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Empirical biomass models of understorey vegetation in boreal forests according to stand and site attributes

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In the early phases of succession, the proportion of biomass comprising understorey vegetation may be considerable and, therefore, it plays a significant role in the annual nutrient and carbon cycling of forest ecosystems. The aim of our study was to identify the most significant forest-site attributes affecting the above-ground biomass of understorey vegetation and to develop models that can be used to predict this biomass in the boreal zone using readily available variables. The study was based on vegetation data consisted of percentage coverage observations collected from a network of permanent sample plots established by the National Forest Inventory in Finland. The coverage data were transformed to biomass with previously published models. According to our results, above-ground biomass can be predicted by such forest stand and site attributes as stand age and site nutrient level. In Scots pine, Norway spruce and broad-leaved forests growing on upland soil, the relative RMSE of predicted above-ground biomass of all understorey vegetation was 16.6%, 22.3% and 31.6%, respectively. In hardwood–spruce mires and paludified forests, the relative RMSE predicted above-ground biomass of all understorey vegetation was 12.2%. In pine mires it was 9.9%. The modelled relationship between biomass and forest site attributes can be used in ecosystem and carbon cycle modelling as a rapid non-destructive method to predict the above-ground biomass of understorey vegetation.

Introduction

The terrestrial biosphere is an important component of the global carbon cycle, and consequently, terrestrial ecosystems can mitigate climate change (Schimel 1995). Forest vegetation and soil may act as significant sinks or sources of atmospheric CO_2 depending on land use, forest management, and environmental conditions. Boreal forests are of particular interest because, among all biomes, they are anticipated to undergo the greatest climatically induced changes during the 21st century (Bonan *et al.* 1992, Myneni *et al.* 1997). Furthermore, accurate estimation of forest biomass is required for greenhouse gas inventories and climate change modelling studies.

The carbon budgets of trees and forest soil have been modelled extensively, but understorey vegetation has not usually been included in these analyses (e.g. Bonan *et al.* 1992, Liski *et al.* 2002, Nabuurs *et al.* 2003). The forest floor is generally completely covered by understorey vegetation in Fennoscandian boreal forests (Palviainen *et al.* 2005a). Approximately 4%–13% of the carbon stock gained in upland forest vegetation is in understorey vegetation (Mälkönen 1974, Havas and Kubin 1983). However, the biomass of understorey vegetation may play an important role in many ecosystem processes, e.g. in the nutrient and carbon cycles (Mälkönen 1974, Yarie 1980, Van Cleve and Alexander 1981, Palviainen *et al.* 2005a), due to the rapid turnover of biomass and the large proportion of easily decomposable litter (Zavitkovski 1976, Chapin 1983, Tappeiner 1989). On upland soils the annual litter production of understorey vegetation may represent a considerable proportion of total litter production, varying from 4% to 30% (Hughes 1970). The understorey vegetation also makes up a sizable amount of the total nutrient storage in forested pine (*Pinus sylvestris*) mires (Paavilainen 1980, Finér and Nieminen 1997). On pristine peatlands most of the organic matter deposited as peat derives from understorey vegetation (Lappalainen and Hänninen 1993). Only on the most nutrient-rich forested mire sites can tree litter be considered to constitute a significant share of the carbon sequestered in the soil. Studies ignoring understorey vegetation may result in underestimation of NPP (net primary productivity) and litter production as well as the carbon stock and sink of soil that are dependent on total litter production.

The development of understorey vegetation in upland forests depends on stand density and the stage of stand development (Mälkönen 1974). Understorey vegetation of boreal upland forests undergoes successional development after clear-cutting or fire disturbance (Alaback 1982). During the regeneration of a stand, the biomass of the understorey vegetation is negligible (Kellomäki and Väisänen 1991, Palviainen *et al.* 2005a). Thereafter, biomass increases in the early successional stages. The importance of understorey vegetation is emphasised during the early successional stages since it becomes the major living vegetation component when trees are removed (Palviainen 2005). However, empirical comprehensive data on the development of understorey biomass over the succession are not available.

In peatlands, especially pine mires, the proportion of understorey vegetation is highly dependent on the water table level and the structure and density of the tree layer (Vasander 1982, Reinikainen *et al.* 1984, Finér and Nieminen 1997, Minkkinen *et al.* 1999, Laiho *et al.* 2003). The obvious reasons for a low biomass are wetness or increasing canopy shading while the nutrient level of the site is only of secondary importance (Laine and Vasander 1996). As the bottom layer (consisting of bryophytes and lichens) is in immediate contact with the water table, due to the structure and physiology of mosses, it is assumed to be the most sensitive indicator of ecological conditions. The development of the moss layer of peatlands, especially pine mires, also depends on the weather (Lindholm 1990). Vasander (1982) observed that at his pine mire study sites the above-ground biomass of the field layer (consisting of herbs and grasses) ranged from 2134 to 5040 kg ha^{-1} and the biomass of the bottom layer from 632 to 2304 kg ha^{-1}. Laiho (1996) reported corresponding biomasses of 690–3480 kg ha^{-1} and 1370–6440 kg ha^{-1}. Laine and Vasander (1996) concluded that the highest understorey biomass values are usually found at dwarf shrub-rich site types.

In general, the dominant and subdominant species represent 85%–97% of the total understorey vegetation biomass (Kubícek and Simonovic 1982). On peatlands the field layer biomass consists of a large variety of life forms and ecological types, ranging from water plants to forest species (Reinikainen *et al.* 1984, Laine and Vasander 1996). The range of life forms in the bottom layer is much more uniform.

Appropriate methods for estimating the biomass of understorey vegetation, applicable to large-scale studies are not available. In many ecosystem models, it is essential to quantify the biomass of understorey vegetation as one component of element cycling. Direct methods for measuring the above-ground biomass of understorey vegetation, again, are destructive, laborious, and time-consuming. Despite numerous studies related to the biomass of understorey vegetation, the relationship between understorey vegetation and tree layer and site characteristics is not yet as well known as the production of biomass in understorey vegetation.

The objective of this study was to develop a new method for estimating understorey biomass according to site and stand attributes. As explanatory variables we used those stand characteristics that are easily quantifiable and widely measured and that we hypothesise to be closely connected to the amount of understorey biomass: dominant tree species, stand age, basal area, stem volume and stem number. These attributes describe the stand structure. As explanatory variables we also used the following site attributes since they describe the physical properties of site potential: nutrient level (*see* Appendix), effective temperature sum, latitude and longitude.

