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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

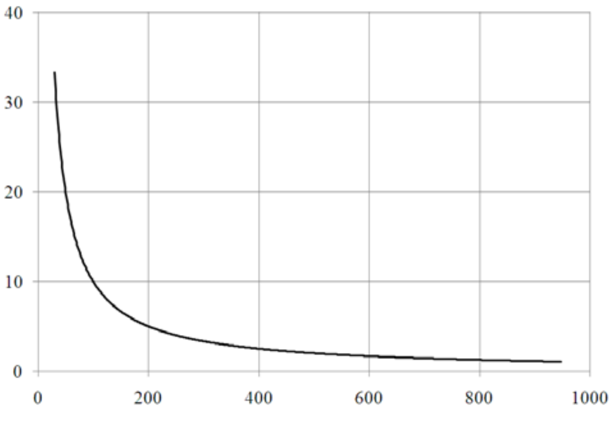
Various methods are used for estimation the length increment of *Sphagnum* mosses (Clymo, 1970; Vitt, 2007). Methods based on the use of artificial markers, such as cranked wire, tied thread, white marks, cutting-off plants for marking starting point of growth are most popular. On the one hand, practical application of these methods is laborious; on the other hand, it displays some artefacts which may distort the results of measurements (Solonevich, 1966; Ilomets, 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; Muldiyarov & 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 (Elina *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

Fig. 1. Individual snow load dependence on *Sphagnum* cover density. Axis X – *Sphagnum* density (plants/dm^2), axis Y – snow load, calculated for open sites, in gram per plant (100 mm water).



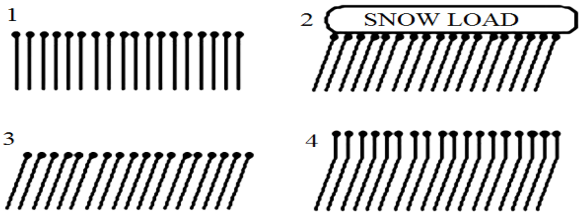


Fig. 2. The nival genesis of geotropic curvature in *Sphagna*: 1 – orthotropic growth; 2 – declination by snow load; 3 – retained declination; 4 – geotropic curvatures formation due to return to orthotropic growth.

subjected to a pressure of 1000–1200 g/dm^2. 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 snowpack 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 inhibitnegative 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.

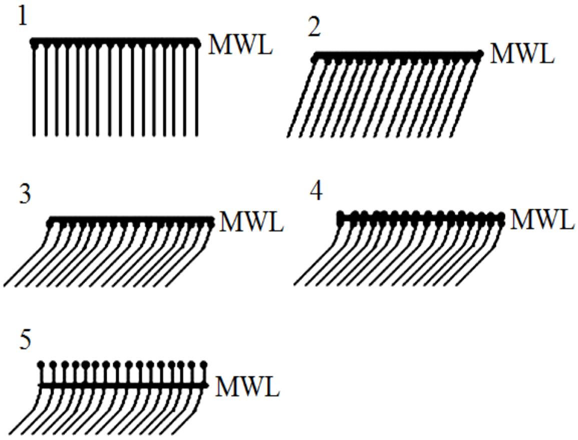


Fig. 3. The aqueous genesis of geotropic curvature in *Sphagna:*1 – orthotropic growth at elevated MWL; 2 – shoot declination as a result of MWL drop; 3 – geotropic curvature formation upon MWL drop; 4 – shoot apices begin to emerge as MWL has dropped critically and further decline can no longer entrain shoots; 5 – shoot growth is steadily orthotropic in spite of further MWL reduction.

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 *Sphagna*, 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).

