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Relationship between Biomass and Percentage Cover in Understorey Vegetation of Boreal Coniferous Forests

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In the present study, the aboveground biomass of the understorey vegetation of boreal coniferous forests was modelled according to the percentage cover. A total of 224 observations from 22 stands in upland forests and 195 observations from 14 different studies in peatland forests were utilized for the present analyses. The relationships between biomass and percentage cover can be used in ecosystem and carbon-cycle modelling as a rapid nondestructive method for estimation of the aboveground biomass of lichens, bryophytes, herbs and grasses, and dwarf shrubs in upland forests and bottom and field layers in peatland forests.

Keywords upland soils, peatlands, biomass models, ground vegetation
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1 Introduction

The boreal forest biome plays an important role in the global carbon cycle. Forest vegetation and soil may act as significant sinks or sources of atmospheric carbon dioxide, depending on land use, forest management and environmental conditions. The carbon budgets of trees and forest soil have been modelled extensively, but understorey vegetation is not usually included in these analyses (Bonan et al. 1992). In comparison to other components of forest ecosystems, the biomass of understorey vegetation is considered to be small and is sometimes dismissed as negligible. However, it may play an important role in many ecosystem processes, e.g. in the nutrient and carbon cycle (Yarie 1980, Van Cleve and Alexander 1981), due to rapid turnover at the biomass level and the presence of easily decomposable litter (Tappeiner and Alm 1975, Zavitkovski 1976, Chapin 1983). In upland soils, the annual litter production of understorey vegetation may represent a considerable proportion of the total litter production, varying from 4% to 30% (Hughes 1970). On pristine peatlands, most of the organic matter deposited as peat derives from understorey vegetation (Lappalainen and Hänninen 1993).

In many ecosystem models it is necessary to quantify the biomass of understorey vegetation as one of the components of nutrient cycling. Since direct methods (e.g. biomass harvesting) for measuring the aboveground biomass of understorey vegetation are destructive, laborious and time-consuming (Hermy 1988, Chiarucci et al. 1999), indirect and nondestructive methods are needed. Nondestructive methods can also be applied when a change in biomass over time within the same sample plot is monitored (e.g. Bråkenhielm and Liu 1998).

The canopy intercept method is used to estimate the aboveground biomass with hits by a stick or sharp needle passed through vegetation and it was suggested that this method could result accurate in estimates of aboveground biomass as well as be sensitive to plant growth form (Jonasson 1988, Frank and McNaughton 1990). In this method, the need to use calibrations according to plant growth form is dependent on the scope of the study and the structure of the vegetation being studied.

Percentage cover analysis is widely used to characterize understorey vegetation (Mueller-Dombois and Ellenberg 1974, Hermy 1988, Chiarucci et al. 1999). Typically, cover is defined as the vertical projection of the crown or shoot area of a species from the ground surface, expressed as the percentage of a reference area. It is essential that the cover be evaluated separately for each vegetation layer, since the understorey vegetation is typically organized into several horizontal layers. Mueller-Dombois and Ellenberg (1974) also concluded that nearly all plant lifeforms, from trees to bryophytes, can be evaluated by the same parameter and thereby in comparable terms. The disadvantage of percentage cover analysis is that observers differ in their tendency to under- or overestimate cover in relation to both species and quadrat size (Hermy 1988).

Several authors have suggested that there is a considerable relationship between the percentage cover and biomass of most species (Kellomäki 1973, 1974, 1975, Kuusipalo 1983, Alaback 1986, Alaback 1987, Jonasson 1988, Yarie and Mead 1989, Chiarucci et al. 1999, Röttgermann et al. 2000). In some studies, the aboveground biomass of understorey vegetation in upland soils was estimated according to multiple variables (Kellomäki 1974, 1975, Mattila and Helle 1978, Mattila 1981, 1988, Kuusipalo 1983). The most often used combination is percentage cover and plant height. In his study, Alaback (1986) estimated the aboveground biomass of understorey species according to the percentage cover, basal shoot diameter or shoot length, using linear regression models. The applicability of such models is limited, since height is not a typically measured attribute in large-scale inventories. In addition, such models are typically built for single species and are based on relatively limited data. Furthermore, all previous studies concerning biomass predictions of understorey vegetation according to the percentage cover or other variables have dealt with upland sites. There are no biomass models available for the understorey vegetation of peatlands, although peatlands are a notable habitat group in the Boreal vegetation zone and play quite a significant role in the carbon cycle and carbon balance.