Material and methods

Material

The biomass/cover equations of Muukkonen *et al.* (2006) were applied to the vegetation data of a systematic network of permanent sample plots (300 m^2) established by the National Forest Inventory in 1985–1986. The sample plots form a regular network of clusters; in southern Finland, each cluster consists of four plots at 400-m intervals, and in northern Finland of three plots at 600-m intervals. In the south, there is one cluster per 16 km × 16 km area, and in the north one cluster per 24 km × 32 km area. Of the 3009 sample plots covering the whole of Finland, 1697 located on upland soils and 592 located on peatlands were selected for our study (Table 1). The percentage cover of plants on (4–6) 2 m^2 squares located systematically within the plots was estimated visually. For further details, *see* Mäkipää and Heikkinen (2003).

The above-ground biomass of understorey vegetation by species group was estimated as a function of percentage cover (Muukkonen *et al.* 2006) and the same models can be used for rapid nondestructive determination of above-ground biomass when only the percentage cover of

Table 1. General description of forest stand data. Pine forests, spruce forests, and broad-leaved forests were studied on 962 sites with 3693 sample squares, 619 sites with 2385 sample squares, and 116 sites with 417 sample squares, respectively. The total number of hardwood-spruce mires and paludified forest sites was 230 with 783 sample squares, while the total number of pine mire sites was 362 with 1403 sample squares.

		Lat. (°N)	Long. (°E)	Elevation (m a.s.l)	Temp. sum (°C)	Age (years)	Stem no. (ha^{-1})	Basal area (m^2 ha^{-1})	Stem vol. (m^3 ha^{-1})
Upland sites									
Pine forests	Min.	59.911	20.052	0	610	3	33	1	1
	Mean	63.407	26.273	135	1078	68	992	9	95
	Max.	69.644	31.429	360	1360	325	8000	47	384
	S.D.	2.19	2.378	68	170	50	772	8	76
Spruce forests	Min.	59.933	21.073	0	680	3	66	1	1
	Mean	62.5	25.985	123	1146	78	891	13	158
	Max.	68.14	31.157	410	1360	305	6222	48	388
	S.D.	1.682	2.318	68	143	45	735	10	85
Broad-leaved forests	Min.	59.915	20.053	0	670	1	37	1	2
	Mean	62.703	26.357	111	1138	55	1142	10	115
	Max.	68.352	30.763	320	1350	145	4133	35	375
	S.D.	1.58	2.468	59	130	30	888	8	84
Peatlands									
Hardwood-spruce mires and paludified forests	Min.	60.076	21.412	0	660	2	124	1	1
	Mean	62.947	26.065	111	1124	74	1320	12	114
	Max.	68.342	31.407	300	1360	195	6777	41	349
	S.D.	1.445	2.445	56	112	38	883	8	72
Pine mires	Min.	60.189	21.384	20	710	4	47	1	1
	Mean	63.432	26.19	129	1075	56	1555	7	45
	Max.	68.123	31.408	260	1340	175	5222	38	275
	S.D.	1.373	2.44	52	101	28	881	6	40

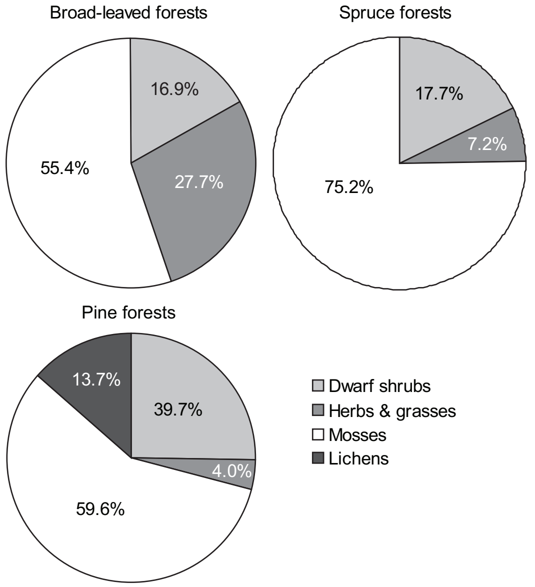

Fig. 1. Proportions of above-ground biomass of species groups in pine, spruce, and broad-leaved upland forests. The values are based on National Forest Inventory vegetation data.

different plant species is recorded. The above-ground biomasses (y) of bryophytes and lichens on upland soils and of the field and bottom layers of peatlands were calculated as a function of percentage cover (x) with a nonlinear model as:

$$y = \frac{x^2}{\left(\beta_0 + \beta_1 x\right)^2}, \qquad (1)$$

where β_0 and β_1 are fixed population parameters (Muukkonen *et al.* 2006). The above-ground biomasses of dwarf shrubs and herbs/grasses on upland soils were modelled with a linear model as:

$$y = \beta_1 x. \qquad (2)$$

Although these models are based on a comparatively small dataset, they represent clear evidence for the existence of relationships between plant cover and above-ground biomass of upland and peatland vegetation. The residuals demonstrated that these models produced unbiased estimates of the above-ground biomass.

The species groups studied were herbs and grasses, mosses, lichens, and dwarf shrubs. The divisions are based on a traditional *a priori* grouping, which is typically defined by discrete and measurable biological trait differences (Reich *et al.* 2003). The bottom layer consists of mosses and lichens only, whereas the field layer includes dwarf shrubs, herbs, and grasses. Dwarf shrubs are low shrubs with perennial above-ground woody stems situated near ground surface. In this study, young tree saplings were also considered dwarf shrubs. Herbs and grasses are annual plants without perennial above-ground woody stems.

The term ‘upland soil’ refers to forest sites on mineral soil. Peatlands are defined botanically as sites supporting a peat-producing plant community (cover of mire vegetation > 70% or depth of peat layer > 30 cm). In this study, peatlands consisted of (1) hardwood-spruce mires and paludified forests, and (2) pine mires. Open fens and bogs were not studied. Our study deals with the boreal vegetation zone according to the division of vegetation zones in northern Europe (Ahti *et al.* 1968: p. 168).

Stand age, basal area, stem volume, stem number, nutrient level, coordinates, elevation, and effective temperature sum were recorded for each stand (Table 1). The effective temperature sum (sum of daily mean temperatures, threshold value +5 °C) was estimated for each site using a surface-fitting model of Ojansuu and Henttonen (1983), which is based on measurements of monthly mean temperature recorded at the Finnish Meteorological Institute weather stations. Stand age was estimated using increment cores from one sample tree that represented the dominant canopy layer. The basal area was estimated as an average of three relascope observations. The nutrient levels of the stands were estimated by a botanist on the basis of the understorey vegetation (*see* Appendix). On peatlands, the drainage status (Paavilainen and Päivänen 1995) was also recorded (*see* Appendix). The dominant tree species was derived using the following procedure: the stand was first compartmentalised into coniferous and broad-leaved forests, after which the dominant coniferous or broad-leaved tree species was determined. The breakdown of data on upland forests by dominant tree species was justified since the share of species groups depended on the dominant tree species (Fig. 1).