Table 1. Characteristics of sample plots with *Sphagna*

Plot #	Species	Position in microrelief	MWL, cm	Nutrient/ moisture
	Nenazvannoye mire (61°47 ′58.92″ N, 33°31′ 29.68″ E)			
I	*S. majus*	hollow	-1 -5	meso-oligotrophic/ stagnant
	S. papillosum	lawn	-5 -10	
II	*S. subsecundum*	hollow	-1 -5	eu- to mesotrophic/ low flowage
	S. obtusum	lawn	-5 -13	
III	*S. fallax*	lawn	-1 -15	mesotrophic / low flowage
	S. riparium	lawn	-1 -15	
	Rittusuo mire (61°46′28.98″ N, 33°31′32.62″ E)			
IV	*S. riparium*	drainage ditch	0 -20	oligomesotrophic/ low flowage
V	*S. fallax*	drainage ditch	0 -3	meso-oligotrophic / stagnant
VI	*S. cuspidatum*	drainage ditch	0 -1	oligotrophic / stagnant

Hollow- and pool-dwelling species, such as *Sphagnum riparium, S. fallax, S. majus, S. cuspidatum, S. jensenii, S. balticum* and *S. lindbergii,* and even the hummock-dwelling species *S. magellanicum* and *S. fuscum*, 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 inpact 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 (Muldiyarov & 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-

