GEOTROPIC CURVATURES OF SPHAGNUM: ENVIRONMENTAL FEATURES OF THEIR GENESIS AND TRIAL APPLICATION FOR ESTIMATION SHOOT LENGTH INCREMENT

ГЕОТРОПИЧЕСКИЕ ИЗГИБЫ ПОБЕГОВ МХОВ РОДА SPHAGNUM: ЭКОЛОГИЧЕСКИЕ ОСОБЕННОСТИ ГЕНЕЗИСА И ПРАКТИЧЕСКОЕ ИСПОЛЬЗОВАНИЕ ДЛЯ ОПРЕДЕЛЕНИЯ ПРИРОСТА ПОБЕГОВ

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Abstract

The genesis of geotropic curvatures in the natural habitat of Sphagnum mosses is described in detail on the basis of in situ observations. A novel method of estimation of length increment of Sphagna shoots is developed, based on their geotropic curvatures, which are the markers of physical impacts. The snow load in northern areas is an example of the most typical impact on Sphagnum cover and further geotropic response of stems. Deviation in stem growth causes the curves which may form after snowmelt or under the snow layer. First attempt to use the snow induced markers, named further as “nival geotropic curvatures”, for estimation of shoot increment rate of Sphagna stems were made in the late 20th century. However, first researchers ignored other than snow cover common factors that are responsible for the formation of similar markers during the growing season. Therefore, measuring increment from these markers may result in incorrect estimation, because they could be formed neither due to the snow load nor the beginning of the growing season. Our method takes into account these shortcomings. Several Sphagnum species were involved in the research for experimental comparison of the novel method with the classical tied thread method. Experimental plots were studied during a two-year period on Karelian mires. The length increment values obtained by both methods show some differences. Shoot increment values obtained by the method of the nival geotropic curvatures markedly exceed values obtained by the classical tied thread method in all cases. The difference ranged from 7.5 to 18.6 % in 2014 and from 20.8 to 45.8 % in 2015. The results could be explained by the negative effect of the tied thread method on the growth of moss, that was described in the literature. The coefficients of variation estimated by the method of nival curvatures are reliably lower than those obtained by the tied thread method for practically all samples. In 2014, mean value of the coefficients of variation were 20.3±4.2 % for samples obtained by tied thread method and 13.0±4.7 % for samples obtained by nival geotropic curvatures method. In 2015, the coefficients of variation were estimated at 21.1±5.3 % and 8.7±2.2 %, respectively. The differences are assumed to be due to the difference in the degree of impact on the structure of Sphagnum cover.

Резюме

На основании наблюдений in situ детально описан генезис геотропических изгибов стеблей в естественной среде обитания сфагнов. Разработан новый метод определения прироста побегов сфагновых мхов, в основу которого положено использование геотропических изгибов, образующихся в результате внешних физических воздействий. Снеговая нагрузка, характерная для северных регионов — пример наиболее типичного физического воздействия, вызывающего геотропическую реакцию побегов. Отклонение растущих побегов вызывает образование изгибов после снеготаяния или под снежным покровом. Первые попытки использования вызываемых действием снега маркеров (называемых нами в дальнейшем «нивальные геотропические изгибы») на стеблях сфагновых мхов для оценки прироста побегов были предприняты во второй половине XX века. В ранних исследованиях игнорировались факторы, кроме снежного покрова, хотя они также вызывают образование геотропических маркеров в течение вегетационного периода. Таким образом, измерение прироста от этих маркеров может приводить к ошибкам, поскольку их образование может быть не связано со снеговой нагрузкой и началом вегетационного периода. Предлагаемый нами метод учитывает эти недостатки. Несколько видов сфагнов было включено

