BIOMECHANICAL PROPERTIES OF THE TERRESTRIAL MOSSES *PLEUROZIUM SCHREBERI* (BRID.) MITT. AND *POGONATUM JAPONICUM* SULL. & LESQ. ALONG ALTITUDINAL GRADIENTS IN NORTHERN JAPAN

БИОМЕХАНИЧЕСКИЕ СВОЙСТВА НАЗЕМНЫХ МХОВ *PLEUROZIUM SCHREBERI* (BRID.) MITT. И *POGONATUM JAPONICUM* SULL. & LESQ. ВДОЛЬ ВЫСОТНОГО ГРАДИЕНТА В ГОРАХ СЕВЕРА ЯПОНИИ

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Abstract

Altitudinal gradients along mountain slopes provide valuable opportunities to study variation in plant traits in response to changes in environmental conditions along such gradients. This study focused on biomechanical traits of two moss species, the more or less horizontally growing *Pleurozium schreberi* and the erect-growing *Pogonatum japonicum,* along altitudinal gradients on two mountains in Hokkaido, northern Japan. We measured stem diameter in two directions to determine the second moment of area I, used three-point bending tests with free stem ends to determine the slope of the force-deflection curve dF/dx, and used these data to calculate Young's modulus and flexural rigidity of the stems. Both species showed much variation in all traits among replicates in the samples at each altitude. Environmental variation associated with altitude had more effect on the biomechanical traits of *P. japonicum* than on those of *P. schreberi*. Stems of *P. japonicum* were thicker (larger I) than those of *P. schreberi* and had a larger Young's modulus and flexural rigidity. Stems tended to become thinner (lower second moment of area) and less rigid (lower flexural rigidity) at increasing altitude in both species.

Резюме

Высотный градиент в горах дает значительные возможности изучения признаков растений в ответ на меняющиеся условия среды вдоль этого градиента. Исследование в данном случае концентрировалось на биомеханических свойствах двух видов мхов, преимущественно плагиотропного *Pleurozium schreberi* и б.ч. прямостоячего *Pogonatum japonicum.* Работа проведена на склонах двух гор на Хоккайдо, Япония. Был измерен диаметр стебля в двух направлениях для определения второго момента площади I, с использованием теста на сгиб по трем точкам, причем концы стебля не были закреплены с целью определить зависимость отклонения кривой dF/dx, и рассчитать модуль Юнга (упругости стебля при растяжении) и упругости стебля на сгиб. Оба вида оказались сильно вариабельными по всем изученным признакам в выборках с отдельных высот. Зависимость от высоты произрастания растений у *P. japonicum* оказалось более явной, чем у *P. schreberi*. Стебли *P. japonicum* были толще, чем у *P. schreberi* и имели больший модуль Юнга и упругости на сгиб. Стебли имеют тенденцию к истончению (имеют более низкий второй момент площади) и становятся менее жесткими (с более низким значением упругости на сгиб) с увеличением высоты для обоих видов.

KEYWORDS: bryophytes, stem, flexural rigidity, altitudinal traits, *Pleurozium, Pogonatum*

INTRODUCTION

Many bryophyte species occur over a range of environments and show variation in their morphology, anatomy and physiology in response to differences in environmental factors along this range. A prime example of such a range is the altitudinal gradient along mountain slopes. This inherently involves a gradient of atmospheric pressure and temperature, although many other factors important for plant life such as moisture and soil development usually also show clear trends (Körner, 2007). Many studies have found both genetically and plastically determined changes in traits relevant for photosynthetic performance and water economy of vascular plants (*e.g.*, Körner *et al*., 1986), including patterns of biomass allocation to stems and roots and root length / leaf area ratios (Körner & Renhardt, 1987). Bryophytes may be expected to show similar patterns, and have done so in some studies (Waite & Sack, 2011), while other studies have shown variation in photosynthesis, respiration and desiccation tol-

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erance hardly related to altitude (Bader *et al*., 2013; Wagner *et al*., 2013).