Statistical modelling

First we checked the correlation coefficients between the derived above-ground biomasses and forest stand and site attributes. Next, the derived above-ground biomasses of the species groups (p) of the understorey vegetation were modelled with the mixed model according to forest stand and site attributes (Table 1). Mixed models accounting for variance derived from different hierarchical levels of the data were used since the sample squares could not be treated as independent units (Fox *et al.* 2001). The hierarchical structure (i.e. sample squares within stands) of the data implies a lack of independence among measurements, since observations from the same stand are correlated.

In the mixed model

$$\sqrt{y_p + 0.5} = \beta_0 + \beta_1 x_1 + \ldots + \beta_k x_k + A + \varepsilon, \quad (3)$$

β's are model parameters, A is a mixed parameter and ε is an error term, and $x_1 \ldots x_k$ are functions of measured forest attributes $z_1 \ldots z_k$; $x = f(z_j, j = 1, 2, ..., k)$, which are either $x = z_1$, $x = z_1 z_2$, or $x = z_1^2$. The square-root transformation was used to avoid negative prediction values. In addition, instead of the $\sqrt{y_p}$ transformation, the $\sqrt{y_p + 0.5}$ transformation was used since dependent variables also contain zero values (Ranta *et al.* 1999).

A criterion for including explanatory variables $x_1 \ldots x_k$ in the model was their statistical significance ($p < 0.05$). The parameters were estimated with an SAS mixed procedure (SAS 1999).

Modelled relationships between above-ground biomass and forest stand and site attributes were tested, reserving a portion of the available material to obtain an independent measure of the model's prediction accuracy. A cross-validation criterion was used (Stone 1974, Snee 1977). Model validation was accomplished with Leave-One-Out (LOO) cross-validation. There the data set is split into a training set on which a model is constructed, and a test set on which the model is evaluated. In this case, the predicted response value $\hat{y}_{(i)}$ was predicted on a model that was estimated for the data set minus the ith observation, while the test set contained only one observation (Stone 1974). The splitting procedure was repeated until all observations had been included in the test set once, and only once. Thus, n models were built, each using $n - 1$ observations for model construction and the remaining observations for model validation. The LOO cross-validation criterion RMSE$_\mathrm{r}$ (relative Root Mean Square Error) was used:

$$\mathrm{RMSE_r} = \frac{\sqrt{\frac{1}{n}\sum_{i=1}^{n}\left(y_i - \hat{y}_{(i)}\right)^2}}{\bar{y}} \times 100, \quad (4)$$

where $\hat{y}_{(i)}$ is the modelled value, y_i the observed value, $\bar{y}$ the mean of the observed values, and n the number of observations in the data set.

Results

Correlations between biomass and forest stand and site attributes

In upland pine forests, the group-wise biomasses of all species groups were significantly ($p < 0.05$) correlated with latitude, elevation, temperature sum, nutrient level, and stand age (Table 2). Longitude, stem volume, basal area, and stem number were significantly correlated with only some of the species groups. The correlation coefficients for dwarf shrubs, mosses, and lichens were always of the opposite sign of the values for herbs and grasses. Of all tested stand variables, stand age showed the highest correlation coefficients with the exception that the biomass of lichens was strongly negatively correlated with stem volume.

At spruce-dominated upland forest sites, the group-wise biomasses of all species groups were significantly ($p < 0.05$) correlated with latitude, elevation, temperature sum, nutrient level, stand age, and basal area (Table 3). The other stand and site attributes studied were significantly correlated with only some of the species groups. Generally, the correlation coefficients for broadleaved upland forest sites were slightly lower than the corresponding values for coniferous forest sites (Table 4). Only nutrient level and elevation were significantly correlated with all species groups. Temperature sum, stand age and stem number correlated with the biomass of dwarf shrubs and mosses.

Table 2. Spearman's correlation coefficients (significant at $p < 0.05$ set in boldface) of forest stand attributes versus above-ground biomass ($\mathrm{kg\ ha^{-1}}$) of pine forest stands on upland sites ($n = 962$ sites with 3693 sample squares).

	Biomass ($\mathrm{kg\ ha^{-1}}$) of						
	dwarf shrubs	herbs and grasses	mosses	lichens	total field layer	total bottom layer	all understorey vegetation
Lat. (°N)	**0.26** ($p < 0.001$)	**–0.29** ($p < 0.001$)	**0.07** ($p < 0.001$)	**0.25** ($p < 0.001$)	**0.14** ($p < 0.001$)	**0.15** ($p < 0.001$)	**0.19** ($p < 0.001$)
Long. (°E)	**0.14** ($p < 0.001$)	–0.03 ($p = 0.073$)	0.01 ($p = 0.508$)	**0.07** ($p < 0.001$)	**0.14** ($p < 0.001$)	0.02 ($p = 0.234$)	**0.07** ($p < 0.001$)
Elevation (m a.s.l)	**0.17** ($p < 0.001$)	**–0.22** ($p < 0.001$)	**0.08** ($p < 0.001$)	**0.24** ($p < 0.001$)	**0.08** ($p < 0.001$)	**0.16** ($p < 0.001$)	**0.16** ($p < 0.001$)
Temp. sum (°C)	**–0.26** ($p < 0.001$)	**0.30** ($p < 0.001$)	**–0.08** ($p < 0.001$)	**–0.26** ($p < 0.001$)	**–0.14** ($p < 0.001$)	**–0.16** ($p < 0.001$)	**–0.20** ($p < 0.001$)
Nutrient level[a]	**0.04** ($p = 0.022$)	**–0.38** ($p < 0.001$)	**0.04** ($p = 0.024$)	**0.52** ($p < 0.001$)	**–0.11** ($p < 0.001$)	**0.29** ($p < 0.001$)	**0.23** ($p < 0.001$)
Age (years)	**0.27** ($p < 0.001$)	**–0.41** ($p < 0.001$)	**0.14** ($p < 0.001$)	**0.04** ($p = 0.007$)	**0.14** ($p < 0.001$)	**0.19** ($p < 0.001$)	**0.24** ($p < 0.001$)
Stem vol. ($\mathrm{m^3\ ha^{-1}}$)	**0.13** ($p < 0.001$)	**–0.11** ($p < 0.001$)	**0.06** ($p < 0.001$)	**–0.25** ($p < 0.001$)	**0.08** ($p < 0.001$)	–0.03 ($p = 0.088$)	0.01 ($p = 0.551$)
Stem no. ($\mathrm{ha^{-1}}$)	**–0.11** ($p < 0.001$)	**0.05** ($p = 0.003$)	–0.03 ($p = 0.053$)	**0.04** ($p = 0.014$)	**–0.10** ($p < 0.001$)	–0.02 ($p = 0.214$)	**–0.06** ($p = 0.001$)
Basal area ($\mathrm{m^2\ ha^{-1}}$)	**0.07** ($p < 0.001$)	**–0.19** ($p < 0.001$)	**0.08** ($p < 0.001$)	–0.01 ($p = 0.516$)	0.01 ($p = 0.728$)	**0.07** ($p < 0.001$)	**0.07** ($p < 0.001$)

[a] See Appendix.