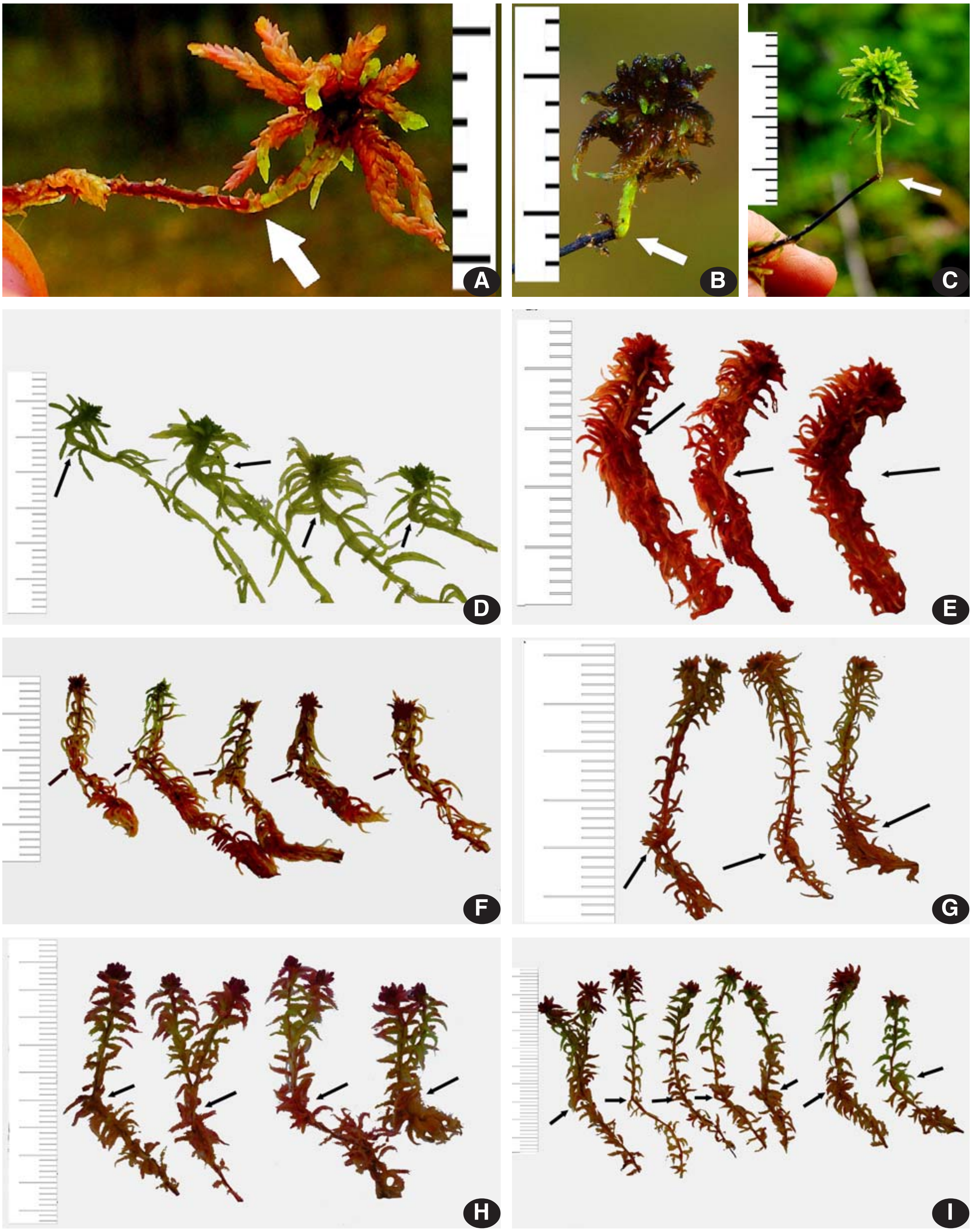


Fig. 6. Samples of nival geotropic curvatures on *Sphagna* shoots under natural conditions (cf. also Figs. 7-8). A: *Sphagnum magellanicum* from ombrotrophic bog site, lawn (May 2016); B: *S. subsecundum* from a minerotrophic mire site, hollow (May 2015); C: *S. wulfianum* from spruce forest, lawn (May 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.

