Evaluating feathermoss growth: a challenge to traditional methods and implications for the boreal carbon budget

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Summary

1 Accurate assessment of net primary production is vital for understanding carbon (C) cycling, both regionally and globally. However, this requires effective methods of measurement that acknowledge the unique characteristics of the subject or area being monitored.

2 Feathermosses dominate the ground layer of boreal upland ecosystems and play a vital role in soil C accumulation, accounting for up to 50% of total photosynthesis. Feathermoss growth is both apical and lateral, with branches of determinate length at maturity produced at consistent frequencies along the stem.

3 Traditional methods of estimating annual production of feathermosses underestimate total plant production because they do not account for lateral growth of the previous year's immature branches. We present a conceptual model of feathermoss growth using *Pleurozium schreberi* that includes apical and lateral annual growth. From this model, we provide a modified method to more accurately estimate *P. schreberi* production. The top 3 cm of 10 *P. schreberi* plants from each of five bog peatlands in Alberta, Canada, were collected. For each plant, distance from the stem apex to branch insertion, branch length and dry mass, and dry mass of 3-mm stem sections were measured and used to define model parameters that, due to lack of significant variability among the sites, can be applied regionally and possibly globally throughout the boreal zone. An additional 20 plants were collected from a sixth site for testing the accuracy of our modified method.

4 Assessment of our method showed an insignificant mean difference between observed and calculated production values. Furthermore, comparison of our method with traditional methods showed a *c*. 25% underestimation of annual production by the latter. Traditional methods underestimate annual biomass production of *P. schreberi* by *c*. 73 g m^{-2}, accounting for more than 14 Tg C year^{-1} across the boreal region.

5 Our study shows that accounting for species-specific growth characteristics when estimating ground layer production has a substantial impact on boreal C budget assessments and therefore the terrestrial C cycle.

Key-words: allometry, boreal forest, bryophyte, ground layer production, growth model, growth morphology, modelling, net primary production, *Pleurozium schreberi*, *Ptilium crista-castrensis*
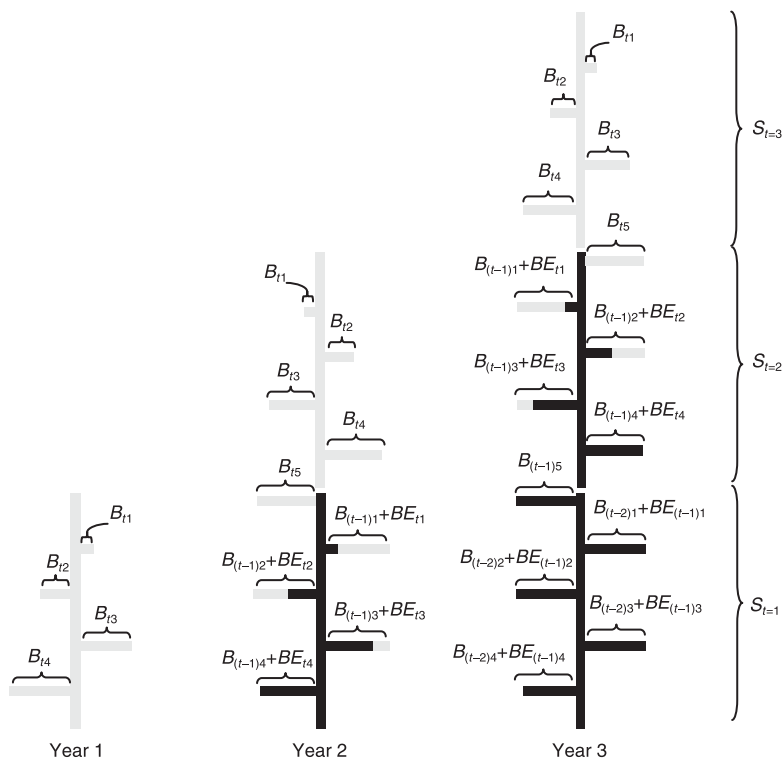
Introduction