In the present study, we investigated the understorey vegetation by species group instead of single species. Despite the relatively wide variability in composition of the flora, dense cover and large number of species, the ground cover in upland soils of boreal forests is often dominated by only a few species, regardless of the phase of stand development (Kubícek and Simonovic 1982, Kellomäki and Väisänen 1991, Reinikainen et al. 2001). In the field and bottom layers, the dominant and subdominant species may represent over 90% of the total aboveground biomass (Mäkipää 1994, 1998). On peatlands, the field layer biomass consists of a large variety of lifeforms and ecological types, and their combinations extend from water plants to forest species (Laine and Vasander 1996). The range of lifeforms in the bottom layer of peatlands is much more uniform than in the field layer.

The objective here was to develop tools for estimating the aboveground biomass of understorey vegetation for conditions corresponding to those in Finland, based on the percentage cover of the plant species groups. We constructed models for the bottom layer (bryophytes and lichens) and field layer (dwarf shrubs, herbs and grasses) at both upland and peatland sites.

2 Material and Methods

2.1 Terms

The term 'understorey vegetation' is used to refer to all vegetation below the overstorey trees. Understorey vegetation may include herbaceous species, grasses and dwarf shrubs, as well as bryophytes and lichens. This definition of understorey vegetation excludes tall shrubs and epiphytes. In boreal forests, however, this exclusion results in only minor underestimates of the biomass of understorey vegetation. The aboveground biomass of understorey vegetation refers to the dry matter of the aboveground parts of the vegetation in the forest understorey.

The bottom layer consists of bryophytes and lichens only. Again, the field layer consists of dwarf shrubs, herbs and grasses. Dwarf shrubs are low shrubs with perennial aboveground woody stems that spreading near the ground surface, and that here included tree saplings with the same height as the dwarf shrubs. Herbs and grasses are annual plants without perennial aboveground woody stems. These divisions are based on traditional a priori grouping, which is typically defined by discrete and measurable biological trait differences (Reich et al. 2003).

The term 'upland soil' refers to those forest sites growing on the mineral soil sites. Peatlands were defined botanically as sites supporting a peat-producing plant community. In the present study, peatlands consist of 1) hardwood-spruce mires and paludified forests, 2) pine mires and 3) drained peatland forests; open fens and bogs were not included.

2.2 Data

The data were compiled from several sources (Tables 1 and 2), with differences in the details of the sampling procedures. However, they in general resulted in comparable observations of the aboveground biomass of the understorey vegetation. The exact sampling procedures for each stand are presented in the corresponding original publications. In each study the percentage cover was estimated visually. The biomass of the aboveground parts was measured either as single species or as species groups such as herbs and grasses, dwarf shrubs, lichens and bryophytes. In some cases, the biomass was measured separately only for the bottom and field layers. A total of 224 sample quadrats were located in the upland soils and 195 on the peatlands.

2.3 Model Development

The hierarchical structure (i.e. sample quadrats within stands) in the data implies a lack of independence among measurements, since observations from the same stand are highly correlated. Correspondingly, we used mixed models that accounted for variance deriving from the different hierarchical levels in the data. Mixed models were used, since the sample quadrats could not be treated as independent units (Fox et al. 2001).