Table 3. Spearman's correlation coefficients (significant at $p < 0.05$ set in boldface) of forest stand attributes versus above-ground biomass of understorey vegetation of spruce forest stands on upland sites ($n = 619$ sites with 2385 sample squares).

	Biomass ($\mathrm{kg\ ha^{-1}}$) of				
	dwarf shrubs	herbs and grasses	mosses	total field layer	all understorey vegetation
Lat. (°N)	**0.40** ($p < 0.001$)	**–0.21** ($p < 0.001$)	**0.22** ($p < 0.001$)	**0.30** ($p < 0.001$)	**0.30** ($p < 0.001$)
Long. (°E)	**0.13** ($p < 0.001$)	0.01 ($p = 0.617$)	0.00 ($p = 0.876$)	**0.15** ($p < 0.001$)	**0.06** ($p = 0.005$)
Elevation (m a.s.l)	**0.27** ($p < 0.001$)	**–0.12** ($p < 0.001$)	**0.13** ($p < 0.001$)	**0.19** ($p < 0.001$)	**0.18** ($p < 0.001$)
Temp. sum (°C)	**–0.41** ($p < 0.001$)	**0.23** ($p < 0.001$)	**–0.22** ($p < 0.001$)	**–0.29** ($p < 0.001$)	**–0.29** ($p < 0.001$)
Nutrient level[a]	**0.41** ($p < 0.001$)	**–0.44** ($p < 0.001$)	**0.35** ($p < 0.001$)	**0.11** ($p < 0.001$)	**0.34** ($p < 0.001$)
Age (years)	**0.42** ($p < 0.001$)	**–0.31** ($p < 0.001$)	**0.35** ($p < 0.001$)	**0.24** ($p < 0.001$)	**0.39** ($p < 0.001$)
Stem vol. ($\mathrm{m^3\ ha^{-1}}$)	0.00 ($p = 0.883$)	**–0.10** ($p < 0.001$)	0.03 ($p = 0.17$)	**–0.11** ($p < 0.001$)	–0.01 ($p = 0.625$)
Stem no. ($\mathrm{ha^{-1}}$)	**–0.06** ($p = 0.002$)	**–0.10** ($p < 0.001$)	**0.07** ($p < 0.001$)	**–0.09** ($p < 0.001$)	0.03 ($p = 0.116$)
Basal area ($\mathrm{m^2\ ha^{-1}}$)	**0.04** ($p = 0.030$)	**–0.18** ($p < 0.001$)	**0.19** ($p < 0.001$)	**–0.08** ($p < 0.001$)	**0.15** ($p < 0.001$)

[a] See Appendix.

In the case of peatlands (hardwood–spruce mires and paludified forests, and pine mires), correlations between biomass values and forest stand and site characteristics were quite similar between the two categories (Table 5). The highest correlation coefficients were found for longitude. The correlation coefficients of the bottom layer and the field layer were generally of the same magnitude and direction.

Models

Two types of models were developed for each species group (Tables 6–9). The first type comprised models with explanatory variables selected from the entire set of forest stand and site attributes while the second type only had age as an explanatory variable (Fig. 2). This was done because the former model type cannot always be applied as variables concerning site location or site type may be unavailable. In addition, the definitions of site types are country-specific and based on Finnish conditions. On the other hand, models with latitude or longitude as an explanatory variable are applicable only to Finnish conditions. Models where only age is an explanatory variable can also be used in other boreal countries. The first model type does, however, provide slightly more accurate estimates than the second type in every case (Tables 6–9). The most common explanatory variables were site nutrient level (*see* Appendix), latitude, and stand age.

For upland pine forests, the relative RMSE_r varied from 16.6% to 147.0%, being lowest for all understorey vegetation (Table 6). The next best accuracies were found for total field layer, total bottom layer, and dwarf shrubs. The models for lichens provided the weakest estimates. The models for upland spruce forests were consistently inferior to the models for pine forests (Table 7). In spruce stands, the lowest RMSE_r values occurred for all understorey vegetation, while the weakest accuracies were found for herbs and grasses. No models were created for

Table 4. Spearman's correlation coefficients (significant at $p < 0.05$ set in boldface) of forest stand attributes versus above-ground biomass of understorey vegetation of broad-leaved forest stands on upland sites ($n = 116$ sites with 417 sample squares).

	Biomass (kg ha^{-1}) of				
	dwarf shrubs	herbs and grasses	mosses	total field layer	all understorey vegetation
Lat. (°E)	**0.17** ($p = 0.001$)	0.06 ($p = 0.254$)	**0.14** ($p = 0.003$)	**0.20** ($p < 0.001$)	**0.23** ($p < 0.001$)
Long. (°E)	**0.20** ($p < 0.001$)	**0.12** ($p = 0.013$)	–0.01 ($p = 0.836$)	**0.17** ($p = 0.001$)	0.08 ($p = 0.115$)
Elevation (m a.s.l)	**0.36** ($p < 0.001$)	**–0.21** ($p < 0.001$)	**0.17** ($p < 0.001$)	0.05 ($p = 0.265$)	**0.15** ($p = 0.002$)
Temp. sum (°C)	**–0.23** ($p < 0.001$)	0.06 ($p = 0.24$)	**–0.15** ($p = 0.002$)	**–0.14** ($p = 0.004$)	**–0.20** ($p < 0.001$)
Nutrient level[a]	**0.47** ($p < 0.001$)	**–0.41** ($p < 0.001$)	**0.36** ($p < 0.001$)	0.07 ($p = 0.16$)	**0.36** ($p < 0.001$)
Age (years)	**0.25** ($p < 0.001$)	–0.06 ($p = 0.233$)	**0.11** ($p = 0.022$)	0.09 ($p = 0.053$)	**0.12** ($p = 0.017$)
Stem vol. (m^3 ha^{-1})	0.05 ($p = 0.337$)	–0.05 ($p = 0.335$)	**–0.10** ($p = 0.033$)	–0.08 ($p = 0.102$)	**–0.15** ($p = 0.003$)
Stem no. (ha^{-1})	**–0.14** ($p = 0.003$)	0.05 ($p = 0.325$)	**–0.12** ($p = 0.013$)	**–0.10** ($p = 0.042$)	**–0.10** ($p = 0.040$)
Basal area (m^2 ha^{-1})	–0.07 ($p = 0.171$)	0.06 ($p = 0.189$)	**–0.11** ($p = 0.019$)	–0.05 ($p = 0.318$)	–0.08 ($p = 0.115$)

[a] See Appendix.

lichens in spruce and broad-leaved forests since the amount of lichen biomass was assumed to be negligible. For the same reason, no models were constructed for the total bottom layer. The RMSE_r values of models for broad-leaved forest stands were similar to those for coniferous stands (Table 8). The best accuracies were observed for the total field layer, and the poorest accuracies for dwarf shrubs and mosses.