The boreal region contains *c*. 40% (709 Pg C; Apps *et al.* 1993) of the global terrestrial carbon pool. The ground layer plays an important role in boreal terrestrial carbon cycling (Kolari *et al.* 2006), with more than 80% of the boreal carbon pool stored in organic soils resulting from biomass inputs from ground layer bryophytes characteristic of these systems (Apps *et al.* 1993; Gower *et al.* 2001; Kolari *et al.* 2006). The bryophyte understory of boreal black spruce forested stands can account for up to 50% of total photosynthesis (Goulden & Crill 1997), and Bond-Lamberty *et al.*

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Fig. 1 Conceptual diagram of growth of *Pleurozium schreberi*. Current year's (*t*) growth is in grey, previous growth in black.

(2004) found bryophytes to be responsible for 2–40% of total net primary production along a chronosequence of well-drained boreal forest stands. However, carbon budget assessments are only as accurate as the methods of measurement. While growth of the dominant peat forming mosses (*Sphagnum* spp.) is well understood (Clymo 1970), the methods used for measuring their production are not applicable to species with different growth characteristics, such as the feathermosses (e.g. *Pleurozium schreberi*, *Hylocomium splendens* and *Ptilium crista-castrensis*) that dominate drier boreal habitats.

Feathermosses are a ubiquitous, dominant component of the boreal upland forest floor (Bonan & Shugart 1989; Esseen *et al.* 1997), permafrost peatlands (Camill *et al.* 2001), and hummocks of mature to over-mature bog peatlands (Gignac *et al.* 1991; Gignac 1992), with *Pleurozium schreberi*, *Hylocomium splendens* and *Ptilium crista-castrensis* comprising > 60% of the boreal forest ground layer. In particular, several studies found *Pleurozium schreberi* in 90–100% of sample plots (LaRoi & Stringer 1976; Økland & Eilertsen 1993; Økland 1996; Pharo & Vitt 2000; Vellak *et al.* 2003; Zackrisson *et al.* 2004), accounting for 15–76% of the total ground cover (LaRoi & Stringer 1976; Pharo & Vitt 2000; Boudreault *et al.* 2002; Vellak *et al.* 2003; Zackrisson *et al.* 2004). Due to their dominance of the ground layer, it is important to accurately assess the contribution of feathermosses to boreal net primary productivity, which requires assessment methods that account for the unique growth characteristics of this group of mosses.

Typically, production of monopodial mosses (e.g. *Sphagnum* spp., *Pleurozium schreberi* and *Ptilium crista-castrensis*) has been measured using cranked wires (Clymo 1970), netting (Bond-Lamberty *et al.* 2004) or marking of the stem (Wallen 1986; Camill *et al.* 2001; Vitt 2007) to assess the annual vertical growth increment of the plant. Vertical growth is multiplied by a species-specific bulk density, obtained by destructively sampling the upper portions of plants, to provide an estimate of annual production. However, *Pleurozium schreberi* and *Ptilium crista-castrensis* also grow laterally, adding relatively large, new branches continuously along the stem from lateral buds and extending the length of the previous year's branches (Fig. 1; Longton & Greene 1969). While use of the bulk density of the upper portion of the stem accounts for new stem production and branch growth thereon, it does not include lateral growth of the previous year's branches, thereby underestimating total annual production.

Here, we present a conceptual model of feathermoss production that includes apical and lateral growth. Based on this model, we describe a modification of the traditional methods that more accurately assesses annual production of feathermosses using *Pleurozium schreberi* as a model species. We compare production assessments using traditional methods with those using our modifications to determine the degree to which boreal net primary production has been underestimated and its importance to the boreal carbon budget.
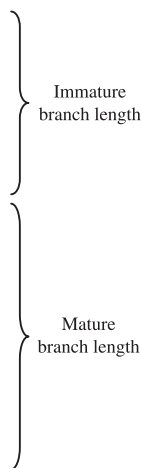
Methods

STUDY SPECIES

Pleurozium schreberi is a pleurocarpous moss that occurs throughout the boreal zone, typically growing in mats on moist, humic soils under a closed canopy. *Pleurozium schreberi* is a prevalent feathermoss in the boreal region, along with *Hylocomnium splendens* and *Ptilium crista-castrensis*, and has been found to have associations with N-fixing *Nostoc* cyanobacteria (DeLuca *et al*. 2002), making it an important constituent of boreal vegetation.