The aboveground biomasses (y) of bryophytes and lichens in upland soils and of the field and bottom layers on peatlands were modelled as a function of percentage cover (x) with a mixed nonlinear model

$$y = \frac{u + x^2}{(\beta_0 + \beta_1 \cdot x)^2} \qquad (1)$$

where β_0 and β_1 are fixed population parameters and u is a random parameter. The parameters were estimated with a nonlinear mixed SAS procedure (SAS Institute 1999). The aboveground biomasses of dwarf shrubs and herbs/grasses in upland soils were modelled with a mixed linear model

$$y = \beta_1 \cdot x + u \qquad (2)$$

Several model structures were tested and compared with the fit-statistics and with the visual examination. Since the species composition may change with the change in total abundance of the species group, both linear and curvilinear relationships between cover and biomass were tested. The final decision between use of the nonlinear and linear models was made based on both evaluation of the differences between these two models and the ecological aspects of the current species group.

3 Results

For the bottom layer (bryophytes and lichens) of boreal coniferous upland forests the relationship between percentage cover and aboveground biomass was curvilinear (Table 3 and Fig. 1a, b and 2a), since the species composition changed according to the total percentage cover of the bottom layer (Fig. 3). The proportion of other bottom layer plant species decreased while that of the pleurocarpous mosses *Pleurozium schreberi* (Brid.) Mitt. and *Hylocomium splendens* (Hedw.) B.S.G. increased. For the field layer (dwarf shrubs, herbs and grasses) the relationship followed a linear form (Table 4 and Figs. 1c, d and 2b), since there was no evident change in species composition.

Table 1. General description of the 23 stands in upland soils gathered for the present study.

Latitude	Longitude	Site type [a)]	No. of sample quadrats	Stand age	Tree species	Further information
61°49´N	29°19´E	MT	10	63	Pine	(Helmisaari and Helmisaari 1992, Mäkipää 1994)
61°24´N	25°2´E	MT	9	42	Pine	(Helmisaari and Helmisaari 1992, Mäkipää 1994)
61°10´N	26°3´E	OMT	10	36	Spruce	(Helmisaari and Helmisaari 1992, Mäkipää 1994)
61°6´N	26°1´E	CT	10	42	Pine	(Helmisaari and Helmisaari 1992, Mäkipää 1994)
62°1´N	24°48´E	VT	9	36	Pine	(Helmisaari and Helmisaari 1992, Mäkipää 1994)
63°23´N	24°17´E	CT	10	53	Pine	(Helmisaari and Helmisaari 1992, Mäkipää 1994)
62°56´N	25°40´E	VT	10	56	Spruce	(Helmisaari and Helmisaari 1992)
67°38´N	24°39´E	EMT	10	52	Pine	(Helmisaari and Helmisaari 1992)
67°20´N	26°39´E	MCClT	10	64	Pine	(Helmisaari and Helmisaari 1992)
66°51´N	27°08´E	EMT	10	53	Spruce	(Helmisaari and Helmisaari 1992)
63°51´N	28°58´E	MT	10	140	Spruce	(Finér et al. 2003)
63°51´N	28°58´E	MT	10	140	Spruce	(Finér et al. 2003)
63°51´N	28°58´E	MT	10	140	Spruce	(Finér et al. 2003)
61°52´N	29°20´E	OMT	16	60	Spruce	(Helmisaari and Helmisaari 1992)
60°42´N	24°10´E	MT	10	60	Spruce	(Mäkipää 1998)
60°42´N	24°10´E	MT	10	60	Spruce	(Mäkipää 1998)
60°42´N	24°10´E	MT	10	60	Spruce	(Mäkipää 1998)
60°42´N	24°10´E	MT	10	60	Spruce	(Mäkipää 1998)
60°42´N	24°10´E	MT	10	60	Spruce	(Mäkipää 1998)
60°42´N	24°10´E	MT	10	60	Spruce	(Mäkipää 1998)
60°42´N	24°10´E	MT	10	60	Spruce	(Mäkipää 1998)
60°42´N	24°10´E	MT	10	60	Spruce	(Mäkipää 1998)

[a)] OMT = Herb-rich heath forest, MT = Mesic heath forest, VT/EMT = Subxeric heath forest, CT/MCClT = Xeric heath forest (Cajander 1949).

Table 2. General description of the 16 previous studies on peatlands gathered for the present study. Main peatland categories: 1) hardwood-spruce mires and paludified forests, 2) pine mires and 3) drained peatland forests (Laine and Vasander 1990, 1996).