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в исследование, посвященное экспериментальному сравнению нового метода с классическим методом перевязок в течение двух лет на болотах Карелии. Значения линейного прироста побегов, полученные обоими методами, показывают некоторые различия. Значения линейного прироста, полученные методом нивальных геотропических изгибов, во всех случаях заметно превышают значения, полученные методом перевязок. Различие варьировало от 7.5 до 18.6 % в 2014 году и от 20.8 до 45.8 % в 2015 году. Результаты можно объяснить известным из литературы отрицательным влиянием метода перевязок на рост побегов. Коэффициенты вариации практически для всех выборок, полученных методом нивальных геотропических изгибов, достоверно ниже по сравнению с данными, полученными методом перевязок. В 2014 году среднее значение коэффициента вариации в выборках, полученных методом перевязок, составило 20.3±4.2 %, а в выборках, полученных методом нивальных геотропических изгибов - 13.0±4.7 %. В 2015 году коэффициенты вариации составили 21.1±5.3 % и 8.7±2.2 %, соответственно. Такие различия, по всей видимости, связаны с различной степенью трансформации естественной структуры сфагнового покрова.

KEYWORDS: Karelia, tied thread method, method of natural markers, artefacts, geotropism, snow load, mire water level, mosses, nival, aqueous, length increment, coefficient of variation.

INTRODUCTION

Various methods are used for estimation the length increment of Sphagnum mosses (Clymo, 1970; Vitt, 2007). Methods based on the use of artificial markers, such as cranked wire, tied thread, white marks, cutting-off plants for marking starting point of growth are most popular. On the one hand, practical application of these methods is laborious; on the other hand, it displays some artefacts which may distort the results of measurements (Solonevich, 1966; Iлометс, 1976). Furthermore, to obtain a large amount of data, several types of markers should be used.

Biological markers of Sphagnum mosses can make methods of estimation of length increment less laborious and provide larger amount of samples. Stem curvatures responsible for the segmented appearance of the shoots are used as markers. First attempts to use these markers for estimation of Sphagnum species shoot increment were made in the late 20th century (Malmer, 1962; Multdyarow & Lapshina, 1983). More recently, it has been concluded that the formation of stem curvatures of Sphagnum mosses is induced by snow cover (further referred as “nival geotropic curvatures”) and, in accordance with this thesis, the distance between consecutive curvatures is consistent with the annual increment (Rochefort et al., 1990; Jauchiainen et al., 1997; Camill et al., 2001; Vitt, 2007). This apparently simple and highly productive method is seldom employed. However, authors of the above mentioned publications attribute the formation of curvatures to the effect of snow alone, ignoring other common factors responsible for the formation of similar curvatures during the growing season. Therefore, measured increment from the upper curvatures may result in incorrect estimation, because curvature formation may be induced by other events than the beginning of the growing season.

Sphagnum grows by the division of apical meristem cells followed by elongation of daughter cells. The negative geotropism of Sphagnum mosses experimentally proved by Bismarck (1959) is responsible for the orthotropic grow of moss on smooth mire surface. Growth pattern in mire slightly differs from growth in heterogenous microrelief conditions. Old shoots of Sphagnum growing in hollows and pools are usually slanting (Elnina et al., 1984; Panov, 2008), though younger parts of plants maintain an orthotropic growth. If shoots deviate, compensatory mechanisms restore the original growth direction. As a result, distinctive geotropic curvatures form on the stem, as described by Bismarck (1959). Thus, negative geotropic reaction can be used for demarcation of Sphagnum length increment before and after shoot deviation. We put this principle for the basis of the novel method for estimating Sphagnum growth (patent RU № 2600827, author V.L. Mironov).

Snow load in northern and mountain areas is an example of the most typical mechanical impact on the mire surface (Camill et al., 2001; Yazaki & Yabe, 2012). A steady snow cover annually forms in most of the territory of Russia, snow amounts usually peaking shortly before the beginning of snowmelt. Prior to thawing, thickness of snow cover is equal to 100–120 mm of water over the most of Karelia (Bondarik, 2004), so mire surface is...
subjected to a pressure of 1000–1200 g/dm². Similar values were reported for mires in southern Finland (Lindholm & Vasander, 1990).