The RMSE_r coefficients for peatland stands (hardwood–spruce mires and paludified forests, and pine mires) were slightly more accurate than those for upland forest stands (Table 9). The relative RMSE_r varied from 9.9% to 36.4%, being lowest for all understorey vegetation of pine mires. The above-ground biomass of all understorey vegetation growing on hardwood–spruce mires and paludified forests can be predicted with nearly identical accuracy.

Discussion

Biomass of understorey vegetation was correlated with site and stand variables that reflected climatic, edaphic and biotic variation of growth conditions across Finland. Importance of both temperature sum and latitude showed the overall effect of climatic variation on understorey vegetation in our data. In general, biomasses of mosses and dwarf shrubs were negatively correlated with temperature sum, whereas those of grasses and herbs showed positive correlation. The observed pattern is consistent with the common understanding of variation in vegetation in boreal zones (Sirén 1955, Kalela 1960, Ahti *et al.* 1968). The nutrient level reflected variation in the edaphic factors of this study and seemed to be more important in the case of spruce or broad-leaved forest stands than with pine dominated

Table 5. Spearman's correlation coefficients (significant at $p < 0.05$ set in boldface) of forest stand attributes versus above-ground biomass of understorey vegetation on peatland sites.

	Biomass (kg ha^{-1}) of					
	hardwood-spruce mires and paludified forests (230 sites with 783 sample squares)			pine mires (362 sites 1403 sample squares)		
	total bottom layer	total field layer	all understorey vegetation	total bottom layer	total field layer	all understorey vegetation
Lat. (°N)	**0.20** ($p < 0.001$)	0.02 ($p = 0.590$)	**0.15** ($p < 0.001$)	**0.10** ($p < 0.001$)	**0.19** ($p < 0.001$)	**0.18** ($p < 0.001$)
Long. (°E)	**0.34** ($p < 0.001$)	**0.13** ($p < 0.001$)	**0.30** ($p < 0.001$)	**0.20** ($p < 0.001$)	**0.11** ($p < 0.001$)	**0.22** ($p < 0.001$)
Elevation (m a.s.l)	**0.27** ($p < 0.001$)	**0.20** ($p < 0.001$)	**0.32** ($p < 0.001$)	**0.15** ($p < 0.001$)	**0.16** ($p < 0.001$)	**0.20** ($p < 0.001$)
Temp. sum (°C)	**–0.24** ($p < 0.001$)	**–0.08** ($p = 0.025$)	**–0.22** ($p < 0.001$)	**–0.16** ($p < 0.001$)	**–0.19** ($p < 0.001$)	**–0.24** ($p < 0.001$)
Nutrient level[a]	**–0.15** ($p < 0.001$)	**0.28** ($p < 0.001$)	**0.13** ($p < 0.001$)	0.01 ($p = 0.583$)	0.04 ($p = 0.153$)	0.05 ($p = 0.087$)
Water table level[a]	–0.05 ($p = 0.179$)	**–0.43** ($p < 0.001$)	**–0.35** ($p < 0.001$)	**–0.09** ($p < 0.001$)	**–0.24** ($p < 0.001$)	**–0.17** ($p < 0.001$)
Age (years)	0.01 ($p = 0.849$)	**0.32** ($p < 0.001$)	**0.26** ($p < 0.001$)	**0.08** ($p = 0.004$)	**0.13** ($p < 0.001$)	**0.12** ($p < 0.001$)
Stem vol. (m^3 ha^{-1})	**–0.22** ($p < 0.001$)	–0.03 ($p = 0.335$)	**–0.15** ($p < 0.001$)	**–0.12** ($p < 0.001$)	–0.02 ($p = 0.549$)	**–0.12** ($p < 0.001$)
Stem no. (ha^{-1})	**–0.10** ($p = 0.006$)	–0.07 ($p = 0.052$)	**–0.10** ($p = 0.005$)	**–0.07** ($p = 0.007$)	**–0.08** ($p = 0.002$)	**–0.10** ($p < 0.001$)
Basal area (m^2 ha^{-1})	**–0.13** ($p < 0.001$)	–0.04 ($p = 0.283$)	**–0.09** ($p = 0.013$)	**–0.12** ($p < 0.001$)	–0.02 ($p = 0.550$)	**–0.12** ($p < 0.001$)

[a] See Appendix.

Table 6. Aboveground biomass (y) (kg ha^{-1}) of understorey vegetation of pine forest stands on upland sites predicted as a function of forest stand and site attributes[a]. The dependent variable is $\sqrt{y_i + 0.5}$ transformation of the above-ground biomass (y) of species group i.

Equation	Correction factor[b]	RMSE$_r$ (%)
Dwarf shrubs		
1. $-10.328 + 0.005z_2z_9 - 0.0004z_9^2 - 0.00003z_4 + 0.0009z_1z_4$	126.91	36.7
2. $16.68 + 0.129z_9 - 0.0004z_9^2$	126.91	37.8
Herbs and grasses		
3. $15.223 + 0.023z_5z_9 - 0.062z_5z_1 + 0.000009z_4^2 - 0.0001z_4z_9 - 0.028z_5z_8$	55.02	90.3
4. $11.725 - 0.098z_9 + 0.0002z_9^2$	55.02	101.0
Mosses		
5. $68.365 + 0.0003z_4z_9 - 0.0003z_6^2 - 0.07z_5z_9 + 0.0002z_6z_3 - 0.2z_5z_1 - 0.00004z_4^2$ $+ 0.014z_5z_4 + 0.01z_8^2$	361.44	46.6
6. $27.329 + 0.138z_9 - 0.0005z_9^2$	361.44	49.1
Lichens		
7. $-53.196 + 0.378z_5z_1 - 0.014z_5z_4 + 0.00002z_4^2$	260.56	126.1
8. $7.975 - 0.0002z_9^2$	260.56	147.0
Total field layer		
9. $13.865 + 0.013z_1z_2 - 2.969z_5 + 0.00003z_4z_9$	96.72	25.2
10. $22.521 + 0.069z_9 - 0.0002z_9^2$	96.72	25.6
Total bottom layer		
11. $8.623 + 0.09z_5z_1 + 0.004z_2z_9 + 0.00003z_3z_4 - 0.0003z_6^2 - 0.0005z_9^2 + 0.0008z_6z_9$	355.13	35.8
12. $32.952 + 0.085z_9 - 0.0000006z_9^3$	355.13	38.7
All understorey vegetation		
13. $22.523 + 0.084z_5z_1 + 0.01z_2z_9 - 0.031z_5z_9 - 0.0007z_9^2 - 0.0003z_6^2 + 0.0006z_6z_9$	231.56	16.6
14. $42.641 + 0.094z_9 - 0.0000008z_9^3$	231.56	17.7