Other physical factors affecting plants, such as snow load, will also vary with altitude, yet biomechanical traits have seldom been studied in relation to altitude. In one of the few existing studies, Eldar pine (*Pinus eldarica* Medw.) showed considerable variation in wood mechanical properties along a gradient from 500 to 1400 m a.s.l. in northern Iran (Kiaei & Samariha, 2011). Biomechanical properties of bryophytes along altitudinal gradients have not yet been studied, although a study of the mechanical properties of two growth forms of *Hylocomium splendens* (Hedw.) Schimp. (Ross *et al*., 1998), one from low-arctic and one from high-arctic conditions, suggests that these traits may also show considerable variation along elevational gradients.

There are only a few studies on the biomechanics of bryophytes in general, perhaps partly because of their small size and often dense canopies, as a result of which strong mechanical forces due to wind are not likely to play a significant role. Yet Niklas (1993, 1994, 1995) showed that the biomechanical properties of moss stems fitted the general allometrical scaling relationships found for vascular plants very well. Sympodial and monopodial plants of the large, usually weft-forming pleurocarpous moss *Hylocomium splendens* originating from low-arctic and high-arctic conditions, respectively, differed markedly in the mechanical properties of their stems (Ross *et al*., 1998). Sympodial plants annually produced a new, initially vertically oriented, stem segment from a meristem on a stem segment of the previous year. Over a period of ca 1.5 year, the new segments branched extensively while gradually changing growth direction from vertical to almost horizontal. After another two years or so, the segments gradually senesced. Over this period the stems gradually became thinner but the material of which they were made became stiffer (higher Young's modulus), and the stem diameter gradually decreased. As a consequence, the stiffness (flexural rigidity) of the stems first increased and after 4-5 years decreased again. Plants with monopodial shoots were usually prostrate, and their stems were thinner and less stiff than those of sympodial plants, with hardly any change over the years. These results were interpreted as a trade-off beween the benefits of vertical growth in terms of light interception and associated carbon gain and the costs of the tissues needed for support (following Givnish, 1986), and as showing that the sympodial plants were mechanically adapted to carry at least their own weight (Ross *et al*., 1998). Transplant studies showed that the difference in growth form was largely a plastic response but probably also genetically determined to some extent (Ross *et al*., 2001).

The work of Biehle *et al*. (1998) on the aquatic species *Fontinalis antipyretica* Hedw. demonstrated the remarkable strength of its stems and showed that variation in its mechanical properties (due to variation in the relative proportion of strengthening tissue in the cortex of the stems) corresponded with the water velocity at the places where the plants were growing.

Finally, Frenzke *et al*. (2011) showed how similar levels of mechanical strength may be achieved using different anatomical designs by comparing the mechanical properties of the tall Polytrichaceous moss *Dendroligotrichum dendroides* (Hedw.) Broth. with those of vascular plants and the few other bryophyte species that have been studied. Detailed anatomical analyses of the conducting tissues in the stem of this species suggested that *D. dendroides* is subject to similar biomechanical constraints as tracheophytes (Atala & Alfaro, 2012).

In this paper we report on a study of biomechanical properties of stems of two bryophyte species differing in growth-form along a gradient of environmental harshness as represented by altitudinal gradients on Mt. Oakan and Mt. Teshio (Japan). *Pogonatum japonicum* Sull. & Lesq. produces tall turfs (sensu Gimingham & Birse, 1957) of leafy, unbranched stems which are usually vertically oriented and anatomically similar to those of *D. dendroides* studied by Frenzke *et al*. (2011) and Atala & Alfaro (2012), while the stems of *Pleurozium schreberi* (Brid.) Mitt. are much more branched and grow more horizontally to produce dense 'wefts', somewhat like the prostrate form of *H. splendens* studied by Ross *et al*. (1998). The stands of *P. schreberi* consisted of several genotypes each and there was clear evidence of genetic differentiation between altitudes (Korpelainen *et al*., 2012). An ecophysiological study on thermal acclimation of photosynthesis and growth in the same species in the same zones on Mt. Oakan showed that stands differed in response to temperature, but did not show consistent trends with altitude (Jägerbrand *et al*., 2014). Based on the assumption that stems may be just as strong and thick as needed in the particular environment in which they are growing, we tested the following hypotheses:

1) Biomechanical tissue properties such as Young's modulus vary consistently along an altitudinal gradient for both species;

2) An erect-growing species will have a higher Young's modulus and flexural rigidity than one with more horizontally growing stems.