Growth of *P. schreberi* is monopodial, with no apparent distinction between annual stem increments. As apical growth occurs, new branches are added in seemingly uniform intervals, with the exception of the top 5-mm of stem, suggesting that new branch growth occurs from portions of the previous year's stem (Fig. 1). Pinnate branching gives *P. schreberi* plants a tapered appearance (Fig. 2), with branches increasing in length with distance from the apex of the stem until a mature, determinate branch length is reached, at which point lateral growth of branches stops. This results in fairly uniform branch length in more mature portions of the plant. Because branch length is deterministic and branches on young portions of the stem are shorter than those on lower portions, continued growth of branches formed the previous year must occur.

DATA COLLECTION

Pleurozium schreberi samples were collected from five bogs in Alberta, Canada. From each sample, 10 plants without visibly missing branches or branching of the main stem were randomly selected and the top 3 cm of each plant was removed. For each plant, the distance from the stem apex to branch insertion point was measured to the nearest 0.25 mm, as was the branch length. For those branches with twinned distal portions, the length of the main branch and each secondary branch was recorded. Each branch was cut from the stem at the insertion point and placed into a catalogued well plate. Following removal of all branches, the stem was sectioned in 3-mm intervals and each section placed into the well plate. The samples were dried at 65 °C for 48 hours and then weighed to the nearest 0.1 μg using an Orion Cahn C-35 microbalance (Thermo Electron Corp., Waltham, MA, USA). The data were then analysed using SAS v9.1 (SAS Institute, Cary, NC, USA).

CALCULATIONS AND RATIONALE

Annual production (P_t) of a *Pleurozium schreberi* plant can be defined as:

$$P_t = \sum_{i=1}^{x} B_{ti} + \sum_{j=1}^{y} BE_{tj} + S_t \qquad \text{eqn 1}$$

where B_t is the mass of new branches (i), BE_t is the mass added by extension of the previous year's branches (j), and S_t is the mass of new stem production. If bulk density of the newly produced stem is used to estimate annual production, B_t and S_t are accounted for, represented by the area under the curve of plant mass vs. stem distance (Fig. 3). However, BE_t is not included with such methods (Fig. 3).

If the branch length vs. distance from stem apex relationship is asymptotic, with branch length remaining constant at maturity, and branch frequency along the stem is constant, then the amount of production added to the previous year's branches (BE_t) can be defined as:
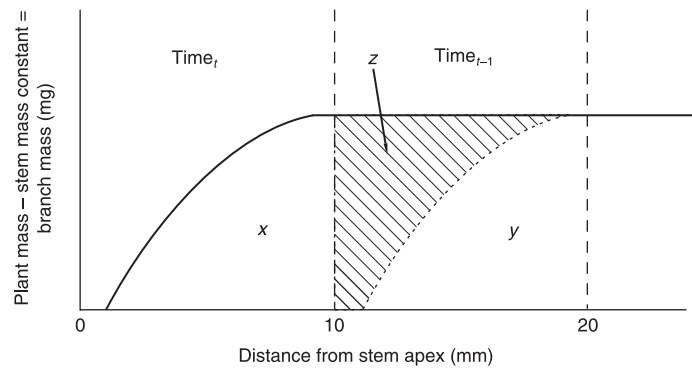
$$\sum_{j=1}^{y} BE_{tj} = \sum_{j=1}^{y} B_{((t-i)@t)j} - \sum_{i=1}^{x} B_{ti} \qquad \text{eqn 2}$$

where $B_{(t-1)@t}$ is the total mass of the previous year's branches at time t (Fig. 3). By combining equations 1 and 2, the new equation can be simplified to

$$P_t = \sum_{j=1}^{y} B_{((t-1)@t)j} + S_t$$

$$= \left(\frac{\sum_{j=1}^{y} B_{((t-1)@t)j}}{L_{stem}} \right) L_{stem} + (L_{stem} \times SM) \qquad \text{eqn 3}$$

where L_{stem} is the length of the stem for which branch masses are summed and SM is the stem mass per length parameter. If stem mass remains constant over time, indicating no initial interannual stem decomposition, then equation 3 represents the biomass of a length of stem produced at time $_{t-1}$ possessing only mature

Fig. 2 Picture of *Pleurozium schreberi* illustrating tapered appearance and zones of maturity.