Importance of the physical impact of the snow cover on the mire surface is commonly underestimated, although recent studies (Yazaki & Yabe, 2012) have shown that snow impact can result in the substantial compacting of Sphagnum hummocks and even in changes of their surface structure. Thus, Sphagnum cover is directly affected by snow load. We have estimated that where snow storage is 100 mm, the snow weight per moss capitulum may be 1.2 g (S. fuscum) to 20 g (Sphagnum riparium), i.e., manifold more than the weight of the capitula. Actual load may be considerably higher than estimated because of additional mire water storage in basal snow layers, which is quite common in microrelief depressions (Eurola, 1975). Thus, known from the literature concepts “permanent bends of the main stem” (Rochefort et al., 1990), “innate seasonal markers” (Jauchiainen et al., 1997); “kinks” (Camill et al., 2001), “snow weighted crooks” (Vitt, 2007), “growth markers created by snow-pack conditions” (Turetsky et al., 2008) and “innate snow-bend markers” (Graham & Vitt, 2016) are consistent with nival geotropic curvatures.

Most of the mentioned above studies refer to the snow impact by its weight pressure rather than consider physiological processes connected with low temperatures or absence of light. It should be stressed, however, that these factors are not the only contributors of the curvatures on Sphagnum shoots. Bismarck (1959) in his classical experimental study revealed a number of factors that inhibit negative geotropic response, i.e., temperature, light, acidity, and weight. The response rate was species specific. According to Banbury (1962), the outcomes of Bismarck’s experiments could be interpreted as well as prove of negative hydrotropism of Sphagnum species.

**METHODOLOGY**

The goal of our study was to update considerably the method for the Sphagnum shoots annual length increment identification and to test this method by the estimation of the Sphagnum length increment in Karelian mires using the updated method of nival geotropic curvatures; the common tied thread method was used for control.

For these purposes, we analyzed the mechanism of interaction of Sphagnum shoots with major natural factors in situ and evaluated their input into the process of stem curvature formation. The methodology is based on the developed within the current study patterns of the formation of the Sphagnum stems curvatures induced by snow cover (nival geotropic curvatures), water level change (aqueous geotropic curvatures) and other environmental factors.

The background pattern for the nival geotropic curvatures

Snow load on individual shoots of Sphagnum mosses (individual snow load) depends hyperbolically on the density of the Sphagnum mat (Fig. 1), and the response of Sphagnum to this load also depends on the degree of its freezing at the time of snowfall (Eurola, 1975), local distribution and density of the snow cover, species affiliations of Sphagnum, capitula density within a mat, degree of submerging of capitula into the water, and a number of random factors.

The impact of snow results in pressing-in and deformation of the Sphagnum cover (Fig. 2) and deviation of shoots from the vertical axis (Camill et al., 2001). It is known from the literature (Camill et al., 2001; Vitt, 2007) that geotropic response to deviation may appear after a snowmelt, but we also observed such response under snow layer. We saw many nival geotropic curvatures in the unfrozen Sphagnum mats in hollows some time after formation of snow cover in late autumn, while in early spring at the same sites moss shoots started to grow long before Sphagnum mat thawing. It should be noted that nival geotropic curvatures at such sites are occasionally formed again in autumn. It depends on how many times the critical mass of snow cover was formed and whether there
were favourable conditions for growth between these periods. Upon a preliminary deep freezing, geotropic curvatures are formed after thawing of Sphagnum cover. We observed this process for hollow and pool species covered by 50 cm of thick snow cover in March to April, while well-defined curvatures in hummocky species were observed in late April to early May, after the snow had fully melted away. Nival geotropic curvatures occur not only in Sphagnum mosses but also in other vertically growing mosses, e.g., Polytrichum, Dicranum, and Meesia.

The background pattern for the aqueous geotropic curvatures

The study is based on the following observations on the interactions between water level and plant shoots. The transition of moss apices from a sub-aqueous (submerged) to supra-aqueous (emerged) position is significant for some carpet-, hollow- and flark-dwelling Sphagnum species. This process is responsible for the formation of stem curvatures of geotropic nature. A basic model can be suggested to describe this process (Fig. 3).