Latitude	Longitude	Main peatland categories	No. of study sites	Further information
61°2´N	25°00´E	2	2	(Vasander 1981a, b, 1982)
62°3´N	24°29´E	2	1	(Kosonen 1976, 1981)
61°2´N–61°24´N	24°58´E–25°3´E	1	4	(Solmari and Vasander 1981, Solmari 1986)
61°2´N	25°2´E	1, 2	7	(Lindholm 1981)
62°3´N	24°29´E	2	5	(Kosonen 1976, Reinikainen 1981)
61°35´N–61°52´N	24°5´E–25°25´E	2	3	(Laiho 1996)
61°48´N	24°19´E	2	3	(Minkkinen et al. 1999)
63°53´N	25°42´E	3	6	Penttilä and Laiho unpublished data
59°38´N	11°18´E	2	1	(Håland and Brække 1989, Håland 1994)
61°35´N–62°5´N	23°50´E–24°55´E	2	82	(Laiho and Laine 1994, Laine et al. 1995)
n/a	n/a	1, 2	42	(Vuorinen et al. 1980, Finér 1989)
n/a	n/a	1, 2	37	(Vuorinen et al. 1980, Finér 1989)
n/a	n/a	3	2	(Solmari 1986)

Table 3. Aboveground biomass (y) (g m^{-1}) of bryophytes and lichens of upland soils predicted as a function of the percentage cover of species (x): Equation 1. The percentage cover used is the sum of the percentage covers for every species in each group.

Biomass of	n	β_0	S.E. of β_0	β_1	S.E. of β_1	
Pine forests						
Bryophytes	68	4.3369	1.1157	0.0128	0.0142	(Model 1)
Lichens	68	1.1833	0.1475	0.0334	0.0037	(Model 2)
Total bottom layer	68	3.8168	1.0679	0.0151	0.0134	(Model 3)
Spruce forests						
Bryophytes	156	1.8304	0.5522	0.0482	0.0073	(Model 4)

Table 4. Aboveground biomass (y) (g m^{-1}) of dwarf shrubs, herbs and grasses of upland soils predicted as a function of the percentage cover of species (x): Equation 2. The percentage cover used is the sum of the percentage covers for every species in each group.

Biomass of	n	β_1	S.E. of β_1	
Pine forests				
Dwarf shrubs	68	2.1262	0.2300	(Model 5)
Herbs & grasses	68	0.8416	0.1701	(Model 6)
Total field layer	68	2.0356	0.2470	(Model 7)
Spruce forests				
Dwarf shrubs	156	1.3169	0.1172	(Model 8)
Herbs & grasses	156	0.6552	0.0436	(Model 9)
Total field layer	156	1.1234	0.2821	(Model 10)