Immature branch length

Mature branch length

Fig. 3 Conceptual model of relationship between plant mass and stem length. Assuming stem mass (*SM*) is constant for Time$_t$ and Time$_{t-1}$, the vertical axis can represent total plant mass or branch mass depending on inclusion or exclusion of *SM*, respectively. Areas *x* and *y* represent total branch biomass production (Σ *B*) in the current (time$_t$) and previous year (time$_{t-1}$), respectively. Area *z* represents biomass resulting from extension of the previous year's branches at time$_t$ (Σ *BE$_t$*). See Methods for explanation of mathematical terms.

Table 1 List of parameters used in production calculations. Calculation of parameter values explained in results

Term	Description	Value
SM	Stem mass per length	0.16-mg mm^{-1} stem
BM	Mature branch mass per stem length	0.30-mg mm^{-1} stem
BF	Branch frequency per stem length	0.86-branch mm^{-1} stem
β	Branch mass per branch length	0.035-mg mm^{-1} branch
L$_{Mature}$	Branch length at maturity	10-mm
M	Plant annual production per stem length	0.46-mg mm^{-1} stem

branches. To further simplify the calculations, if there is a linear relationship between branch mass and length, and branch frequency is constant, and we define mature branch length, then the bracketed term in equation 3 and associated variance can be defined as a single parameter, requiring only measurement of linear growth in the field. The revised equation then becomes

$$P_t = BM \times L_{stem} + SM \times L_{stem} = L_{stem}(BM + SM)$$
$$\text{eqn 4}$$

where *BM* is the branch mass per stem length parameter. Combination of the parameters reduces the equation to

$$P_t = L_{stem} \times M \qquad \text{eqn 5}$$

where *M* is the plant annual production per stem length parameter. Variability in the branch and stem mass parameters can be incorporated into equation 5 by addition of a variance parameter. Production of an individual plant (*P$_t$*) can be extrapolated to an areal expanse by multiplying by the density of plants within a local population.

Results

Uniformity of stem mass was assessed using a randomized complete block design by site to determine if mass varied between sections at different distances from the apex. Because stem sections for each plant are not independent, PROC MIXED in SAS v9.1 was used to include fixed and random effects and Levene's test was used to assess homogeneity of the sample variances. The top 3-mm section was excluded from this analysis because the high density of young leaves surrounding the apical bud places additional mass on this section. No significant difference between sections was observed within sites ($F_{8,359} = 0.90$, $P = 0.516$) or among sites ($F_{8,391} = 0.85$, $P = 0.557$). Therefore, the stem mass per length parameter (*SM*) was defined as the mean stem section mass across all 50 plants divided by 3 mm, resulting in a value of 0.16 ± 0.03 mg mm^{-1} (Table 1).

To assess consistency of branch frequency along the stem, branch frequency was calculated for 5-mm sections of the stem. The frequency of branches on each stem section was compared within and among plants and sites using chi-square analyses. For all 50 plants, branch frequency was found to be constant among sections ($P > 0.05$). As some frequencies were < 5, the EXACT CHISQ option in PROC FREQ was used. The section branch frequencies were constant among plants within each site. Using the total data set, the top 5-mm section had fewer branches than the other sections, which were not significantly different from each other. However, the assumption of constant branch frequency still holds true for the model because there is no variability within each plant and there is constancy for all sections below 5 mm. Furthermore, the overall variability in branch frequency between the

top 5-mm section and all other sections suggests there is a delay in branch production just beneath the stem apex and that new branch growth occurs on the previous year's stem. Using branch frequencies for the section > 5 mm from the apex, we calculated a mean branch frequency (*BF*) of 0.86 ± 0.02 branches mm^{-1} of stem (Table 1).