At elevated mire water levels (MWL) taking place in spring, hollow-dwelling Sphagnum species acquire the orthotropic direction of capitulum growth, although their stems remain fully submerged at that time (stage 1). Later on, as MWL declines and shoots are elongated, moss capitula gradually get to deflect from the initial position (stage 2). Significant factors in this process are water surface tension forces, stem resilience, capitulum weight and size. When a deflection threshold is reached, geotropic response is enacted to correct the growth direction, and stem curvature is formed as a result (stage 3). MWL drop may take a while, entraining capitula and gradually increasing the angle of their declination from the vertical axis. Meantime, compensatory mechanisms continuously rectify the direction of capitulum growth. Thus, if this stage is prolonged, stem curvatures may become quite long and subdued. When the critical MWL is reached, the further water drop no longer has the capacity to drag Sphagnum capitula along. Capitula emerge from water to air (stage 4). The direction of growth is then stabilized, and the formation of geotropic curvatures stops (stage 5).

Hollow- and pool-dwelling species, such as Sphagnum riparium, S. fallax, S. majus, S. cuspidatum, S. jenseni, S. balticum and S. lindbergii, and even the hummock-dwelling species S. magellanicum and S. fascum, which rarely grow in Karelia as carpets together with S. balticum, typically have geotropic curvatures of aqueous genesis. Aqueous geotropic curvatures are commonly more gentle than nival ones, but if the shoots deviate markedly, they can hardly be distinguished from nival curvatures. Obviously, estimation of annual increment of Sphagnum may be much lower than real value, if only snow impact is considered and aqueous genesis of geotropic curvatures is ignored. It is probably the reason why the increment values obtained by some authors using similar markers (Muldyyarov & Lapshina, 1983; Camill et al., 2001; Vitt, 2007; Turetsky et al., 2008), are lower than ours.

On the contribution of other factors to the formation of geotropic curvatures

Among other natural factors responsible for the formation of geotropic curvatures, pouring of rain and hail are worth to mention. Our studies show that they have a crucial effect on the formation of curvatures in Sphagnum moss carpets when shoot increment (especially in S. riparium) is rather high. In this case, abundant precipitation often results in the shoot deviation, contributing to their geotropic reaction. The curvatures thus formed commonly do not look like nival varieties, but can occasionally be taken for aqueous curvatures. Therefore, they are directly identified by consecutive observations. Furthermore, abundant precipitation can exert an indirect effect, causing a rise in MWL and another immersion of shoots into the water. As a result, aqueous curvatures are formed.

The noteworthy factor for the geotropic curvatures formation could be physical impact on the Sphagnum mats, such as trampling. In the Karelian mires, physical impact is a consequence of the recreation and animal activities. Such impacts considerably disturb natural structure of the mat, inflicting massive damage on shoots and altering their spatial orientation. Nonetheless, the apical meristems of a majority of the damaged shoots remain functional, so the shoots retain capacity for growth and compensatory response. This mechanism secures a rapid recovery of the natural structure of Sphagnum mat.

Other hints for method improvement

Areas of mires with a smooth, undamaged, complete Sphagnum cover without any footprints are most suitable for study. Thin grass cover and small variations in MWL over the entire vegetative season are also desirable. Our study shows that nival shoot curvatures are more conspicuous in such Sphagnum moss sites. Furthermore, differences in the density distribution of small branches and contrast between the living and dead tis-

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Table 1. Characteristics of sample plots with Sphagnum