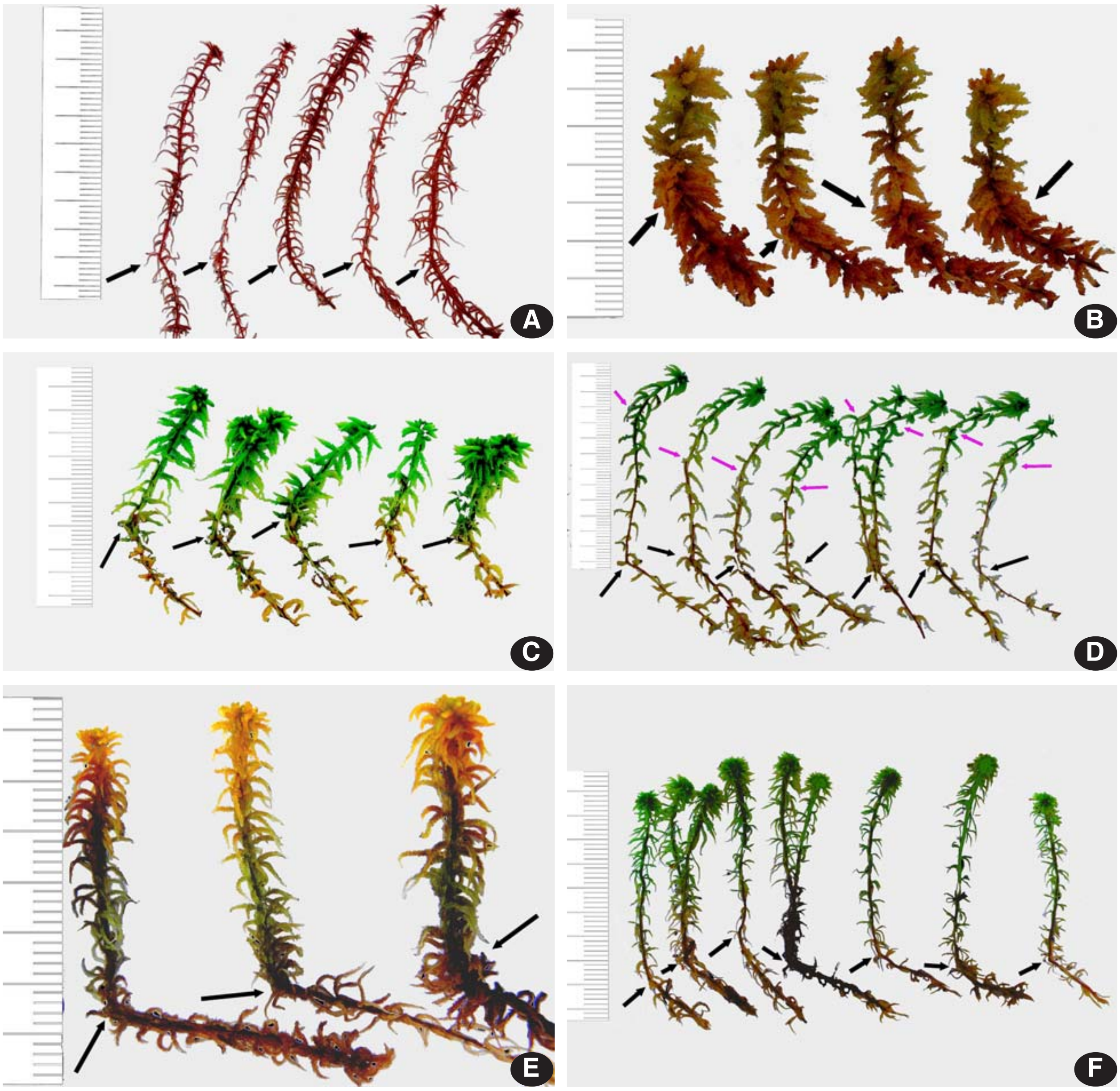


Fig. 7. Samples of nival and other geotropic curvatures on *Sphagna* shoots under natural conditions (cf. Figs. 6 and 8). A: *S. warnstorfii* from a rich fen site, lawn (October 2015); B: *S. papillosum* from a minerotrophic mire site, lawn (September 2015); C: *S. centrale* from an open minerotrophic 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.

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. 8. Samples of nival and other geotropic curvatures on *Sphagna* shoots under natural conditions (fr. Figs. 6–7). A: *S. girgensohnii* from spruce forest, lawn (September 2014); B: *S. riparium* from a minerotrophic mire site, lawn (September 2015). Scale intervals 1 cm / 2 mm. Black arrows point positions of nival curvatures, yellow arrows indicate aqueous curvatures, red arrows show rainfall curvatures.

MATERIALS AND METHODS

The surveys were carried out in 2014 and 2015 in mires Nenazvannoye 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 Nenazvannoye 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 Nenazvannoye 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.

Table 2. Shoot length increments of *Sphagnum* in the control and the experiment in 2014 and 2015

Species	control N	increment, cm	experiment N	increment, cm	difference between control and experiment, %
		2014, Nenazvannoye mire			
S. riparium	35	7.2±1.35	33	7.9±1.00	8.9
S. obtusum	33	6.2±1.44	51	6.7±1.17	7.5
S. subsecundum	41	4.0±0.68	96	4.4±0.33	9.1
S. majus	32	2.8±0.70	89	3.3±0.56	15.2
S. fallax	–	–	86	3.5±0.52	–
		2014, Rittusuo mire			
S. riparium	34	7.7±1.85	96	8.8±0.83	12.5
S. fallax	27	5.1±1.01	32	5.8±1.08	12.1
S. cuspidatum	13	7.0±0.95	30	8.6±0.71	18.6
		2015, Nenazvannoye mire			
S. riparium	39	18.1±3.39	30	32.6±2.26	44.5
S. obtusum	26	9.7±1.83	50	17.5±2.32	44.6
S. subsecundum	35	6.7±1.18	20	9.1±0.73	26.4
S. papillosum	28	1.6±0.75	30	2.4±0.37	33.3
S. fallax	20	5.1±0.71	30	6.8±0.54	25.0
		2015, Rittusuo mire			
S. riparium	30	26.6±3.97	40	41.5±2.07	35.9
S. fallax	37	15.8±2.78	30	31.0±1.59	45.8
S. cuspidatum	15	16.4±3.40	32	20.7±1.63	20.8