MATERIAL AND METHODS

Collection of samples

Pleurozium schreberi samples of approximately 10 cm diameter were collected from 10 sites along an altitudinal gradient from 460 to 1350 m a.s.l. at Mt Oakan (43°45'N, 144°16'E) (Table 1) on 29-30 June 2007. Where possible, from these samples 20 stems with a length of at least 4 cm were selected, but in most cases the actual number of available stems was slightly lower (Table 1). Almost all shoots sampled at 545 m a.s.l. were too short to be used in the tests, and this sample

Table 1. Summary of mechanical properties of *Pleurozium schreberi* on Mt. Oakan, Hokkaido, Japan (averages ± S.E.). E: Young's modulus; I: second moment of area; E*I: flexural rigidity.

Alt (m asl)	#replicates	E (MPa)	I (mm^4)	E*I (N mm^2)
460	19	604 ± 91	0.0028 ± 0.0004	1.516 ± 0.274
670	20	662 ± 119	0.0016 ± 0.0002	0.757 ± 0.122
750	19	651 ± 99	0.0016 ± 0.0002	0.911 ± 0.151
870	15	759 ± 117	0.0013 ± 0.0002	0.803 ± 0.183
965	19	732 ± 130	0.0012 ± 0.0001	0.739 ± 0.093
1055	17	724 ± 156	0.0011 ± 0.0003	0.487 ± 0.06
1185	17	572 ± 112	0.0016 ± 0.0002	0.77 ± 0.162
1260	10	978 ± 115	0.0003 ± 0.00003	0.323 ± 0.047
1350	19	635 ± 61	0.0012 ± 0.0001	0.714 ± 0.073

was therefore excluded. *Pogonatum japonicum* was collected at 8 sites on Mt Eniwa (42°47'N, 141°28'E) on 15-24 August 2006 along an altitudinal gradient from 320 to 1219 m a.s.l. (Table 3), in Hokkaido, Northern Japan. At each site samples were carefully collected a few m apart, ensuring that the moss stems were not damaged. The collected samples were approximately 10 cm in diameter, and the number of samples used from each site varied depending on the number of sufficiently long (over 4 cm) stems available (see Table 3). At Mt Oakan, *Pleurozium schreberi* occurred in the understory of coniferous forests and at higher altitudes beneath shrubs (*e.g.*, *Pinus pumila* (Pall.) Regel). At Mt Eniwa, *Pogonatum japonicum* grew in the understory of mixed forest, for example comprising oak, ash and conifers, from the lowest to the highest altitudes. After collection, the samples were dried and sent to Utrecht. There they were kept dry until the study of their mechanical properties in 2008.

Mechanical properties

Stems with lengths of at least 3 cm were carefully remoistened by spraying with tap water and kept in plastic bags until the measurement, which took place within a period of one hour.

To address our hypotheses we focused on Young's modulus (E), obtained from measurements of the force needed to bend the stems. We used a 3-point bending test with free stem ends, as the results of this method are most likely to allow interpretation in terms of resistance against mechanical failure in the field (Ross *et al*., 1998). In order to keep the ratio of span L over diameter D above 20 to minimize effects of shear (Ross *et al*., 1998), we used a span of 2 or, if possible, 3 cm, as stem diameter did not exceed 1 mm. Tests were carried out with an Instron 5542 universal testing machine with a sensitive load cell (maximum force 5N). This measured the applied force F (in N) and the extension x (mm). After measurement we determined stem radius r (mm) of the material while still fresh by measuring the diameters of cross sections in two directions under a microscope.

After plotting force F against extension x we calculated (or estimated from the graph) the initial gradient of the force-deflection curve dF/dx. Using this value, we calculated the flexural rigidity (a stem property, dependent on span L and radius r):

Flexural rigidity $E_bI = L^3 (dF/dx) / 48$

Where I represents the second moment of area.
From this formula, Young's modulus E_b was calculated:

$$E_b = L^3 (dF/dx) / 48\ I = L^3 (dF/dx) / (12\ \pi\ r^4)$$

Often the stem cross section was elliptical rather than round, in which case we determined short and long radii r_a and r_b, respectively, and used the formula:

$$E_b = L^3 (dF/dx) / (12\ \pi\ r_b\ r_a^3)$$

Stems of *Pogonatum japonicum* mostly approached a triangle in cross section. For this species we calculated I using

$I = b.d^3 / 36$ (with b width, d height)

And used this in the calculation of EI and E.
Since the stems did not break during the test, calculation of breaking force F_{max} and stress at yield σ was not possible.