<table>
<thead>
<tr>
<th>Plot #</th>
<th>Species</th>
<th>Position</th>
<th>MWL, cm</th>
<th>Nutrient/ in microrelief moisture</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>S. majus</td>
<td>hollow</td>
<td>-1 -5</td>
<td>meso-oligotrophic/ stagnat</td>
</tr>
<tr>
<td>II</td>
<td>S. papillosum</td>
<td>lawn</td>
<td>-5 -10</td>
<td>eu- to mesotrophic/</td>
</tr>
<tr>
<td>III</td>
<td>S. obtusum</td>
<td>lawn</td>
<td>-5 -13</td>
<td>low flowage</td>
</tr>
<tr>
<td>IV</td>
<td>S. riparium</td>
<td>lawn</td>
<td>-1 -15</td>
<td>mesotrophic / low flowage</td>
</tr>
<tr>
<td>V</td>
<td>S. fallax</td>
<td>drainage</td>
<td>0 -20</td>
<td>oligomesotrophic / low flowage</td>
</tr>
<tr>
<td>VI</td>
<td>S. cuspidatum</td>
<td>drainage</td>
<td>0 -1</td>
<td>oligotrophic / stagnat</td>
</tr>
</tbody>
</table>

Nenazvannoye mire (61°47’58.92" N, 33°31’29.68” E)
Rittusuo mire (61°46’28.98" N, 33°31’32.62” E)

Areas of mires with a smooth, undamaged, complete Sphagnum cover without any footprints are most suitable for study. Thin grass cover and small variations in MWL over the entire vegetative season are also desirable. Our study shows that nival shoot curvatures are more conspicuous in such Sphagnum moss sites. Furthermore, differences in the density distribution of small branches and contrast between the living and dead tis-
Fig. 6. Samples of nival geotropic curvatures on Sphagna shoots under natural conditions (cf. also Figs. 7-8). A: Sphagnum magellanicum from ombrotrophic bog site, lawn (May 2016); B: S. subsecundum from a minerotrophic mire site, hollow (May 2015); C: S. wulfianum from spruce forest, lawn (May 2016); D: S. riparium from a minerotrophic mire site, lawn (March 2015); E: S. capillifolium from an ombrotrophic bog site, hummock (October 2014); F: S. fuscum from an open ombrotrophic bog site, hummock (October 2015); G: S. fuscum from a forested (pine) ombrotrophic bog site, hummock (October 2015); H: S. magellanicum from an open ombrotrophic bog site, hummock (October 2015); I: S. magellanicum from a forested (pine) ombrotrophic bog site, hummock (October 2015). Scale intervals 1 cm / 2 mm. Arrows point positions of nival curvatures.
sues reported also by other authors (Muldiyarov & Lapshina, 1983; Vitt, 2007), were observed around the curvature of some moss samples. “Colorful” species (such as Sphagnum fuscum, S. magellanicum, S. wulfianum, S. lindbergii) sometimes also have a locally modified sclerenchyma pigmentation around the curvature. At early growth stages, their sclerenchyma has no colour yet. Therefore, the old coloured and the young colourless parts around the curvature are clearly contrasting. To identify nival curvatures, one should keep in mind that the latter precede aqueous curvatures that had been developed at an early growth stage before changes of the water level.

In mesotrophic and eutrophic environments, shoots can be contaminated by mud particles. The well-defined boundary between the dark submerged part of the shoot and the light emerged part of the shoot is often observed after leaving the aquatic environment. This technique can be used to rule out curvatures of aqueous origin.

Transformed sites with damaged Sphagnum cover and sites which display a complex fluctuating Sphagnum cover dynamics during the growing season are less suitable for the study of shoot increment over a long period of time. Nival curvatures on shoots are very similar to the impact and aqueous curvatures.

Fig. 7. Samples of nival and other geotropic curvatures on Sphagna shoots under natural conditions (cf. Figs. 6 and 8). A: S. warnstorffii from a rich fen site, lawn (October 2015); B: S. papillosum from a minerotrophic mire site, lawn (September 2015); C: S. centrale from an open minerotrophic mire site, hummock (September 2015); D: S. centrale from paludified spruce forest, footprint on low hummock (October 2015); E: S. subsecundum from a minerotrophic mire site, hollow (September 2014); F: S. wulfianum from spruce forest, lawn (October 2015). Scale intervals 1 cm / 2 mm. Black arrows point positions of nival curvatures, purple arrows indicate positions of artificially induced curvatures.
**MATERIALS AND METHODS**