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° C 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° C 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

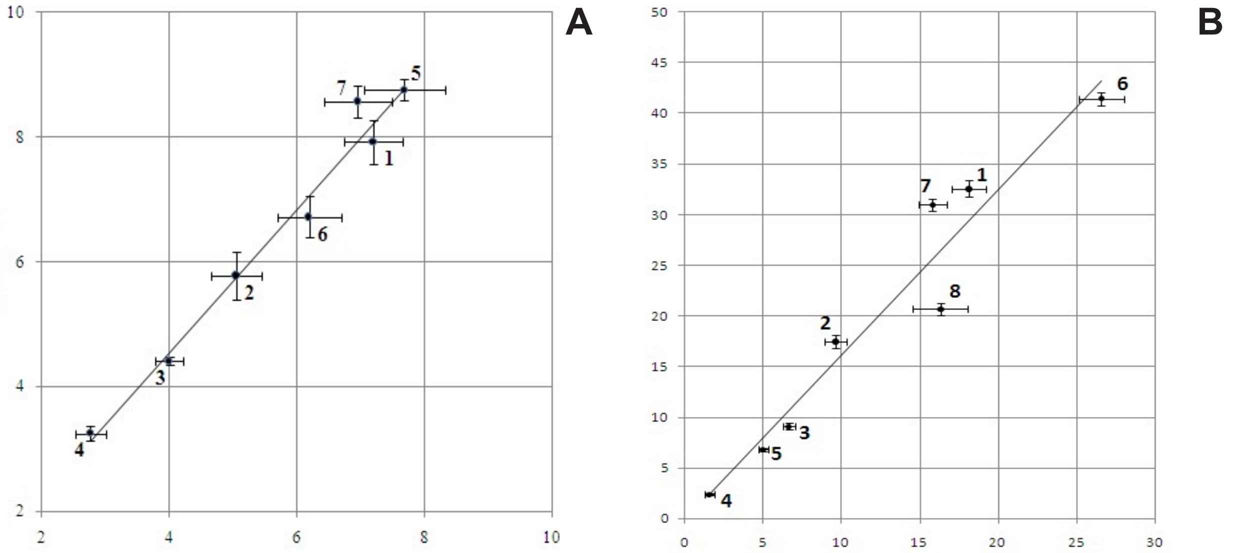


Fig. 4. Shoot length increment in control and experiment in 2014 (A) and 2015 (B). Axis X – control, axis Y – experiment. In (A) Nenazvannoye mire: 1 – *Sphagnum riparium*, 2 – *S.obtusum*, 3 – *S.subsecundum*, 4 – *S.majus*; Rittusuo mire: 5 – *S.riparium*, 6 – *S.fallax*, 7 – *S.cuspidatum*. In (B) 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.