Statistical analysis

As the data from several parameters were heteroscedastic, these were subjected to Ln- or Sqrt-transformation to ensure homoscedasticity (see tables 2, 4). One-way ANOVA (GLM) was used to test whether biomechanical tissue properties differed between sites differing in altitude. To investigate if these properties varied with altitudinal elevation we performed linear regressions with altitude (m a.s.l.) as the independent variable (SPSS 22).

RESULTS

For both species at all altitudes there was much variation in biomechanical traits between individuals. Additionally, both species showed significant variation in all four parameters along the altitudinal gradients, but differences between samples from different altitudes were more obvious than any linear trends over the full length of the gradient (Figs. 1 and 2, Tables 1-4).

The Young's modulus (E_b) decreased with altitude in *Pogonatum japonicum* (Fig. 1, Table 4), but did not show a consistent altitudinal trend in *Pleurozium schreberi*: the data of the site at 1260 m a.s.l. differed from those at
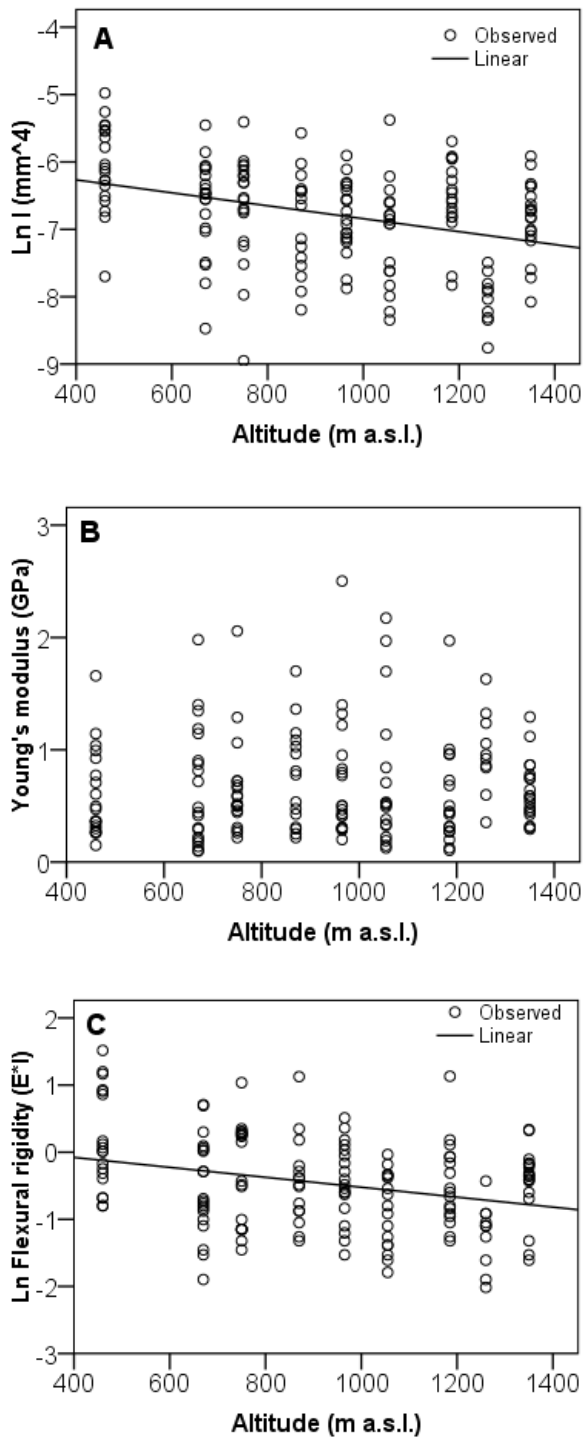
Fig. 1. Plots of (A) second moment of area I, (B) Young's modulus E, (C) flexural rigidity of stems of *Pleurozium schreberi* along an altitudinal gradient on Mt. Oakan, Hokkaido, Japan
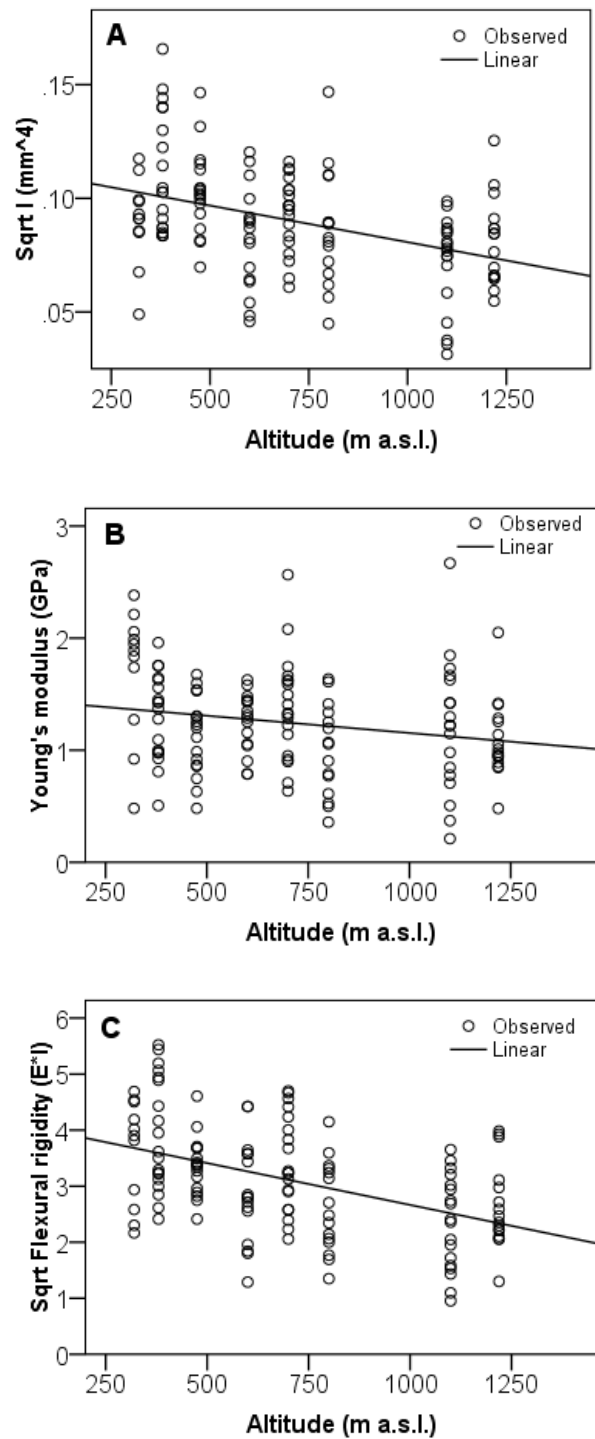
Fig. 2. Plots of (A) second moment of area I, (B) Young's modulus E, (C) flexural rigidity of stems of *Pogonatum japonicum* along an altitudinal gradient on Mt. Eniwa, Hokkaido, Japan

the other altitudes (Fig. 2, Table 2). Second moment of area (I) and flexural rigidity (E*I) decreased with increasing altitude in both species.

