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Effects of simulated shade on growth, number of branches and biomass in *Hylocomium splendens* and *Racomitrium lanuginosum*

Annika K. Jägerbrand and Heinjo J. During

The effects of simulated shade in terms of reduced light quantity (PPFD) and changed red:far-red ratio (R:FR ratio) on the growth in length, in number of branches and in biomass, were examined in a greenhouse experiment with *Hylocomium splendens* and *Racomitrium lanuginosum*, two species from habitats with different light conditions (with *H. splendens* often in more shaded microsites). Using ten intact moss turfs per species which had been collected on Iceland at 4 m distance between replicate turfs, we tested, whether light quantity affected growth and biomass, whether changes in light quantity and red:far-red ratio affected the number of branches, and whether the two species differed in these responses. Reduced light quantity (i.e. PPFD level) caused a greater length increase, decreased biomass, and biomass:length ratio in both species, but the magnitude of response varied greatly between species. Furthermore, in *R. lanuginosum* spectral shade (i.e. reduced PPFD and a lower R:FR ratio) generally caused stronger responses than neutral shade, with only a reduction in PPFD. *H. splendens* (from the shaded habitat) responded less strongly to the shade treatments than *R. lanuginosum* (from the open habitat) did. In addition to these effects of shading, there were strong effects of the turf of origin in both species, and in many cases the interaction between turf of origin and shading treatment was significant as well.

The light intensity rapidly declines with depth in natural moss patches (van der Hoeven et al. 1993) and in dense moss cushions the light extinction in the upper few centimetres is nearly complete (Clymo and Hayward 1982, Rydin and McDonald 1985, Skre et al. 1983). Owing to the shortage of light, bryophyte shoots and leaves may turn brown (van der Hoeven et al. 1993), and moss parts situated deeper in the canopy become brown and apparently dead (Skre et al. 1983, Rydin 1995). Thus, even with the rather low light compensation points (Kallio and Heinonen 1973, Skre and Oechel 1981) and low light saturation points (Skre and Oechel 1981) displayed by many bryophytes, light may become limiting for photosynthesis. Light limitation is further enhanced when bryophytes grow beneath a dense cover of canopy plants (Pedersen et al. 2001). Light limitation combined with burial by vascular plant litter brought about by the increase in vascular plants has been suggested to be the cause of the decline of bryophytes.
of radiation and moisture, as a higher radiation level 

Interpretations of the light reduction experiments in 

increase, biomass or the morphology in two species. 

significant effects of a decreased R:FR ratio on the length 

diminished the cover of vascular plants in a field expe- 


By bryophytes, a reduction in PPFD has been 

shown in laboratory, greenhouse or garden experi- 

ments to cause decreased growth rates in terms of 

absolute biomass increment (Rincon 1993, van der 

Hoeven et al. 1998, van der Wal et al. 2005) as well 

as biomass-based relative growth rates (Rincon 1993). 

Other studies found little or no effect of shading on 

biomass increment rates, but an increase in length 

increment rates (Bakken 1995, Rincon and Grime 


removed the cover of vascular plants in a field expe- 

riment, and found that this did not significantly af- 

fect biomass of the bryophyte shoots, but led to a lower 

length increment and a higher branch density of the 

main axis. These results are consistent with the set 

of responses known as the “shade avoidance syn- 

drome” (Smith and Whitham 1997) in phanerogams, 

which is a response to a reduction in R:FR ratio in 

plant-induced shade or dense canopies. Phytochromes 

play an important role in this respect (Morgan and 

Smith 1979, Smith 1982). Phytochromes occur widely 

in bryophytes (Schneider-Poetsch et al. 1994, 1998, 

Lamparter and Bruecker 2004). They play a role in 

diagavitropic responses (Rethy et al. 1990), and have 

been assumed to be involved in bryophyte responses 

to shade as well (Bates 1998). Yet, effects of a reduc- 

tion in R:FR ratio of the light falling on bryophytes 

have received little attention.

Hoddinott and Bain (1979) showed that in the bryo- 

phytes studied such a decreased R:FR ratio led to a 

decreased mean height, which is in the opposite di- 

rection to the observations made on vascular plants. 

However, van der Hoeven et al. (1998) found no sig- 

nificant effects of a decreased R:FR ratio on the length 

increase, biomass or the morphology in two species. 

Interpretations of the light reduction experiments in 

bryophytes are complicated by the interacting nature 

of radiation and moisture, as a higher radiation level 

will inevitably lead to faster desiccation of bryophy-

tes and consequently a reduced growth (van der Ho- 

ev et al. 1998).