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-

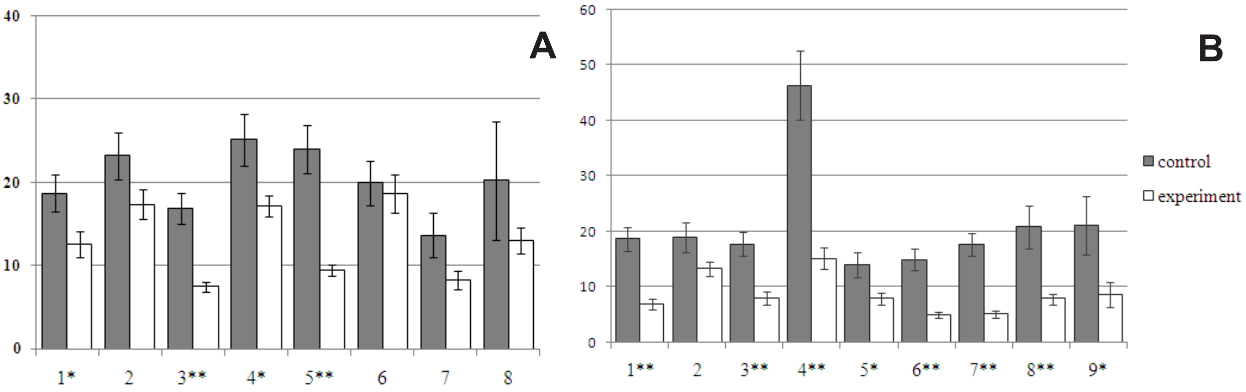


Fig. 5. Difference of coefficients of variation for the control and the experiment in 2014 (A) and 2015 (B). In (A) Nenazvannoye mire: 1 – *Sphagnum riparium*, 2 – *S.obtusum*, 3 – *S.subsecundum*, 4 – *S.majus*; Rittusuo mire: 5 – *S.riparium*, 6 – *S.fallax*, 7 – *S.cuspidatum;* ; 8 – mean value. In (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.

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.

	Length increment				Coefficients of variation			
	2014		2015		2014		2015	
	df	$t_{act.}$	df	$t_{act.}$	df	$t_{act.}$	df	$t_{act.}$
Nenazvannoye mire								
S. riparium	66	2.509*	67	21.112**	66	2.245*	67	5.110**
S. obtusum	82	1.747	74	16.031**	82	1.745	74	1.923
S. subsecundum	135	3.590**	53	9.388**	135	4.861**	53	3.950**
S. majus	119	3.425**	–	–	119	2.336*	–	–
S. fallax	–	–	48	9.485**	–	–	48	2.486*
S. papillosum	–	–	56	5.015**	–	–	56	4.804**
Rittusuo mire								
S. riparium	128	3.258**	68	18.768**	128	4.867**	68	4.941**
S. fallax	57	2.643**	65	27.980**	57	0.356	65	5.799**
S. cuspidatum	41	5.483**	45	4.691**	41	1.861	45	3.298**
				Mean:	12	1.439	14	2.184*

monly induced by snow and groundwater level fluctuations. To estimate an annual increment of shoots, measurements should be made from the nival geotropic curvatures. However, in accordance with the early version of the method (Camill *et al*., 2001), all shoot segments between 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 aqueous 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 aqueous 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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LITERATURE CITED

ALDOUS, A.R. 2002. Nitrogen translocation in *Sphagnum* mosses: effects of atmospheric nitrogen deposition. – *New Phytologist* **156**(2), *241-253.*

BANBURY, G.Y. 1962. Geotropism of lower plants. *In: Handbuch der Pflanzenphysiologie. Ed. by W.Ruhland et al. Band XVII, Teil 2. Berlin-Gottingen-Heidelberg: Springer-Verlag: 344–377.*

[BEGAK, D.O.] БЕГАК Д.О. 1927. О приросте торфяников. – [On the peatlands growth] *Торфяное дело [Torfyanoe delo]* **11-12**: *300–306.*

BERG, A., E. DANIELSSON & B.H. SVENSSON. 2013. Transfer of fixed-N from N2-fixing cyanobacteria associated with the moss *Sphagnum riparium* results in enhanced growth of the moss. – *Plant and Soil* **362** (1): *271-278.*

BISMARCK, R. VON. 1959. Über den Geotropismus der Sphagnen. – *Flora (Jena)* **148**: *23–83.*

[BONDARIK, N.L.] БОНДАРИК Н.Л. 2004. Динамика стокообразующих факторов. – [Dynamics of discharge forming factors] *В кн: Климат Карелии: изменчивость и влияние на водные объекты и водосборы (отв. ред. Филатов, Н.Н.) Петрозаводск, КарНЦ РАН. [in Filatov, N.N. Climate of Karelia: variability and influence on water objects and watersheds, Petrozavodsk, KarRC RAS]: 34–54.*

CAMILL, P., J.A. LYNCH, J.S. CLARK, J.B. ADAMS & B. JORDAN. 2001. Changes in biomass, aboveground net primary production, and peat accumulation following permafrost thaw in the boreal peatlands of Manitoba, Canada. *– Ecosystems* **4(5)**: *461–478.*

CLYMO, R.S. 1970. The growth of *Sphagnum*: methods of measurement. *– Journal of Ecology.* **58**: *13–49*.