Regression analysis was used to assess the relationship between branch mass and length. Branches with secondary branching and visibly broken branches were excluded. For this analysis, the combined data set from all 50 plants was used to increase the sample size for determining an overall relationship and the *y*-intercept was set to zero. A significant linear relationship, $F_{1,897} = 14556.1$, $P < 0.0001$; Fig. 4). Therefore, length can be used in place of mass using the relationship

$$B_t = L_{branch} \times \beta \qquad \text{eqn 6}$$

where L_{branch} is the length of the branch and β is the slope of the mass vs. length relationship (0.035) in units of mg mm^{-1} (Table 1). The slope of the regression (β) is approximately equal to the mean of the individual branch mass divided by the branch length (0.035 ± 0.01 mg mm^{-1}). Branch mass variability can be estimated using the error root mean square from the regression ($RMS_{error} = 0.08$).

Length of the main branch was plotted against distance from the stem apex for each plant, revealing a logarithmic relationship (Fig. 5). Upon testing several logarithmic functions, a second-order model provided the best fit to the data. The relationship appears relatively uniform among plants, particularly for immature
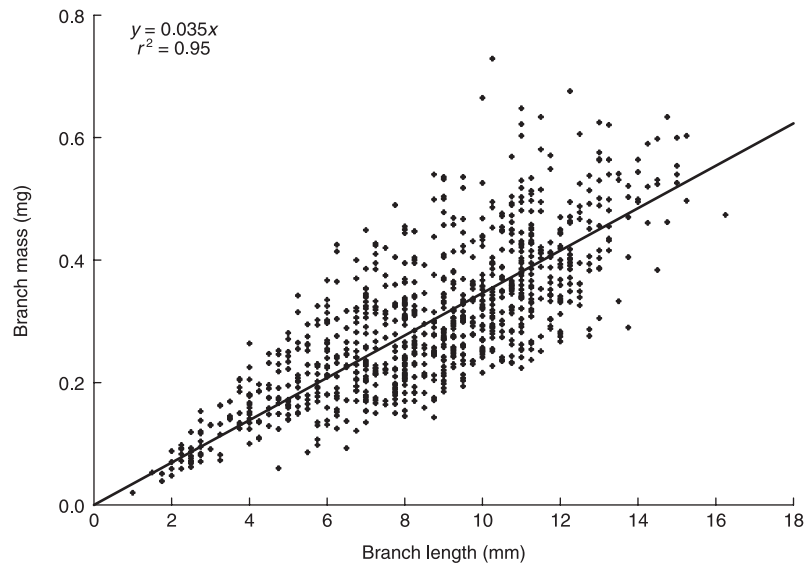

Fig. 4 Relationship between branch length and branch mass for all 50 plants. Visibly broken or aberrant branches were excluded.
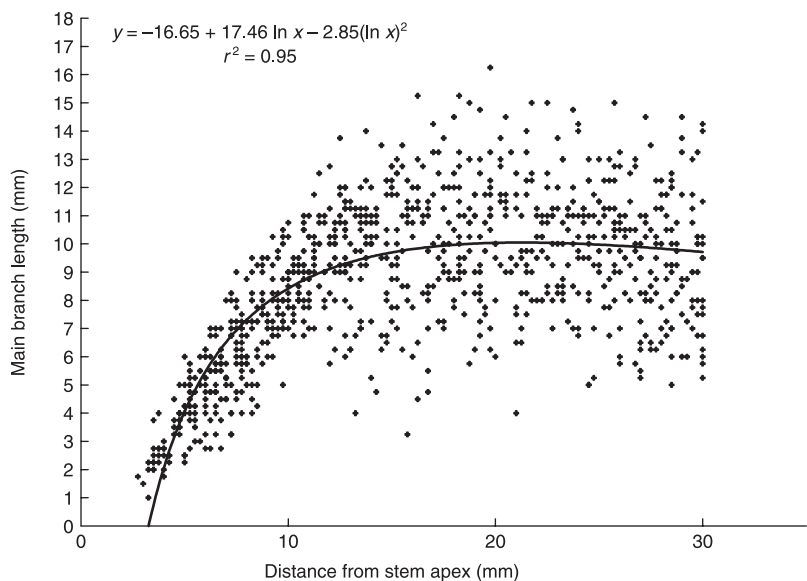

Fig. 5 Relationship between distance from the stem apex and main branch length for all 50 plants. Visibly broken or aberrant branches were excluded.

branches (top *c*. 12 mm of stem), with approximately equal degrees of variability in the relationship observed within sites as among sites.