The surveys were carried out in 2014 and 2015 in mires Nenazzvannoye and Rittusuo, where the growth of *Sphagnum* mosses has been annually studied by the tied thread method in permanent sample plots on a long-term basis (Grabovik, 1994; Grabovik & Nazarova, 2013). The species measured for increment were *Sphagnum fallax*, *S. obtusum, S. subsecundum, S.majus, S. riparium*, and *S. papillosum* in Nenazzvannoye mire, and *S. riparium, S.fallax*, and *S. cuspidatum* in Rittusuo mire (Table 1).

One sampling polygon 30 × 30 cm, where the increment of dominant species was measured by the traditional tied thread method (Begak, 1927) and the method of natural markers, was installed on six permanent sample plots. Each polygon was divided into two equal parts. In the first part (control) 50 moss stems were marked by the tied thread method. We tied the thread on each stem below 1 cm of the top of the capitulum. The stems were marked on May 11 and 14 in 2014, and on May 20 and 21 in 2015. In the second part (experiment) the *Sphagnum* mat was left intact, but shoots around the polygon were pre-checked for nival geotropic curvatures.

The surveys were completed on September 10 and 11 in 2014, and on September 22 and 23 in 2015. When observations have been completed, *Sphagnum* was harvested from both parts of the polygon. The length increment of the tied shoots was measured in the control, and the length increment of shoots from nival geotropic curvatures was measured in the experiment. In the control, length increment was estimated by measuring the distance between the tied thread position and the top of the capitulum, excluding initial distance 1 cm. In the experiment, after identifying nival geotropic curvatures, length increment was estimated by measuring the distance between the curvature and the top of the capitulum. Later on, based on the direct measurements, samples were made. This data were processed by statistical methods (Ivanter & Korosov, 2003) and compared against each other. Differences between values of length increment and between the coefficients of variation of the samples were estimated by Student’s t-test.

**RESULTS**

In 2014, most shoots in the control of *S. fallax* in Nenazzvannoye mire dried out, thus length increment was determined only in experiment for this species. The length increment values (Table 2) obtained for control and experiment display distinctive differences. Experiment increment values exceed control values for all the samples compared by 12.0±3.81 % in 2014 and by 35.0±10.21 % in 2015. Such differences are reliable for all samples compared in 2014, except for *S. obtusum* (Table 3). Control and experiment samples were clearly shown to correlate (Fig. 4). Pearson’s correlation coefficient for the samples compared was 0.99 in 2014 and 0.97 in 2015.
The coefficients of variation (CV) obtained for control and experiment samples also exhibit some peculiarities. In 2014, mean value of CV was 20.3±4.2 % for control samples and 13.0±4.7 % for experiment samples. In 2015, CV were estimated at 21.1±5.3 % and 8.7±2.2 %, respectively. The greatest internal scatter for all samples compared during the study period was obtained for control samples and the least range for experiment samples (Fig. 5). In 2014 reliable differences were found for four of seven pairs compared: Sphagnum riparium and S. subsecundum on Nenazvannoye mire and S. majus and S. riparium on Rittusuo mire (Table 3). In 2015, reliable differences were found for all pairs compared, except for S. obtusum from Nenazvannoye mire.

**DISCUSSION**

Differences in the length increment values estimated with natural and artificial markers have been discussed in literature. For example, Pouliot et al. (2010) reported similar results obtained by estimating the increment of some mosses from polygonal mires by various methods. The difference in increment values in their study varied from 32 to 113 %. In our study, increment values obtained for experiment were higher than for control at 7.5 % – 18.6 % in 2014, and at 20.8 % – 45.8 % in 2015. Systematic differences between the control and experiment samples are most probably due to some characteristics of the methods employed.