[ELINA, G.A., O.L. KUZNETSOV & A.I. MAKSIMOV] ЕЛИНА Г.А., О.Л. КУЗНЕЦОВ, А.И. МАКСИМОВ. 1984. Структурно-функциональная организация и динамика болотных экосистем Карелии. – [*Structure-functional organization and dynamics of mire ecosystems in Karelia*] *Л., Наука* [*Leningrad, Nauka*]: *128 pp.*

EUROLA, S. 1975. Snow and ground frost conditions of some Finnish mire types. *– Annales Botanici Fennici* **12**: *1–16.*

[GRABOVIK, S.I.] ГРАБОВИК С.И. 1994. Влияние климатических условий на линейный прирост сфагновых мхов южной Карелии. – [The effect of climatic conditions on the annual increment of *Sphagna* in Southern Karelia] *Ботанический журнал* [*Botanicheskyi zhurnal*] **79** (4): *81–86.*

[GRABOVIK, S.I. & O.L. KUZNETSOV] ГРАБОВИК С.И., КУЗНЕЦОВ О.Л. 2016. Рост и продуктивность ценопопуляций сфагновых мхов на естественных и трансформированных болотах Карелии. – [Growth and productivity of cenopopulationsof Sphagnum mosses in natural and transformed mires of Karelia] *Труды Карельского научного центра РАН. Серия Экологические исследования* [*Transactions of the Karelian Research Centre of the Russian Academy of Sciences. Ecological studies series*] **4**: *59–69.*

GRABOVIK, S.I. & L.E. NAZAROVA. 2013. Linear increment of *Sphagnum* mosses on Karelian mires (Russia). *– Arctoa* **22**: *23–26.*

GRAHAM, J.A. & D.H. VITT. 2016. The limiting roles of nitrogen and moisture on *Sphagnum angustifolium* growth over a depth to water table gradient. *– Plant and Soil* **404**(1): *427–439*.

HO, A. & P.L. BODELIER. 2015. Diazotrophic methanotrophs in peatlands: the missing link? *– Plant and Soil* **389**(2): *419–423*.

HULME, P.D. & A.W. BLYTH. 1982. The annual growth period of some Sphagnum species on the Silver Flowe National Nature Reserve, southwest Scotland. *– Journal of Bryology* **12**(2): *287–291*.

[IVANTER, E.V. & A.V. KOROSOV] ИВАНТЕР Э.В., А.В. КОРОСОВ. 2003. Введение в количественную биологию. – [Introduction in quantitative biology] Петрозаводск. *Петрозаводский государственный университет* [*Petrozavodsk, Petrozavodskij gosudarstvennii universitet*]: *302 pp.*

[ILOMETS, M.A.] ИЛОМЕТС М.А. 1976. Продуктивность сфагнового покрова на примере Гусиного болота. – [Productivity of *Sphagna* cover on Gusinoe mire model] *Труды Печеро-Илычского государственного заповедника* [*Trudy Pechero-Ilychskogo gosudarstveogo zapovednika*] **13***: 40–57.*

JAUHIAINEN, J., J. SILVOLA, K. TOLONEN & H. VASANDER. 1997. Response of *Sphagnum fuscum* to water levels and CO2 concentration. *– Journal of Bryology*, **19**(3): *391–400*.

LINDHOLM, T. & H. VASANDER. 1990. Production of eight special of *Sphagnum* at Suurisuo mire southern Finland. *– Annales Botanici Fennici* **27**: *145–157.*

MALMER, N. 1962. Studies on mire vegetation in the Archean area of southwestern Gotaland (South Sweden) II. Distribution and seasonal variation in elementary constituents on some mire sites. *– Opera botanica.* **7**(2): *1–67*.