A second-order logarithmic function was fitted to the plot of branch length vs. distance from the stem apex (Fig. 5). The branch length at which the fitted curve levelled off (10 mm) was used as the expected branch length at maturity (L_{mature}) for our *P. schreberi* production model (Table 1). Using this length in equation 6, we defined branch mass at maturity ($B_{(t-1)@t}$) as 0.35-mg branch^{-1}. The mature branch mass and mean branch frequency (0.86 branches mm^{-1}) were used to calculate the *BM* parameter as follows:

$$BM = \frac{B_{(t-1)@t}(BF \times L_{stem})}{L_{stem}}$$

$$= \frac{0.35 \times 0.86}{1} = 0.30\text{-mg mm}^{-1}$$

eqn 7

where *BF* is the mean branch frequency (branches per stem length) and L_{stem} = 1 mm (Table 1). Combined with the stem mass per length parameter ($SM = 0.16 \pm 0.03$-mg mm^{-1}), the plant mass per linear increment parameter (*M*) was calculated as

$$M = BM + SM = 0.30 + 0.16 = 0.46 \text{ mg mm}^{-1} \quad \text{eqn 8}$$

EFFECTIVENESS ASSESSMENT

The ability of the overall method to approximate *Pleurozium schreberi* annual production was assessed by comparing estimated values generated using the parameters against actual production values obtained from 20 additional random samples. Based on the assumptions of the method (illustrated in Fig. 3), the observed annual biomass production was obtained by sampling 10-mm lengths of stems possessing only mature branches (identified by relative uniformity of branch length) from 20 randomly selected plants. The 10-mm samples were dried and weighed, and these observed plant masses were compared with an expected mass of 4.6 mg plant^{-1} for a 10-mm plant length. Because the differences between observed and expected values were normally distributed, a paired *t*-test was used, resulting in no significant difference between values ($t = -0.06$, d.f. = 19, $P = 0.9547$). On average, the expected values overestimated the actual biomass by 0.02 ± 1.16 mg, which can be used to define variability in the method.

We then compared our method using the biomass parameter *M* with the traditional method using the bulk density of the upper portion of the plant. Using an expected annual plant production for 15 mm of linear growth calculated using equation 5 (6.9 mg plant^{-1}) and a mean population density of 3.0 ± 0.9 plants cm^{-2} obtained from the samples, we calculated a ground layer production for a mat of *Pleurozium schreberi* of 207 ± 62 g m^{-2}. We then calculated ground layer production

using the traditional method. For this, we determined the mean total mass of the top 15 mm of the 50 plants sampled (5.21 ± 1.33 mg plant^{-1}) and, using the same mean population density, calculated a ground layer production of 156 ± 62 g m^{-2}, a *c*. 25% lower value than that obtained using our modifications of the method.

To quantify production underestimation using traditional methods, we calculated the annual biomass added to the previous year's stem and branches (ΣBE_t), represented as area *z* in Fig. 3. Because the section of stem possessing immature branches, and therefore experiencing second-year growth, is constant, we can calculate the point along the stem marking the transition from mature to immature branches. The top 1 cm of the plant possesses only immature branches, so regression of branch length vs. distance from the apex ($r^2 = 0.70$, $F_{1,252} = 591.98$, $P < 0.0001$) was used to calculate the stem distance corresponding to branch length of L_{Mature}, resulting in a stem distance of 11.5 mm. For each of the 50 plants, the mass of the top 11.5-mm section and underlying 11.5-mm section was calculated, with the difference representing the mass from second-year branch extension (*z*), resulting in a mean value of 2.43 ± 2.23 mg plant^{-1}.