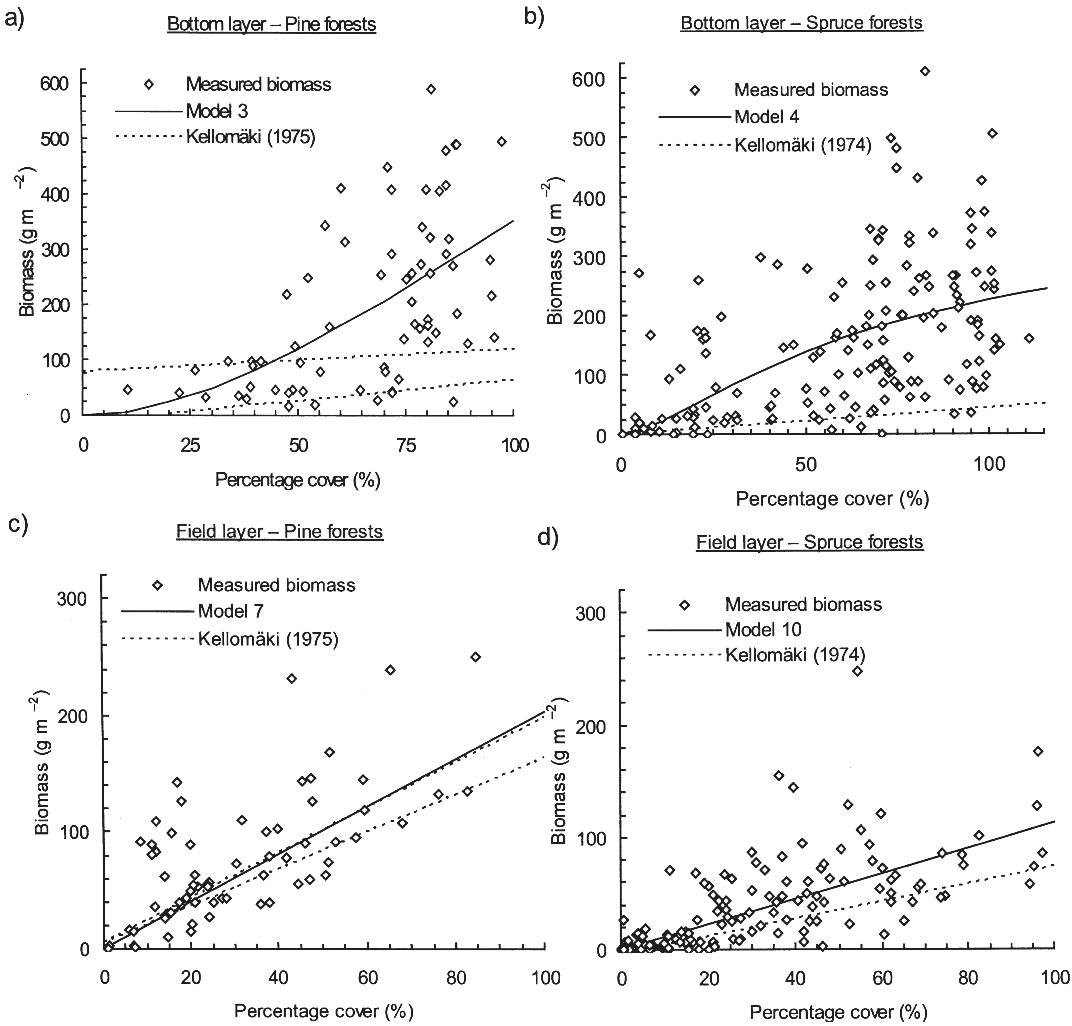


Fig. 1. Aboveground biomass of understorey vegetation in upland soils according to the percentage cover.