[MULDIYAROV, E.YA. & E.D. LAPSHINA] МУЛЬДИЯРОВ Е.Я., Е.Д. ЛАПШИНА. 1983. Датировка верхних слоев торфяной залежи, используемой для изучения космических аэрозолей. – [Dating of the top layer in peat deposit, using for cosmic aerosol research] *В кн: Метеоритные и метеорные исследования, Новосибирск* [*In: Meteoritnye i meteornye issledovaniya, Novosibirsk*]: 75-84.

[PANOV, V.V.] ПАНОВ В.В. 2008. Функциональная неоднородность деятельного слоя сфагновых болот. – [Functional heterogeneity of acrotelm in mires] *Вестник Томского государственного педагогического университета* [*Vestnik Tomskogo gosudarstvennogo pedagogicheskogo universiteta*] **4**: *21–26*.

POULIOT, R., M. MARCHAND-ROY, L. ROCHEFORT & G. GAUTHIER. 2010. Estimating moss growth in arctic conditions: a comparison of three methods. *– Bryologist* **113** (2): *322–332*.

RAGHOEBARSING, A.A., A.J. SMOLDERS, M.C. SCHMID, W.I.C. RIJPSTRA, M. WOLTERS-ARTS, J. DERKSEN, M.S.M. JETTEN, S. SCHOUTEN, J.S.S. DAMSTÉ, L.P.M. LAMERS, J.G.M. ROELOFS, H.J.M. OP DEN CAMP & M. STROUS. 2005. Methanotrophic symbionts provide carbon for photosynthesis in peat bogs. – *Nature* **436**(7054): *1153–1156*.

ROCHEFORT, L., D.H. VITT & S.E. BAYLEY. 1990. Growth, production, and decomposition dynamics of *Sphagnum* under natural and experimentally acidified conditions. *– Ecology* **71**(5): *1986–2000*.

RYDIN, H. & R. S. CLYMO. 1989. Transport of carbon and phosphorus compounds about *Sphagnum*. *– Proceedings of the Royal Society of London: Biological Sciences* **237**(1286): *63–84*.

[SMOLYANICKIJ, L.YA.] СМОЛЯНИЦКИЙ Л.Я. 1977. Некоторые закономерности формирования дернины сфагновых мхов. – [Some regularities of formation of Sphagnum moss turfs] *Ботанический журнал* [*Botanicheskiy Zhurnal*] **62** (9): *1262–1272.*

[SOLONEVICH, N.G.] СОЛОНЕВИЧ Н.Г. 1966. К биологии сфагновых мхов. – [On the *Sphagna* biology] *Ботанический журнал* [*Botanicheskiy Zhurnal*] **51** (9): *1297–1302.*

SONESSON, M., S. PERSSON, K. BASILIER, & T.A. STENSTRÖM. 1980. Growth of *Sphagnum riparium* Engstr. in relation to some environmental factors in the Stordalen mire. *– Ecological Bulletins* **30**: *191–207*.

TURETSKY, M.R., S.E. CROW, R.J. EVANS, D.H. VITT & R.K. WIEDER. 2008. Trade-offs in resource allocation among moss species control decomposition in boreal peatlands. *– Journal of Ecology* **96**(6): *1297–1305*.

VITT, D.H. 2007. Estimating moss and lichen ground layer net primary production in tundra, peatlands and forests. *In: Fahey, T.J. & A.K. Knapp (eds) Principles and Standards for Measuring Primary Production. Oxford University Press, New York: 82–105.*

YAZAKI, T. & K. YABE. 2012. Effects of snow-load and shading by vascular plants on the vertical growth of hummocks formed by *Sphagnum papillosum* in a mire of northern Japan. *– Plant Ecology* **213**: *1055–1067*.