B/L ratio between 0.62 and 0.75 (Appendix 1, Fig. 1A, 2A). This B/L ratio slightly overlaps between both subspecies which is in agreement with plants growing in similar poor-acidic conditions (Flatberg 1987). I recorded mixed stands of *S. majus* subsp. *majus* and *S. majus* subsp. *norvegicum* from Brackvenn (Table 1: F8.56), from Konnerzvenn (Table 1: F8.46) and from Schwarzbach (Table 1: G8.15). The three populations of subsp. *majus* fit well with features defining this subspecies. To the reverse subsp. *norvegicum* is a more variable taxon. In Konnervenn's populations, several very robust green specimens show intermediate features with stem leaf B/L ratio of 0.72, stem leaf apex acute-obtuse, branch leaf B/L ratio of 0.25. The branch leaf apex is hardly involute and exhibits a *majus*-like porosity. At Malchamps, collected specimens fit very well with the features of subsp. *norvegicum* concerning stem leaf and pore features, but branch leaves are falcate and strongly involute. At Allgemeines Venn, a population growing in a somewhat shaded location has *majus*-like pores but otherwise fits with typical subsp. *norvegicum* features. *Sphagnum majus* is known for its high variability and the value of both subspecies are not always accepted (Crum 1997, Guerra and Cros 2007). Effectively there is no clearcut morphological feature distinghising both subspecies and subsp. *norvegicum* shows considerable morphological variation in his various habitats. Even the lectotype of *S. majus* is difficult to assign to one of these subspecies (Flatberg 1987). Thus the main difference between these subspecies are the shape of the capitulum and the ability of subsp. *majus* to produce large amount of brown secondary pigments.

Male plants of the *S. majus* subsp. *norvegicum* are reported to be rare in central Norway (Flatberg 1987). In view of the small studied population, male plants of subsp. *norvegicum* are common in Wallonia. During autumn 2019, I found male plants of this subspecies at Malchamps (two ombrotrophic locations), at Brackvenn (one ombrotrophic location, Fig. 4E) and at Allgemeines Venn (one oligotrophic location, Fig. 4D). The antheridial branches appear at the end of summer. The antheridial growth is rapid but spermatogenesis lasts for approximatively two months (Pujos 1992). Nevertheless I observed antheridial dehiscence and swimming antherozoids from freshly collected *S. majus* subsp. *norvegicum* on mid-October. At this time archegonia are at the beginning of their development and thus totally immature. This time shift between the maturity of antherozoids and archegonia could certainly reduce the number of antherozoids available for fertilization especially after a hot autumn or after warm spells during winter. Futhermore during autumn 2019 and after the severe drought of that summer, I did not observe any antheridia in the fertile population of Malchamps but male plants were easily spotted by their rusty brown coloration

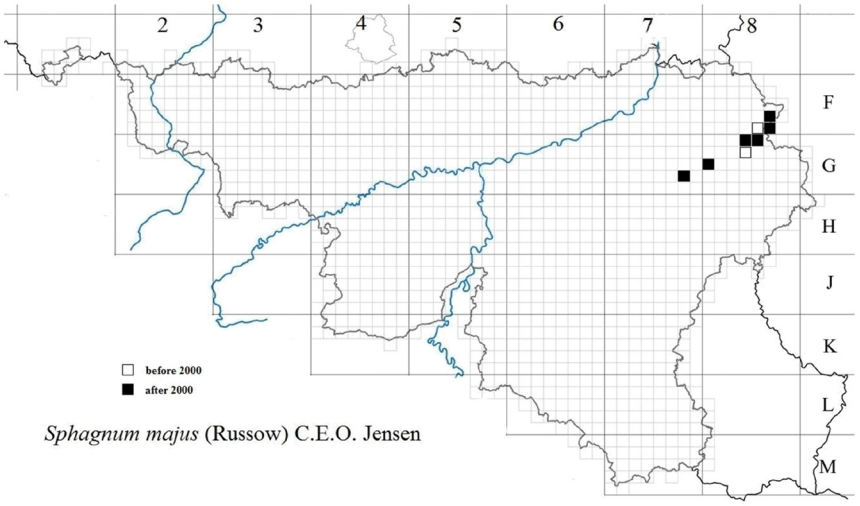


Figure 3. Distribution map of *Sphagnum majus* in Wallonia (IFBL grid).


Figure 4. (A) Oligotrophic mire dominated by *S. cuspidatum* (green-yellowish) and *S. majus* subsp. *majus* (brown) (Konnerzvenn, 07 IV 2019). (B) Large green-yellowish capitulum of *S. majus* subsp. *norvegicum* among small dirty mottled green-brown capitula of *S. majus* subsp. *majus* (Konnerzvenn, herb. Graulich no. SMAJUS26/19, 01 VI 2019). (C) Fertile population of *Sphagnum majus* subsp. *norvegicum* in an ombrotrophic bog (Malchamps, herb Graulich no. SMAJUS32/19, dupl. TRH, 09 VI 2019). (D) Mixed stand of male (light rusty) and female (green) *Sphagnum majus* subsp. *norvegicum* associated with male *Sphagnum cuspidatum* (dark rusty) (Allgemeines Venn, herb. Graulich no. SMAJUS39/19 dupl. TRH, 13 X 2019). (E) Male plants of *Sphagnum majus* subsp. *norvegicum* growing in an open ombrotrophic bog (Brackvenn, herb. Graulich no. SMAJUS44/19 dupl. TRH, 26 X 2019).

and the presence of antheridial bracts in some branches. These observations comfirm that antheridial growth and maturation are very sensitive to climatic factors with end-summer drought being probably the most limitating factor for capsule production where male and female plants grow in mixture.