The plastic response to shade differs between spe- 

cies, depending on their ecology and tolerance to low 

light levels. For vascular plants, evidence suggests 

that species from open habitats (e.g. grassland) should 

have a stronger shade avoidance response than spe- 

cies from shaded habitats, e.g. understorey vegeta- 

tion (Corré 1983, Morgan and Smith 1979, Smith 

1982). For bryophytes, the study of Rincon and Grime 

(1989) points in the same direction. They found that 

bryophytes of more productive habitats (mesic grass- 

land) showed stronger plastic responses to different 

irradiances (although without any change in R:FR 

ratio) than bryophytes of unproductive (shaded wood- 

land floor) habitats.

In this paper, we compared the responses to simu- 

lated shade (both neutral shade, only affecting the 

PPFD, and spectral shade with changed PPFD and 

R:FR ratio) on the growth in terms of biomass, 

number of branches and the shoot length of two cir- 

cumpolar bryophytes, Hylocomium splendens (Hedw.) 

B.S.G. and Racemitrium lanuginosum (Hedw.) Brid. 

The experiment lasted seven months and was con- 

ducted in an unheated greenhouse in Utrecht, the 

Netherlands.

Both species have a wide distribution. H. splen- 

dens is probably the most common moss in the North- 

ern Hemisphere (Persson and Vierieck 1983), where- 

as R. lanuginosum is cosmopolitan (Tallis 1958). Both 

species are ecologically important as they can be very 

dominant and locally reach high abundance. Despite 

the fact that they can be found within the same area, 

they have very different habitat preferences, H. splen- 
dens prefers mesic habitats, and can be very domi- 
nant in understorey vegetation (Tamm 1953), whereas 

R. lanuginosum prefers more exposed and open ha- 

bitats (Vitt and Marsh 1988, Ellis and Tallis 2003), 

and is especially favoured when the presence of vas- 

cular plants is reduced (Tallis 1964). Their ecologi- 
cal differences are also reflected in their different 

ecophysiologies, H. splendens having a lower light 

compensation point for photosynthesis (ca 20 µmol 

m-2 s-1 at 5°C as compared to ca 60 µmol m-2 s-1 at 

5°C for R. lanuginosum) and a higher temperature 

optimum for growth than R. lanuginosum has (20°C 

vs 5–10°C; Kallio and Heinonen 1973, Furness and 

Grime 1982). In fact, the light saturation level of R. 

lanuginosum (some 1750 µmol m-2 s-1) is one of the 

highest found among mosses (Kallio and Heinonen 

1973).

We hypothesized, that a reduction in PPFD will 

lead to less growth in biomass, while a reduction in 

R:FR ratio will result in shoot elongation and reduced 

branching. We further assumed, that especially the 

morphogenetic responses to a reduced R:FR ratio will
be less pronounced in the understorey species (H. splendens) than in the species from an open habitat (R. lanuginosum).

Material and methods

Site of collections

Moss samples were collected in Thingvellir National Park (64°17′N 21°05′W), in SW Iceland. The site is situated at 120 m a.s.l. on a post-glacial lava-field, and has a maritime subarctic climate. Annual mean temperature at Thingvellir was 2.8°C during the period 1974–1988, and the mean annual precipitation was 1438 mm (Einarsson 1992). The area has been protected from sheep grazing since 1928 (Jónasson 1992), and one of the most extensive vegetation types is the well-developed R. lanuginosum moss heath (Thorsteinsson and Arnalds 1992). The moss heath vegetation is low-productive with few vascular plants and few trees (Thorsteinsson and Arnalds 1992), resulting in direct exposure of the moss during sunshine and clear days. In the same area, but with less cover, there are scattered Betula pubescens Ehrh. trees and dwarf-shrub heath vegetation dominated by different Salix spp. (Thorsteinsson and Arnalds 1992). The dwarf-shrub heath has a more species-rich vegetation, and common bryophytes are H. splendens and Pleurozium schreberi (Brid.) Mitt (Jägerbrand 2004).

The highest amounts of global radiation in Thingvellir is found during the summer period (Einarsson 1992). Mosses in the subcanopy shade of the dwarf shrub heath are protected from large amounts of the insulation.