[a] z_1 = lat. (°N), z_2 = long. (°E), z_3 = elevation (m a.s.l), z_4 = temperature sum (°C), z_5 = nutrient level (*see* Appendix), z_6 = stem vol. (m^3 ha^{-1}), z_7 = stem no. (ha^{-1}), z_8 = basal area (m^2 ha^{-1}), z_9 = stand age (years).

[b] Corrected biomass estimate derived with the equation $\hat{y}_i = f\left(z_p, p = 1,2,\ldots,p\right)^2 - 0.5 + c$, where c is the correction factor (Lappi 1993).

Table 7. Aboveground biomass (y) (kg ha^{-1}) of understorey vegetation of spruce forest stands on upland sites predicted as a function of forest stand and site attributes[a]. The dependent variable is $\sqrt{y_i + 0.5}$ transformation of the above-ground biomass (y) of species group i.

Equation	Correction factor[b]	RMSE$_r$ (%)
Dwarf shrubs		
15. $10.903 + 0.027z_5z_9 + 0.045z_5z_1 - 0.000006z_4^2$	87.14	50.1
16. $10.375 - 0.033z_9 + 0.001z_9^2 - 0.000004z_9^3$	87.14	53.4
Herbs and grasses		
17. $21.49 - 0.05z_5z_1 - 0.006z_5z_6 - 0.008z_5z_9$	44.60	63.3
18. $15.058 - 0.113z_9 + 0.0003z_9^2$	44.60	68.9
Mosses		
19. $9.672 + 0.029z_5z_9 + 0.078z_5z_1 + 0.186z_8$	264.82	38.0
20. $19.282 + 0.164z_9 - 0.000001z_9^3$	264.82	39.3
Total field layer		
21. $-42.593 + 0.981z_1 - 0.008z_8^2 + 0.002z_8z_9$	67.15	29.9
22. $15.399 + 0.036z_9$	67.15	31.0
All understorey vegetation		
23. $22.522 + 0.026z_5z_9 + 0.11z_5z_1 - 0.003z_5z_4$	206.67	22.3
24. $27.349 + 0.157z_9 - 0.000001z_9^3$	206.67	22.9

[a] for explanations *see* Table 6.

[b] for explanations *see* Table 6.

stands. The observed high correlation between stand variables and the biomass of understorey vegetation indicate that variation in understorey vegetation is controlled also by biotic factors, particularly by tree stand development.

Herbs and grasses have the greatest amount of biomass during the early succession of upland forests stands, which gradually decreases over time (*see* Fig. 2). This is in agreement with Lindholm and Vasander (1987), who reported

Table 8. Aboveground biomass (y) (kg ha^{-1}) of understorey vegetation of broad-leaved forest stands on upland sites predicted as a function of forest stand and site attributes[a]. The dependent variable is $\sqrt{y_i + 0.5}$ transformation of the above-ground biomass (y) of species group i.

Equation	Correction factor[b]	RMSE$_r$ (%)
Dwarf shrubs		
25. $3.217 + 0.034z_5z_3 - 0.0003z_3^2 + 0.0005z_3z_9 - 0.077z_5z_8$	77.67	85.1
26. $7.102 + 0.0004z_9^2$	77.67	96.9
Herbs and grasses		
27. $-192.32 - 3.451z_5 + 0.117z_1z_2 - 0.00001z_3z_4 - 0.065z_2^2 + 0.002z_1z_4 - 0.003z_2z_4$	55.55	37.2
28. $20.58 - 0.423z_9 + 0.004z_9^2 - 0.00002z_9^3$	55.55	42.7
Mosses		
29. $20.931 + 0.096z_5z_1 - 0.0006z_2z_4$	236.6	85.8
30. $13.555 - 0.056z_9$	236.6	91.9
Total field layer		
31. $-95.393 + 0.094z_1z_2 - 0.000001z_7z_4 - 0.106z_2^2 + 0.0005z_1z_4$	55.40	25.4
32. $18.831 + 0.0002z_9^2$	55.40	26.6
All understorey vegetation		
33. $19.8 + 0.691z_5z_1 - 38.578z_5$	156.51	31.6
34. $25.645 + 0.037z_9$	156.51	33.7

[a] for explanations *see* Table 6.
[b] for explanations *see* Table 6.

Table 9. Aboveground biomass (y) (kg ha^{-1}) of peatland soil understorey vegetation predicted as a function of forest stand and site attributes[a]. The dependent variable is $\sqrt{y_i + 0.5}$ transformation of the above-ground biomass (y) of species group i.

Equation	Correction factor[b]	RMSE$_r$ (%)
Hardwood-spruce mires and paludified forests, total bottom layer		
35. $-3.182 + 0.022z_1z_2 + 0.0002z_3z_9 - 0.077z_5z_2 - 0.003z_2z_6 + 0.0002z_6^2$	98.10	21.9
36. $25.923 + 0.000001z_9^3$	98.10	24.1
Hardwood-spruce mires and paludified forests, total field layer		
37. $23.24 - 1.163z_{10}^2 + 1.515z_5z_{10} - 0.00002z_6z_7 + 0.00008z_4z_9 + 0.00001z_7z_3$	162.58	32.4
38. $19.334 + 0.094z_9$	162.58	36.4
Hardwood-spruce mires and paludified forests, all understorey vegetation		
39. $35.52 + 0.001z_2z_3 - 1.1z_{10}^2 - 0.00002z_6z_7 + 0.00004z_7z_9 + 0.139z_2z_{10}$	116.54	12.2
40. $36.655 + 0.0004z_9^2$	116.54	13.6
Pine mires, total bottom layer		
41. $31.809 + 0.008z_2z_3 - 0.0003z_7z_8 + 0.00006z_7z_9 - 0.188z_3$	222.22	27.3
42. $36.039 + 0.000003z_9^3$	222.22	28.6
Pine mires, total field layer		
43. $48.12 - 0.00001z_4^2 + 0.013z_5z_9 - 0.04z_6z_{10} + 0.026z_5z_6$	133.26	16.0
44. $35.861 + 0.026z_9$	133.26	16.9
Pine mires, all understorey vegetation		
45. $50.098 + 0.005z_2z_3 - 0.00001z_6z_7 + 0.026z_5z_9 - 0.0001z_3z_4 - 0.014z_6z_{10}$	167.40	9.9
46. $51.877 + 0.042z_9$	167.40	10.7