Stems of *Pogonatum* were thicker (larger I) than those of *Pleurozium* and had a larger Young's modulus and flexural rigidity.

DISCUSSION

All three biomechanical traits of *Pogonatum japonicum* showed significant negative correlation with altitude, but for *Pleurozium schreberi* this applied only to second moment of area and flexural rigidity. The full sets of samples of both species showed a large amount of

Table 2. Results of regressions against altitude and ANOVA for mechanical properties of *Pleurozium schreberi* on Mt. Oakan, Hokkaido, Japan. Data were transformed as indicated to make them homoscedastic.

parameter	transformation	Significance	R square	R squared (GLM)
I (mm^4)	Ln	P< 0.001 ***	0.118	0.309
Young's modulus (MPa)	None	P<0.603 [n.s.]	0.003	0.042
Flexural rigidity (N mm2)	Ln	P<0.001 ***	0.087	0.211

variation in these properties, but most of this represented variation between replicates. For most traits the differences between sites were substantial (the only exception being Young's modulus in *P. schreberi*) and only a small part of the variation was explained by altitude, as shown by the low R square for both species. Stems at different altitudes primarily seemed to vary in thickness, with consequently different values for second moment of area. Together with the gradual decrease in Young's modulus with increasing altitude in *P. japonicum* this may explain why flexural rigidity of the stems decreased for samples of this species collected at higher altitude. Stems of *P. schreberi* did not differ in Young's modulus with altitude.