The main factors responsible for the described differences are probably: a) the difference in time between the beginning of the active growth of shoots and the time of application of artificial markers and b) artifacts associated with the inevitable damage of natural structure of the Sphagnum mat inflicted, for example, by threads. It is known from the literature (Solonevich, 1966; Ilomets, 1976; Smolyanitsky, 1977) that such events considerably increase the loss of water by a Sphagnum carpet and result in either drying of shoots or retardation of their growth. Subnival growth observed occasionally (unpublished data) could also be responsible for the differences described above.

The differences between the pairs compared in 2014 and 2015 seem to be due to the features described above. We believe that they were essential at the beginning of 2014 and 2015 growing seasons. As there was little snow in the winter of 2014, the mires were subjected to deeper freezing, and transition of mean daily temperatures via 5° С in spring took place as late as May 9, immediately before the beginning of experiments. Therefore, Sphagnum mosses must have started to grow actively after the tying of threads, and the differences between control and experimental samples were not sufficient. Different background was observed in winter of 2015, when the mires were snow-bound. Early snowfalls retarded deep freezing and contributed to subnival moss growth. The transition of mean daily temperatures via 5° С in spring took place on April 28, 3.5 weeks before the beginning of the experiments. Obviously, the reason for considerable differences is that Sphagnum mosses had begun to grow actively in this environment long before threads were tied.

It should be stressed that the shoot length increment values obtained for some species with nival geotropic curvatures are higher than the values estimated for the study area (Grabovik & Kuznetsov, 2016) and other regions. This could be due to some artifacts and the delayed checking of the beginning of shoot growth due to the use of artificial markers. The growth of Sphagnum mosses is badly affected not only by tied threads but
also by the cutting-off the plants to known initial length – a method used to estimate the increment of pool moss species. As a result, natural translocation within a shoot is disturbed (Rydin & Clymo, 1989; Aldous, 2002), the surfaces and cavities colonized by diazotrophic and methanotrophic microorganisms are considerably reduced (Raghoebarsing et al., 2005; Ho & Bodelier, 2015) and the natural assimilation and transport of biogenic chemical elements are disturbed. It seems to be the reason why the increments estimated by this method are so low even for rapidly growing species (Sonesson et al., 1980; Hulme & Blyth, 1982). One should keep in mind that the selected habitats (especially drainage ditches) are inundated at an optimum level favourable for the growth of Sphagnum.

The above mentioned differences in CV are also consistent with earlier data (Pouliot et al., 2010). In that study, CV obtained for samples with natural markers were 17 % – 31 %, while those obtained with artificial markers were as high as 37 % – 56 %. Together with other authors (Solonevich, 1966; Ilomets, 1976), we attribute higher CV obtained for samples with artificial markers to the disturbance of the natural structure of the Sphagnum mat. As a result, the growth of some shoots was either retarded or terminated, while the growth of other shoots was not substantially affected. As such phenomena do not occur in samples obtained with natural markers, their values vary less markedly.

A geotropic reaction is favoured by various natural factors (Figs. 6–8). In northern regions it is most com-

![Fig. 4. Shoot length increment in control and experiment in 2014 (A) and 2015 (B). Axis X – control, axis Y – experiment. In (A) Nenazvannoye mire: 1 – Sphagnum riparium, 2 – S.obtusum, 3 – S.subsecundum, 4 – S.majus; Rittusuo mire: 5 – S.riparium, 6 – S.fallax, 7 – S.cuspidatum. In (B) Nenazvannoye mire: 1 – Sphagnum riparium, 2 – S.obtusum, 3 – S.subsecundum, 4 – S.papillosum, 5 – S.fallax; Rittusuo mire: 6 – S.riparium, 7 – S.fallax, 8 – S.cuspidatum. Bars correspond to double standard error of the mean.](image)