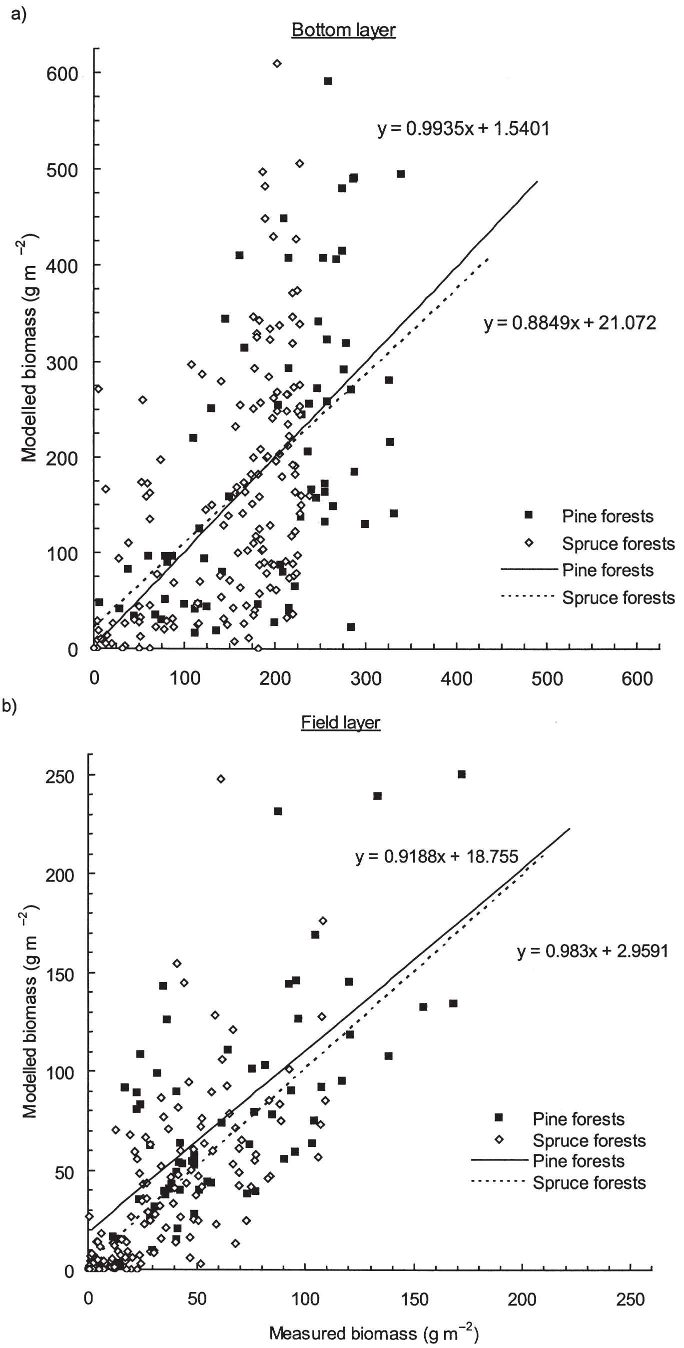


Fig. 2. Measured and modelled aboveground biomasses of understorey vegetation in upland soils.

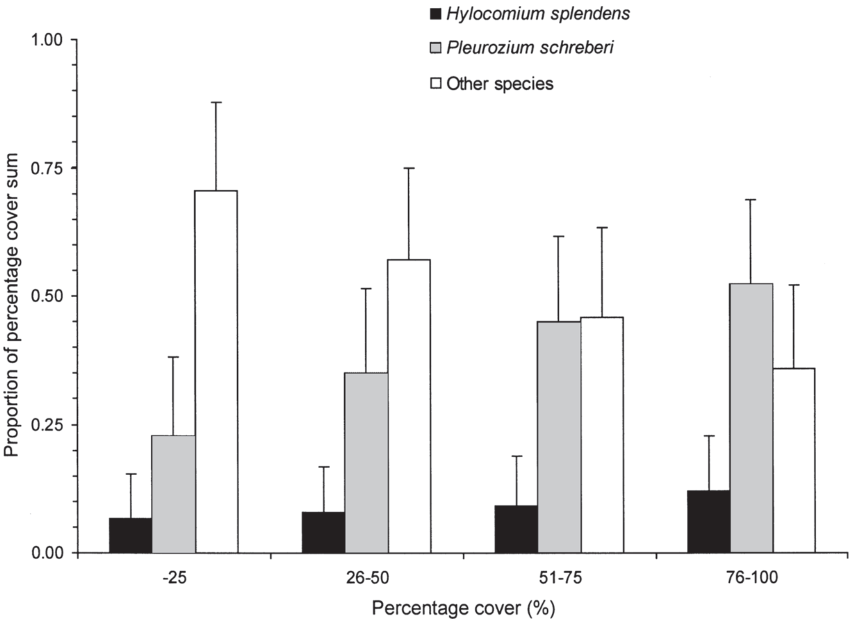


Fig. 3. Proportion of bottom layer species in upland soils according to the total percentage cover of the bottom layer.

The residuals demonstrated that the models developed resulted in unbiased estimates of the aboveground biomass of upland sites, according to the percentage cover (Fig. 4). Although residual clouds showed heteroskedastic phenomena, transformations could not be done since the zero values of the dependent variable are needed to describe the nature of the relationship between the percentage cover and the aboveground biomass of understorey vegetation.