The species

Hylocomium splendens and R. lanuginosum are long-lived perennial species with clonal growth (During 1979). The species have quite different morphology, H. splendens has primary, secondary and tertiary branching and is a web-forming pleurocarpous bryophyte with sympodial or monopodial growth (La Farge-England 1996). Hylocomium splendens may initiate a new segment every year by sympodial branching (Tamm 1953), with distinct annual markers of growth (Callaghan et al. 1978, 1997, Økland 1995). Racomitrium lanuginosum has a main stem with a variable number of lateral primary branches (Tallis 1959a, 1959b), and grows monopodially (La Farge-England 1996).

Simulated shade experiment

On 8 September 1998, 10 samples (20 × 20 cm) were collected along a transect at every 4 m for each species in Thingvellir National Park. The samples were transported to Utrecht, the Netherlands, under dark and relatively dry conditions. The 10 samples for each species were cut to a depth of ca 7 cm (which included all green parts plus some of the brown lower parts of the shoots) and carefully divided into 3 containers (9 × 9 cm, depth 7 cm), and the containers were systematically assigned to one of the treatments: hyaline cage, green shade cage or black shade cage. For each species, two containers were placed in a treatment cage (five of each treatment) in a greenhouse in Utrecht. The cages consisted of a bottomless thin wooden frame, which was covered with either one layer of colourless plastic film (i.e. hyaline cage, or controls), alone or together with black gauze (to reduce light quantity), or a green plastic film (Lee Colortran International, Andover, Hants, UK; film no. 122, Fern green) simulating canopy shade. The cages could be opened from above and measured 20×43 cm, with a height of 20 cm.

The hyaline cage functioned as control because this foil had hardly any effect on light quantity and quality (Fig. 1), and it produced the same microclimatic conditions (increased moisture levels) as both types of shade cage (Huber 1997). Light spectra of cages were measured with a Li-Cor 1800 spectroradiometer (Fig. 1). The green and black shade cages reduced the PPFD with approximately 60% (Fig. 1). PPFD above the cages varied continuously, but was usually in the range of 50–200 µmol m⁻² s⁻¹. Additionally, in the green cages the red:far-red ratio was also reduced, from 1.12 for the controls and black cages to 0.20, thereby simulating a canopy shade (Fig. 1). The experiment was started 24 September 1998. The mosses were watered every day with demineralized water.
and three times during the experiment with a strongly diluted Hoagland nutrient solution. The experiment was terminated 1 May 1999, as the apex of many *H. splendens* shoots for unknown reasons turned dark brown.

Measurements were taken on: length increase of the shoots; number of branches (on the new shoot part); biomass increase (dry weight of the new shoot parts, including the branches); and branch density (number of new branches divided by length increase). Furthermore, the biomass per unit shoot length of the newly formed parts was calculated. Measurements were performed on six shoots from each container, chosen in a systematical way. In some cases, the fragile shoots were destroyed, leaving 176 shoots for *H. splendens* (59 from controls, 59 from green cages, and 58 from black cages), and 179 shoots for *R. lanuginosum* (59 from green cages). As the climate in the greenhouse in Utrecht contrasted with the Icelandic climate, the point of new growth (i.e. from the start of the experiment) was often clearly visible on both species. For *R. lanuginosum* the new parts were more green, probably because of the documented ability of the hair points and awn teeth to change lengths and forms (Tallis 1959a, Vitt and Marsh 1998). For *H. splendens* it was also possible to use markers of annual growth (the sympodial branching pattern; see Tamm 1953, Økland 1995), the change in its growth direction towards light, or, as in some cases, leaf characters. Biomass was measured after drying to constant dry weight in 72 h at 70°C.

**Statistical analyses**

Prior to analyses all variables were transformed to zero skewness and expressed on a 0 to 1 scale to meet the assumptions of homogeneity of variances and normality (Økland et al. 2003). To test for differences between species and treatments, separate two-way ANOVAs were used for each response variable. Treatment effects and differences between the ten turfs of origin per species were tested by two-way mixed-model ANOVAs, followed by Tukey-Kramer post-hoc-tests for the treatment effects, suitable when sam-

![Fig. 2. Effects of a simulated shade on growth in length (A, D), in number of branches (B, E) and in biomass (C, F) of *Hylocomium splendens* (A-C) and *Racomitrium lanuginosum* (D-F). Bars indicate ± 1 SE. Bars with different letters indicate significant differences analysed by Tukey-Kramer post-hoc-tests (p<0.05, and + = p<0.10, see Table 2 for the ANOVA). ns=non-significant.](image)
Table 1. Two-way ANOVAs testing differences between species and the shade treatments in separately analyses on the increase in length, number of new branches, new biomass produced, dry weight:length ratio of new mass, and branch density per cm new shoot in Hylocomium splendens and Racomitrium lanuginosum from a greenhouse experiment in Utrecht.