[a] z_{10} = drainage status, for other explanations *see* Table 6.
[b] for explanations *see* Table 6.

that in boreal forests vegetation is initially dominated by herbs and grasses. After closure of the canopy, the group-wise biomasses change steadily as the composition of the plant community shifts and the vegetation of the stand becomes more characteristic of forest vegetation with the dominance of mosses and slow growing clonal dwarf shrubs.

The importance of age in explaining variation in biomass in upland forests has also been reported in other studies describing succession development (e.g. Lindholm and Vasander 1987, Crowell and Freedman 1994). For instance, understorey vegetation of the boreal zone undergoes successional development after clear-cutting or fire disturbance (Alaback 1982). Immediately after clear-cutting, the biomass of mosses and field layer plants decreases drastically (Palviainen *et al.* 2005a, 2005b). The biomass of mosses does not return to pre-treatment levels for five years. However, after the initial decrease, the field layer biomass increases to levels greater than before clear-cutting. These relatively short-term changes are not, however, detected by the models used here, which were constructed to describe long-term changes in understorey biomass (Fig. 2).

One main conclusion can be drawn from this study: the age of a stand predicts the understorey biomass of upland forest stands much better than any other tree stand variable alone. Although the production of understorey vegetation has been reported to increase as basal area decreases (Pase and Hurd 1958), our findings did not support this conclusion. The basal area of the stand and the characteristics of a single plant species might, however, behave in this manner. When the biomasses of all understorey plant species are pooled, and then examined according to stand age, the species-specific relationship may lose its meaning since the species composition changes during canopy closure. In addition, stand age indicates how long understorey vegetation has had time to grow. Stand age is normally also correlated with other tree stand variables such as volume and basal area, but extreme exceptions also do occur.

The biomass values of bottom and field layers were higher in pine mires than hardwood-spruce mires and paludified forests. The correlations between tree characteristics (stem volume, stem number, and basal area) and biomass of the understorey vegetation in hardwood-spruce mires and paludified forests and pine mires were negative (Table 5), which is in agreement with the findings of Reinikainen *et al.* (1984) and Laine and Vasander (1996).

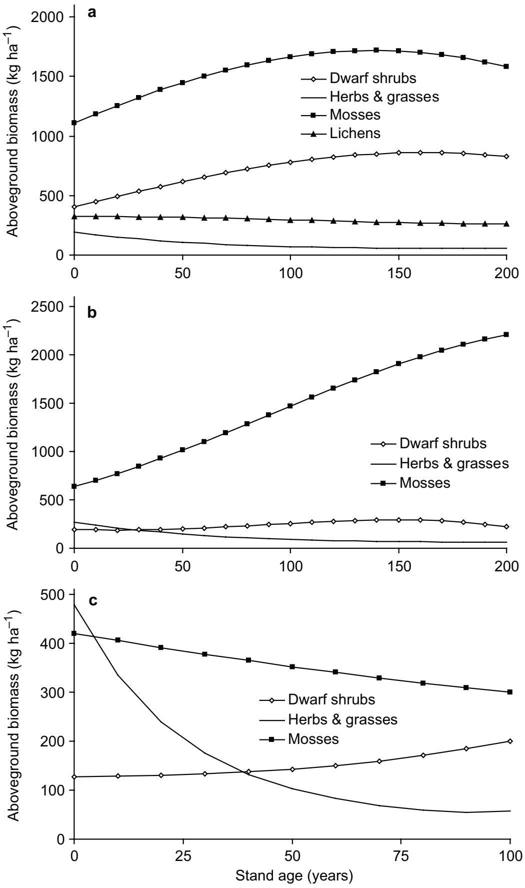

Fig. 2. Group-wise above-ground biomass of understorey vegetation in upland forests during stand development. — **a**: pine forest, — **b**: spruce forest, — **c**: broad-leaved forests.

Mälkönen (1974) reported that in his pine-dominated upland study areas in southern Finland (three 28- to 47-year-old forest stands), the total above-ground biomass of understorey vegetation ranged from 2800 to 3300 kg ha^{-1}, which is very close to our results (Fig. 3). Havas and Kubin (1983) calculated that on their spruce-dominated upland study site in northern Finland, the total above-ground biomass of understorey vegetation was 5527 kg ha^{-1}, which

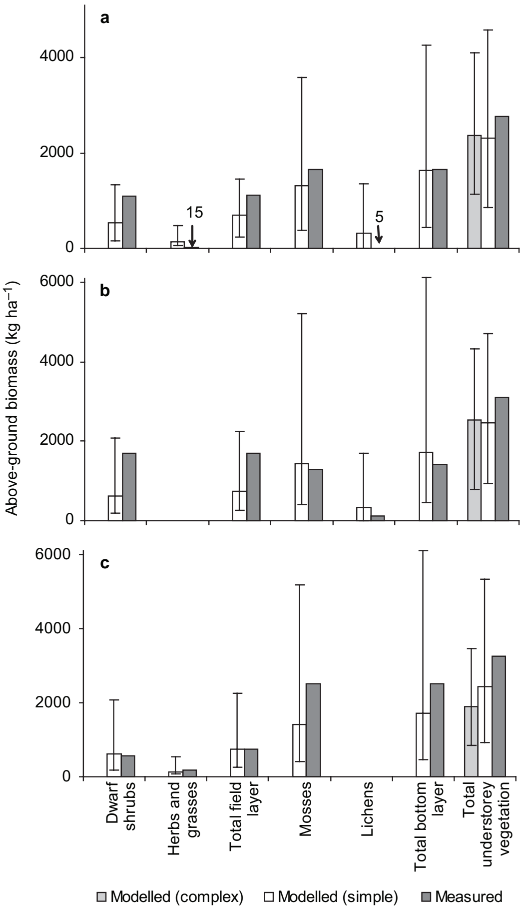

Fig. 3. Comparison of modelled and measured above-ground biomass of understorey vegetation in three pine forest stands (**a**: 28-year-old stand, **b**: 47-year-old stand, **c**: 47-year-old stand) measured and reported by Mälkönen (1974). The 95% confidence limits of predictions are also shown.