Overall, in both species studied here shoots tended to be thinner (lower I) and less rigid (lower flexural rigidity) with increasing altitude, at least partially supporting our first hypothesis. It is tempting to speculate, that this pattern is related to altitudinal variation in growth conditions, with plants growing less well under the harsher conditions found at higher altitudes. These would include thickness and duration of snow cover, which will affect the length of the growing season as well as physically putting weight on the shoots. The large variation around the mean among and within the different sites observed in the study of Jägerbrand *et al*. (2014) as well as in this study indicates that plasticity in the physiological and biomechanical traits is large, perhaps larger than that due to difference in altitude. Size variation among shoots may be considerable at higher densities, however (*e.g.*, Økland & Økland 1996, Van der Hoeven & During 1997), and it is possible that shoots of various sizes in dense turfs share the load of the snow cover, as Frenzke *et al*. (2011) seem to suggest. Regrettably, we did not collect data on plant traits such as shoot density and dry weight of individual shoots together with their bio-

mechanical properties, nor environmental data such as duration and average depth of snow cover in winter along the altitudinal gradients.

A comparison of our results with those of previous studies is a bit difficult because of differences in methodology. Yet, in a study of biomechanics of sporophytes of some bryophytes in comparison with the properties of a range of vascular plants using Multiple Resonance Frequency Spectrum analysis (MRFS) Niklas (1995) found values for Young's modulus that were remarkably close to those of *P. schreberi* and *P. japonicum* in bending tests (Table 5). Values for Young's modulus of the plants of *Fontinalis antipyretica* studied by Biehle *et al*. (1998) using tension tests were also of the same order of magnitude (Table 5).

The stems of *P. schreberi* are more or less similar in thickness and structure to those of *Hylocomium splendens* (Ross *et al*., 1998). Young's modulus of the *Pleurozium* stems resembled that of the prostrate growth form of *H. splendens* as well, but it was less than that of the self-supporting plants of this species. In the study of Ross *et al*. (1998) too, most of the variation was found between replicates rather than between the two sites (which differed in latitude as well as in the growth form of the plants found there). *Pogonatum japonicum* is taxonomically and anatomically related to *Dendroligotrichum dendroides* (Frenzke *et al*., 2011), though the plants are much smaller than in that species. Young's modulus in *P. japonicum* was considerably lower than that in *D. dendroides*, but both species show rather higher values than are found in the other bryophytes studied so far (Table 5), most of which are characterized by more or less horizontally directed growth. This may be seen as support for our second hypothesis, but it may also simply reflect the phylogenetical constraints formed by the anatomy and the massive structure of the stems of the Polytrichaceae (Atala & Alfaro, 2012).

Table 3. Summary of mechanical properties of *Pogonatum japonicum* on Mt. Eniwa, Hokkaido, Japan (averages ± S.E.). E: Young's modulus; I: second moment of area; E*I: flexural rigidity.

Alt (m asl)	#replicates	E (MPa)	I (mm^4)	E*I (N mm^2)
320	11	1702 ± 174	0.0084 ± 0.001	13.79 ± 1.93
380	19	1291 ± 88	0.013 ± 0.0014	16.33 ± 1.88
475	17	1132 ± 85	0.0109 ± 0.001	11.52 ± 3.66
600	16	1247 ± 67	0.0072 ± 0.001	9.16 ± 0.89
700	19	1379 ± 108	0.0089 ± 0.0007	12.27 ± 1.36
800	15	1002 ± 105	0.0081 ± 0.0013	7.5 ± 1.14
1100	18	1204 ± 141	0.0055 ± 0.0006	6.14 ± 0.92
1219	16	1095 ± 87	0.0068 ± 0.0008	7.52 ± 1.09