Male plants of subsp. *majus* were observed at Konnerzvenn (oligotrophic location). Interestingly, plants from this population show some fascicules with three antheridial branches (Fig. 1A). This presence of antheridia on pendent branches was not known within subgenus *Cuspidata* and is probably due to the fact that branches are nearly isomorphic in *S. majus* (Daniels and Eddy 1985). Morever this population is lush and very vigourous which could also explain this exceptional presence of functional antheridia in pendent branches.

As many dioecious *Sphagnum* species, the occurence of sporophytes is rare to occasional in *Sphagnum majus* (Cronberg 1991, Hill 2004). In United Kingdom, sporophytes of subsp. *norvegicum* were found only at Glen Affric in Scotland (Blockeel et al. 2014) and according to Flatberg (1987), the sporophytes of both subspecies are not common in Norwegian material. Effectively several factors may

influence the production of capsules: climatic factors during the formation of sex organs, dispersal abilities of gametes, frequency of male and female plants and availability of water during fertilization period (Cronberg 1991, Sundberg 2000). Nevertheless when all favourable conditions are fulfilled, the production of capsules may be abundant as I observed at Malchamps bogs on June 2019 (Fig. 4C). In the examined herbarium material, one sample from Malchamps collected in 1967 shows also several sporophytes. I observed sporophytes only at Malchamps despite attempts at finding them in other locations. The presence of spore-producing populations at Malchamps may explain the abundance of *S. majus* in this location. Effectively *S. majus* occurs in nearly all lithalsas and hollows in the eastern part of this bog and by this way is much more common that *S. cuspidatum* in this small area.

## Conclusion

Even if both subspecies of *S. majus* are easily differentiated in the field, several specimens show intermediate microscopic features. Taking into account the high variability of taxa of the subgenus *Cuspidata*, the taxonomic split within *Sphagnum majus* is still unclear. Futher field observations, culture experiments and genetic evaluations will probably elucidate the relationship between these taxa and their real taxonomic values.

In Wallonia, *Sphagnum majus* is only reported from a limited area totally included in the protected nature reserve of Hautes-Fagnes. Moreover, subsp. *majus* was only observed in three locations. Subspecies *norvegicum* appears to be more common and less threatened as this taxon is able to thrive in various biotopes (bogs and ditches). An increase in temperature associated with reccurent droughts is know to reduce the *Sphagnum* growth, thus reducing carbon accumulation (Bragazza et al. 2016). In the context of global warming, boreal peatmoss populations isolated in temperate area are probably strongly threatened. This update on distribution of *Sphagnum majus* in Wallonia will help to monitor the evolution of this population in the ongoing context of climate change.

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## Appendix 1

Additional data for B/L ratio calculation, the measurements were made from n stem leaves per stem. Each ratio corresponds to a single stem.

| Herbarium no. | Location | B/L ratio | n |
|---|---|---|---|
| subsp. *norvegicum* | | | |
| 02/19 | Brackvenn | 0.77 | 7 |
| 09/19 | Konnerzvenn | 0.78 | 9 |
| 10/19 | Konnerzvenn | 0.82 | 7 |
| 12/19 | Konnerzvenn | 0.74 | 10 |
| 14/19 | Brackvenn | 0.81 | 9 |
| 20/19 | Malchamps | 0.77 | 8 |
| 21/19 | Malchamps | 0.86 | 9 |
| 22/19 | Malchamps | 0.92 | 9 |
| 23/19 | Malchamps | 0.85 | 5 |
| 23/19 | Malchamps | 0.83 | 19 |
| 26/19norv | Konnerzvenn | 0.72 | 5 |
| 27/19norv | Konnerzvenn | 0.82 | 7 |
| 28/19norv | Brackvenn | 0.73 | 7 |
| 29/19 | Malchamps | 0.75 | 5 |
| 31/19 | Malchamps | 0.90 | 5 |
| 32/19 | Malchamps | 0.79 | 7 |
| 39/19 | Allgemeines Venn | 0.82 | 8 |
| 39/19 | Allgemeines Venn | 0.90 | 8 |
| 39/19 | Allgemeines Venn | 0.92 | 8 |
| 39/19 | Allgemeines Venn | 0.82 | 8 |
| 39/19 | Allgemeines Venn | 0.89 | 8 |
| 39/19 | Allgemeines Venn | 0.84 | 8 |
| 39/19 | Allgemeines Venn | 0.84 | 8 |
| 39/19 | Allgemeines Venn | 0.79 | 8 |
| subsp. *majus* | | | |
| 03/19 | Brackvenn | 0.67 | 12 |
| 03/19 | Brackvenn | 0.68 | 7 |
| 03/19 | Brackvenn | 0.63 | 12 |
| 11/19 | Konnerzvenn | 0.70 | 11 |
| 11/19 | Konnerzvenn | 0.75 | 5 |
| 25/19 | Konnerzvenn | 0.69 | 11 |
| 26/19maj | Konnerzvenn | 0.70 | 12 |
| 27/19maj | Konnerzvenn | 0.69 | 9 |
| 28/19maj | Brackvenn | 0.67 | 10 |
| 28/19maj | Brackvenn | 0.62 | 5 |