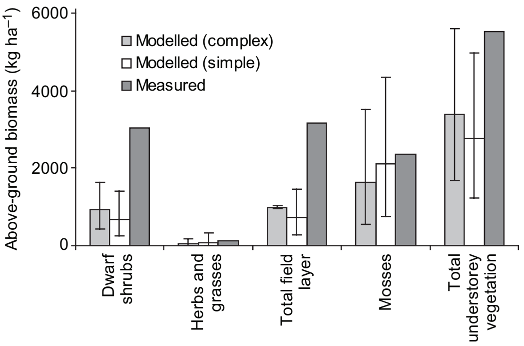

Fig. 4. Comparison of modelled and measured above-ground biomass of understorey vegetation in a spruce forest. Results of our biomass models were compared with the measurements of Havas and Kubin (1983). The 95% confidence limits of predictions are also shown.

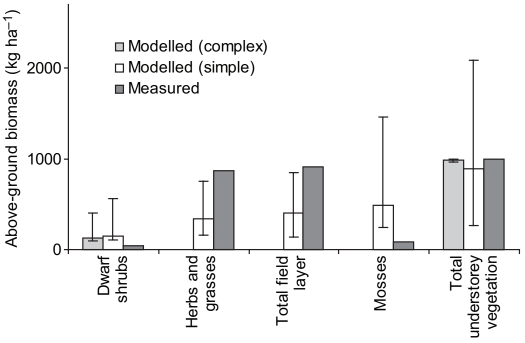

Fig. 5. Comparison of modelled and measured above-ground biomass of understorey vegetation in a broad-leaved forest. Results of our biomass models were compared with the measurements of Mälkönen (1977). The 95% confidence limits of predictions are also shown.

lies just slightly beyond the 95% confidence intervals of the models presented here (Fig. 4). The difference can be explained by the relatively large amount of dwarf shrubs. Mälkönen (1977) observed on a birch-dominated study site in southern Finland a total aboveground biomass of understorey vegetation of 1100 kg ha^{-1}, which is quite close to the estimate predicted by our models (Fig. 5).

The models and equations developed in this study can be applied when modelling carbon dynamics of forest ecosystems in addition to regional carbon stock assessments. When applying the simple models (only age as an explanatory variable) presented here, the authors recommend using general-level species groups instead of detailed-level groups, when detailed group-wise predictions are not essential. Detailed group-wise predictions might be important when the study deals with litter production or carbon flow from living vegetation to the soil system. Our models for predicting understorey biomass are applicable to boreal coniferous upland forests aged up to 200 years. For broad-leaved upland forests and peatland forests, the upper limit is 100 years. An upper limit is given since the number of older stands in our data was small. For stands older than the upper limit, the biomass for the upper limit should be applied. Our study is based on nationwide vegetation data from a network of permanent sample plots established by the National Forest Inventory in Finland. The results are thus representative of the proportions of managed and unmanaged forest stands.

The biomass models of understorey vegetation developed here consider only above-ground biomass. Thus, our estimates cover the total living biomass of mosses and lichens but only part of the biomass of the field layer species. The proportion of the biomass of field layer vegetation located in belowground parts is estimated to be about 70% of the total biomass (Mälkönen 1974, Perina and Kvet 1975, Kubícek and Simonovic 1982, Havas and Kubin 1983, Kubícek *et al.* 1994, Palviainen *et al.* 2005a). The annual biomass production of bryophytes and lichens was estimated to be 1/3 (Tamm 1953, Kellomäki *et al.* 1977, Havas and Kubin 1983, Nakatsubo *et al.* 1997) and 1/10 (Longton 1992, Kumpula *et al.* 2000) of the total biomass, respectively. These proportions are also approximations of the annual litter production of these functional groups. The annual biomass production of the above-ground parts of herbs and grasses is approximated to be 1/1 of the total above-ground biomass since most of the above-ground parts of herbs and grasses change into litter at the end of the growing season. The annual biomass production of the above-ground parts of dwarf shrubs is assumed to be 1/4 of total above-ground biomass (Mork 1946, Mälkönen 1974, Havas and Kubin 1983). Normally the mean annual biomass production and, therefore, the mean annual litter production of the belowground parts of herbs, grasses, and dwarf shrubs is estimated to be 1/3 since the life expectancy of roots is about 2–3 years (Head 1970). Until more accurate models and estimates are developed, our biomass models supplemented with the mentioned litter approximations can be used to estimate litter production of understorey vegetation in modelling the carbon dynamics of forest ecosystems.

Understorey vegetation is a highly diverse component of the forest ecosystem that cannot be easily predicted on the basis of forest stand and site attributes. Many factors other than those easy to observe affect the biomass of understorey vegetation. Interspecies relationships can drastically impact the occurrence and abundance of a plant species therefore influencing the species composition and total biomass of the understorey vegetation of a stand. However, empirical models based on large data with wide geographic coverage on species abundances provide robust tools to estimate the mean biomass of understorey vegetation for large areas in boreal conditions.

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Appendix. Nutrient levels of uplands and peatlands and drainage status of drained peatlands.

Nutrient levels (1–7) of the upland sites are based mainly on the classification of Cajander (1926, 1949):

1. Herb-rich forest.
2. Herb-rich heath forest.
3. Mesic heath forest.
4. Sub-xeric heath forest.
5. Xeric heath forest.
6. Barren heath forest.
7. Rock, cliff, or sand.

Nutrient levels (1–5) of peatland sites follow the classification:

1. Herb-rich hardwood-spruce swamps, herb-rich pine fens; herb-rich fens (mesotrophic).
2. *Vaccinium myrtillus* or tall sedge spruce swamps; tall sedge pine fens; tall sedge fens (meso-oligotrophic).
3. *Carex globularis* and *Vaccinium vitis-idaea* spruce swamps and spruce-pine swamps; *Carex globularis* pine swamps; low sedge fens (oligotrophic).
4. Low sedge, dwarf-shrub, and cottongrass pine bogs; low sedge *Sphagnum papillosum* bogs (ombro-oligotrophic).
5. *Sphagnum fuscum* pine bogs; ombrotrophic and *Sphagnum fuscum* low sedge bogs (ombrotrophic).

Drainage status (1–4) of peatlands (Paavilainen and Päivänen 1995):

1. Undrained.
2. Recently drained; slight effect on understorey vegetation, no or little effect on tree stand.
3. Transforming drained mires; clear effect on understorey vegetation and tree stand.
4. Transformed drained mires; vegetation resembles corresponding upland forest site type, tree stand forest-like.