Discussion

The results of this study provide a non-destructive method of measuring *Pleurozium schreberi* production that is more accurate than traditional methods using the bulk density of the upper segment of the plant. Although a narrow range of habitats was examined in this study, extensive circum-boreal observations by the authors suggest the pattern of *P. schreberi* growth is consistent regardless of location, but future study is required to quantitatively support this. While population specific calibrations can be employed, the results of this study indicate that variability within a population is greater than among populations, allowing for regional parameters. Furthermore, this method may be applicable to other feathermoss species with similar growth characteristics, such as *Ptilium crista-castrensis* and *Rhytidiadelphus triquetrus*.

Other methods of measuring growth characteristics and production of feathermosses and other bryophytes have been proposed. Økland (1995) used a non-destructive technique for repeated monitoring of individual *Hylocomium splendens* plants by marking the stems and branches with distinct bands and using transition matrix modelling to assess the population biology of the species. While this method is highly effective and provides insights into growth of individual plants, it is time and labour intensive, requiring long-term monitoring of many individuals, whereas our proposed method can be quickly calibrated regionally (if necessary) or for different species with similar growth morphology.

Hanslin (1999) employed the sequential harvesting technique of Rincon & Grime (1989) to assess growth

Table 2 Published rates of *Pleurozium schreberi* biomass production (mean ± SD) based on traditional methods and estimated rate (modified) using method proposed in this study

Study	Biomass production (g m^{-2} year^{-1})		Region
	Traditional	Modified*	
Asada *et al.* (2003)	305 ± 70	378 ± 74	British Columbia, Canada
Longton & Greene (1979)	93.8 ± 16.1	167 ± 28	Glasshouse
Palviainen *et al.* (2005)	55.6 ± 18.7	129 ± 29	Finland
Solga *et al.* (2005)	128.7 ± 60.1	202 ± 64	Germany
Zechmeister (1997)	161 ± 56	234 ± 60	Austria
This study	156 ± 62†	207 ± 62†	Alberta, Canada

*Underestimated biomass production (72.9 ± 22.3 g m^{-2} year^{-1}) added to published value.
†Calculated in results.

characteristics of five boreal bryophytes. However, this destructive technique limits the repeatability and duration of monitoring, as well as introducing confounding variables due to changes in population structure through sampling (e.g. competition, water relations, population density, etc.).

Our modified method of measuring feathermoss production results in more accurate assessments of boreal ground layer production. Compared with our method, traditional methods may underestimate *Pleurozium schreberi* annual biomass production by *c*. 73 g m^{-2}, which would increase published production values by 19–56% (Table 2). Because *P. schreberi* dominates the boreal forest floor and is ubiquitous throughout the boreal region globally, inclusion of this underestimated production could substantially increase published regional annual net primary production estimates (180–430 g C m^{-2} year^{-1}, Harden *et al.* 2000; 52–868 g C m^{-2} year^{-1}, Gower *et al.* 2001; 106–406 g C m^{-2} year^{-1}, Bond-Lamberty *et al.* 2004). Although future study with direct application of this method will be required to address regional or spatial variation in *P. schreberi* production, the potential impact of accurate production assessment of feathermosses is significant. Assuming an average *P. schreberi* ground cover of 20% (a conservative estimate based on LaRoi & Stringer 1976; Pharo & Vitt 2000; Boudreault *et al.* 2002; Vellak *et al.* 2003; Zackrisson *et al.* 2004) across 1.9×10^6 km^2 of spruce/feathermoss boreal forest (Harden *et al.* 2000), boreal ground layer net primary production based on direct biomass measurements has been underestimated by more than 14 Tg C year^{-1}. This represents a minimum value, as very conservative estimates of *P. schreberi* cover and boreal forest extent were used. Furthermore, if this method is used for the other dominant boreal feathermoss species (*Hylocomium splendens* and *Ptilium crista-castrensis*), which along with *P. schreberi* account for > 60% of the boreal forest ground layer, this underestimated value will be greatly increased, providing a more accurate assessment of the global carbon budget.

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