<table>
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<tr>
<th>Variable</th>
<th>DF</th>
<th>F</th>
<th>P</th>
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</thead>
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<td>Length increase</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Species</td>
<td>1</td>
<td>0.31</td>
<td>.5800</td>
</tr>
<tr>
<td>Treatments</td>
<td>2</td>
<td>13.50</td>
<td>&lt;0.001</td>
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<tr>
<td>Species X treatments</td>
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<td>1.00</td>
<td>.3690</td>
</tr>
<tr>
<td>Residual</td>
<td>349</td>
<td></td>
<td></td>
</tr>
<tr>
<td>No.of branches</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Species</td>
<td>1</td>
<td>4.93</td>
<td>.0270</td>
</tr>
<tr>
<td>Treatments</td>
<td>2</td>
<td>0.50</td>
<td>.6063</td>
</tr>
<tr>
<td>Species X treatments</td>
<td>2</td>
<td>5.95</td>
<td>.0029</td>
</tr>
<tr>
<td>Residual</td>
<td>349</td>
<td></td>
<td></td>
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<tr>
<td>Dry weight new shoot</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Species</td>
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<td>.4038</td>
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<td>Treatments</td>
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<td>.0440</td>
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<td>1.39</td>
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</tr>
<tr>
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<td></td>
</tr>
<tr>
<td>Biomass:length ratio</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Species</td>
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<td>7.70</td>
<td>.0058</td>
</tr>
<tr>
<td>Treatments</td>
<td>2</td>
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<td>&lt;.0001</td>
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<td>3.51</td>
<td>.0310</td>
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<td>Residual</td>
<td>349</td>
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<tr>
<td>Branch density</td>
<td></td>
<td></td>
<td></td>
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<tr>
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<td>&lt;.0001</td>
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</tr>
<tr>
<td>Residual</td>
<td>349</td>
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</tbody>
</table>

Results

Shading led to significantly greater length increase, lower biomass production, and lower biomass:length ratio of new parts in both species (Table 1, Fig. 2, 3). Significant differences between the species were found in the number of branches, biomass:length ratio and branch density (Table 1), with higher values for H. splendens in all cases. Significant interaction effects between species and treatments were found for biomass production, biomass:length ratio and branch density (Table 1). For H. splendens, both shade treatments (spectral and neutral shade) caused similar increases in length and decreases in biomass:length ratio (Table 2, Fig. 2, 3). In R. lanuginosum, biomass:length ratio was also reduced by a decrease in PPFD, but there was an additional effect of a decrease in R:FR ratio (Fig. 3c). Branch density was not significantly affected by a reduction of the PPFD alone, but significantly responded to a reduced R:FR ratio in this species (Fig. 3d). Biomass production and length increase differed strongly among the replicate moss turfs in both species (biomass marginally significant in H. splendens), and the interaction term was clearly significant for both species for almost all variables (Table 2), indicating markedly different responses of the turfs to the shade treatments (see Fig. 4 for an example).

Discussion

Although the differences between the different original turf sections obscured some of the patterns in the results for both species, the general hypotheses were confirmed. Absolute biomass increase was little affected by the shade treatments when analysed per species (for unknown reasons), but when analysing responses of both species simultaneously, there were significant treatment effects on biomass production, thereby confirming our first hypothesis. Under
shade conditions, the reduced PPFD may cause a lower photosynthetic rate, directly affecting length growth and biomass production. In this study a decreased PPFD did indeed cause a length growth increase, a reduced biomass increment and a lower biomass:length ratio, which is in accordance with previous studies (Rincon and Grime 1989, Bakken 1995).

The spectral shade treatment caused a greater reduction in biomass, biomass:length ratio, and branch density in *R. lanuginosum* than the black-gauze shade treatment, but the same responses were not found in *H. splendens*. Thus, there is also support for the two hypotheses on R:FR ratio effects: that a reduced R:FR ratio causes a stronger length increase and reduces the number of branches, and that a change in R:FR ratio has a stronger morphogenetic effect on the species from open habitats (*R. lanuginosum*) than on the understory species (*H. splendens*). In addition, our results for *R. lanuginosum* also show (for the first time) that a reduced R:FR ratio caused an additive shade effect in bryophytes, compared with a shade treatment reducing the PPFD level per se (esp. biomass:length ratio).