![Fig. 5. Difference of coefficients of variation for the control and the experiment in 2014 (A) and 2015 (B). In (A) Nenazvannoye mire: 1 – Sphagnum riparium, 2 – S.obtusum, 3 – S.subsecundum, 4 – S.majus; Rittusuo mire: 5 – S.riparium, 6 – S.fallax, 7 – S.cuspidatum; 8 – mean value. In (B) Nenazvannoye mire: 1 – Sphagnum riparium, 2 – S.obtusum, 3 – S.subsecundum, 4 – S.papillosum, 5 – S.fallax; Rittusuo mire: 6 – S.riparium, 7 – S.fallax, 8 – S.cuspidatum, 9 – mean. Asterisks mark significant difference: * – p<0.95, ** – p<0.99. Bars correspond to standard error of CV.](image)
Table 3. Verification of the hypothesis on the difference between values of the shoot length increment and difference between coefficients of variation in the control and the experiment: \( df \) – number of degrees of freedom; \( t_{act} \) – actual Student’s \( t \)-test value; significance: * \( p>0.95 \), ** \( p>0.99 \).

<table>
<thead>
<tr>
<th></th>
<th>Length increment</th>
<th>Coefficients of variation</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>2014 ( df )</td>
<td>2015 ( df )</td>
</tr>
<tr>
<td><strong>Nenazvannyoe mire</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S. riparium</td>
<td>66</td>
<td>67</td>
</tr>
<tr>
<td>S. obtusum</td>
<td>82</td>
<td>74</td>
</tr>
<tr>
<td>S. subsecundum</td>
<td>135</td>
<td>53</td>
</tr>
<tr>
<td>S. majus</td>
<td>119</td>
<td>–</td>
</tr>
<tr>
<td>S. fallax</td>
<td>–</td>
<td>48</td>
</tr>
<tr>
<td>S. papillosum</td>
<td>–</td>
<td>56</td>
</tr>
<tr>
<td><strong>Rittusuo mire</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S. riparium</td>
<td>128</td>
<td>68</td>
</tr>
<tr>
<td>S. fallax</td>
<td>57</td>
<td>65</td>
</tr>
<tr>
<td>S. cuspidatum</td>
<td>41</td>
<td>45</td>
</tr>
<tr>
<td><strong>Mean:</strong></td>
<td>12</td>
<td>1.439</td>
</tr>
</tbody>
</table>

Theoretically, mire ridges and hummocks and in the forest habitats, mat, then no nival geotropic curvatures are formed on cover is preceded by the deep freezing of the tional markers. For instance, if the formation of snow hard and even impossible to identify in a variety of other factors. Geotropic curvatures of nival genesis are dealt with, is not a problem in conducting dynamic observations or external control (artificial markers on the shoots). Geotropic curvatures actually may be taken for an annual increment, because the method ignores curvatures formed due to other factors.

Tracing of shoot increment from the nival curvatures horizon, even if genetically different curvatures are dealt with, is not a problem in conducting dynamic observations or external control (artificial markers on the shoots). Geotropic curvatures of nival genesis are hard and even impossible to identify in a variety of other curvatures without permanent monitoring or additional markers. For instance, if the formation of snow cover is preceded by the deep freezing of the Sphagnum mat, then no nival geotropic curvatures are formed on mire ridges and hummocks and in the forest habitats. Theoretically, Sphagnum mosses growing at considerable water depth, where shoots are unaffected by snow load, are expected to have no markers. Another factor to be taken into account is that these markers can be lost in the course of transformation of lower shoot portions into peat. Thus, the nival geotropic curvatures of Sphagnum riparium growing in some mesotrophic sites were lost as a result of the decomposition of the lower shoot fragments by the end of the growing season. In species growing in a hyperhydrophilic environment with considerable water level fluctuations (Sphagnum fallax, S. majus), nival geotropic curvatures are sometimes unrecognizable because of a variety of aequous curvatures. Therefore, their increment cannot be precisely estimated.

To sum up, our in situ monitoring shows that stem curvatures of Sphagnum mosses are of geotropic origin and that they are formed by some environmental triggers such as widespread nival and aequous physical impact. The method for estimation of the length increment of Sphagnum known from the literature was updated on the basis of the technique for identification of nival geotropic curvatures described earlier. Comparison of this method with the tied thread method has revealed similarities and differences between length increment values and variation indices. This shows the distinctive characteristics of the methods employed.

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