Table 4. Results of regressions against altitude and ANOVA for mechanical properties of *Pogonatum japonicum* on Mt. Eniwa, Hokkaido, Japan. Data were transformed as indicated to make them homoscedastic.

parameter	transformation	Significance	R square	R square (GLM)
I (mm⁴)	Sqrt	$P< 0.001$ ***	0.159	0.262
Young's modulus (MPa)	None	$P<0.005$**	0.041	0.042
Flexural rigidity (N mm2)	Sqrt	$P<0.001$ ***	0.215	0.294

The populations of *P. schreberi* on Mt. Oakan have also been used in studies of responses in growth and photosynthesis to temperature regimes connected with altitudinal variation and of the amount of genetic variation along the same gradient. In a growth chamber experiment employing three different temperature regimes, stems of *P. schreberi* from exactly the same sites sampled in our study were tested for responses in growth, branching and maximum quantum yield of photosynthesis (Jägerbrand *et al*., 2014). Just as in our study, much of the variation found was related to site rather than altitude, although length increment (under standard conditions) over a period of four weeks tended to increase in plants from higher altitudes. At all altitudes, populations consisted of several genotypes, with a positive relationship between genetic diversity and altitude (Korpelainen *et al*., 2012). This may indicate that differences in growth, physiology and biomechanical traits might partly be due to genetic variation.

Bryophytes have been shown to respond to factors associated with altitude in studies from several perspectives. First, most species are clearly restricted in the range of altitudes at which they grow (*e.g.*, Lloret & González-Mancebo, 2011; Ah-Peng *et al*., 2012). Populations at various altitudes may also differ in life history traits such as reproductive phenology and performance (Hassel *et*

al., 2005a, c; Maciel-Silva *et al*., 2012) and in morphology, anatomy, growth and physiology (*e.g.*, Zechmeister, 1995; Waite & Sack, 2011). Altitudinal variation involves changes in many environmental factors (Körner, 2007), but most of these responses have been attributed to differences in temperature or associated water stress along the altitudinal gradient. These factors do not always provide a satisfactory explanation for the observed responses, however (Bader *et al*., 2013, Wagner *et al*., 2013). Transplant experiments have shown that differences between sites may be at least as large as differences connected with altitude, and suggest that genetic variation may partially underlie these patterns (Hassel *et al*., 2005b, Hedderson & Longton, 2008). Perhaps this also applies to biomechanical traits such as Young's modulus, but addressing this question may require cultivation in a common garden experiment.

Table 5. Average values (with, if applicable, standard deviation ([1]) or standard error ([2]) as given in the original publications) of Young's modulus E of sporophytes (Spor; mostly setae) or gametophyte stems (Gam) of some bryophytes differing in growth form and taxonomical position using pull tests (tension), bending tests or Multiple resonance frequency spectrum analysis (MRFS).

name	E (MPa)	Spor/gam	method	source
Anthoceros sp.	735	Spor	MRFS	Niklas 1995
Dicranum sp.	165	Spor	MRFS	Niklas 1995
Fissidens sp.	87	Spor	MRFS	Niklas 1995
Fontinalis sp.	49	Spor	MRFS	Niklas 1995
Polytrichum commune	419	Spor	MRFS	Niklas 1995
Polytrichum juniperinum	256	Spor	MRFS	Niklas 1995
Tortella sp.	203	Spor	MRFS	Niklas 1995
Fontinalis antipyretica in fast-flowing water	633 ± 171[1]	Gam	tension	Biehle et al. 1998
Fontinalis antipyretica in slow-flowing water	488 ± 160[1]	Gam	tension	Biehle et al. 1998
Hylocomium splendens self-supporting	2591 ± 245[2]	Gam	bending	Ross et al. 1998
Hylocomium splendens prostrate growth form	718 ± 70[2]	Gam	bending	Ross et al. 1998
Dendroligotrichum dendroides	4545 ± 1355[1]	Gam	bending	Frenzke et al. 2011
Pleurozium schreberi	685 ± 38[2]	Gam	bending	This study
Pogonatum japonicum	1243 ± 40[2]	Gam	bending	This study

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