There were large differences in the magnitude of response between the species. For example, *H. splendens* had a mean length increment of 2.48 cm, whereas that of *R. lanuginosum* was only 1.19 cm. These differences probably reflect their contrasting eco-

![Fig. 4. Biomass(DW):length ratio of the new shoot parts of *Hylocomium splendens* shoots, average values of 5-6 replicate shoots from ten moss turfs collected at distances of 4 m along a line transect in Iceland, cultivated in hyaline, black and green shade cages.](image)

<table>
<thead>
<tr>
<th>variable</th>
<th>Treatment</th>
<th>Moss turf</th>
<th>Trmt × Turf</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F 2</td>
<td>p</td>
<td>F 9</td>
</tr>
<tr>
<td><em>Hylocomium splendens</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length increase</td>
<td>3.77</td>
<td>0.04</td>
<td>4.11</td>
</tr>
<tr>
<td>No. of branches</td>
<td>2.09</td>
<td>0.15</td>
<td>1.96</td>
</tr>
<tr>
<td>Dry weight new shoot</td>
<td>0.14</td>
<td>0.87</td>
<td>2.25</td>
</tr>
<tr>
<td>Biomass:length ratio</td>
<td>7.17</td>
<td>0.005</td>
<td>0.95</td>
</tr>
<tr>
<td>Branch density</td>
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<td>0.27</td>
<td>1.64</td>
</tr>
<tr>
<td>Residual DF: 146</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Racomitrium lanuginosum</em></td>
<td>2.63</td>
<td>0.10</td>
<td>3.24</td>
</tr>
<tr>
<td>No. of branches</td>
<td>1.41</td>
<td>0.27</td>
<td>0.82</td>
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<td>Dry weight new shoot</td>
<td>2.97</td>
<td>0.08</td>
<td>3.39</td>
</tr>
<tr>
<td>Biomass:length ratio</td>
<td>20.9</td>
<td>0.000</td>
<td>1.44</td>
</tr>
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<td>Branch density</td>
<td>2.90</td>
<td>0.08</td>
<td>0.74</td>
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<tr>
<td>Residual DF: 149</td>
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</table>
ergy, *H. splendens* exists in a more productive habitat (the dwarf shrub heath), whereas the *R. lanuginosum* moss heath is nutrient-poor and low-productive. This is supported by measurements of nitrogen and chlorophyll content, with concentrations in *H. splendens* often twice as high as those in *R. lanuginosum* (Jägerbrand et al. 2006).

In vascular plants, shade effects may cause a reduction in branching density (Huber and Stuefer 1997). The shade responses in branching densities reported by previous studies on mosses did not conform to this pattern, however: higher branching densities in response to decreased light quantity (Bergamini and Peintinger 2002) or to decreased R:FR ratio (Hoddinott and Bain 1979), or no effects at all (van der Hoeven et al. 1998). The length growth increase shown by both species under shade conditions and the morphogenetic responses to a reduced R:FR ratio shown by *R. lanuginosum* suggest, that at least some elements of the shade avoidance syndrome may also be found among bryophytes. The effects of the green-shade treatment suggest, that phytochromes may be involved in bryophytes as they do in phanerogams, but a role for blue-light-sensitive cryptochromes (Liscum et al. 2003) as a cause of the increased elongation in the treatment of reduced PPFD shown by both species cannot be excluded, since such photoreceptors have been found in bryophytes as well (Suetsugu and Wada 2003).

A rather unexpected result of this study was the large difference in almost all respects between the shoots extracted from the ten replicate moss turf patches of both species, collected along a transect in a fairly homogeneous area at distances of only 4 m. Although genetically based differences between the patches cannot be excluded, other influences seem more likely. The patches differed visually in shoot density and turf height, and perhaps, interactions between the canopy structure and the conditions in the shade cages caused the differences found (Peder sen et al. 2001). The strong interaction effects showing the large differences in even the direction of the responses to shade among the patches (Fig. 4) remain enigmatic, however.

**Acknowledgements** – We would like to thank the National park of Thingvellir, Iceland who allowed us to collect samples to carry out this study, and the staff in the greenhouses of the Utrecht Botanical Garden, the Netherlands. AKJ would also like to thank Magnus Popp and Gudjon Helgi Thorvaldsson for practical help with the experiments. We thank Håkan Rydin for constructive comments and suggestions. This study was supported by fundings from Helge Ax:son Johnsons fond, the Swedish Royal Forestry and Agricultural Academy (Grant No. SF-339), Göteborgs Universitets överskottsfond and NorFa to AKJ.

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phytogeography of Racemitrium lanuginosum and R.