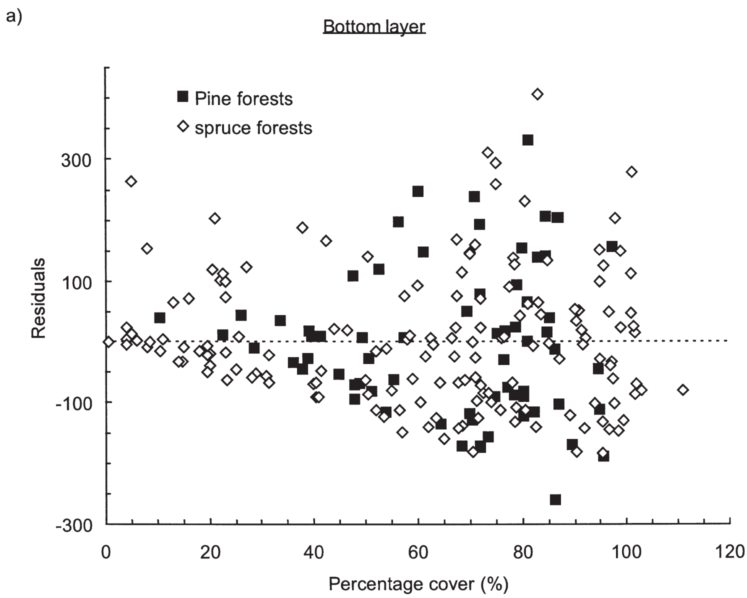
The models of the aboveground biomass of peatland understorey vegetation were predicted using Eq. 1 (Table 5, Figs. 5 and 6). The relationship between percentage cover and biomass of the understorey vegetation was weaker on the pine mires and on the drained peatlands than on the hardwood-spruce mires and in the paludified forests (Fig. 6). Due to the low number of observations, it was impractical to fit the basic mixed nonlinear model (Eq. 1) to the field layer of drained peatland forests.

We also tested whether the available stand characteristics could be used together with the percentage cover to estimate the aboveground biomass of understorey vegetation in upland soils and peatlands. The use of such characteristics did not improve the statistical models.

4 Discussion

4.1 Developed Models and Comparison with Previous Studies

The models used to predict the aboveground biomass of the field layer in upland soils were similar to those previously developed by Kellomäki (1974, 1975), as shown in Figs. 1c and 1d. In addition, Kellomäki's (1974, 1975) models accounted for a noticeably lower biomass for the bottom layer than did the data and models of the present study (Figs. 1a, b). Kellomäki's (1974, 1975) equations were based on material from a single forest stand per forest site type (mesic, subxeric and xeric heath forests) (Cajander 1949), while our equations were based on more extensive data.



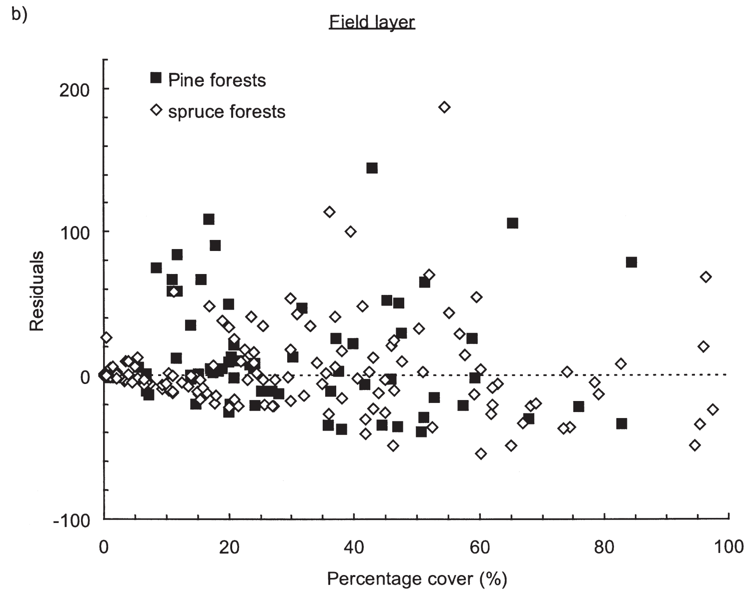
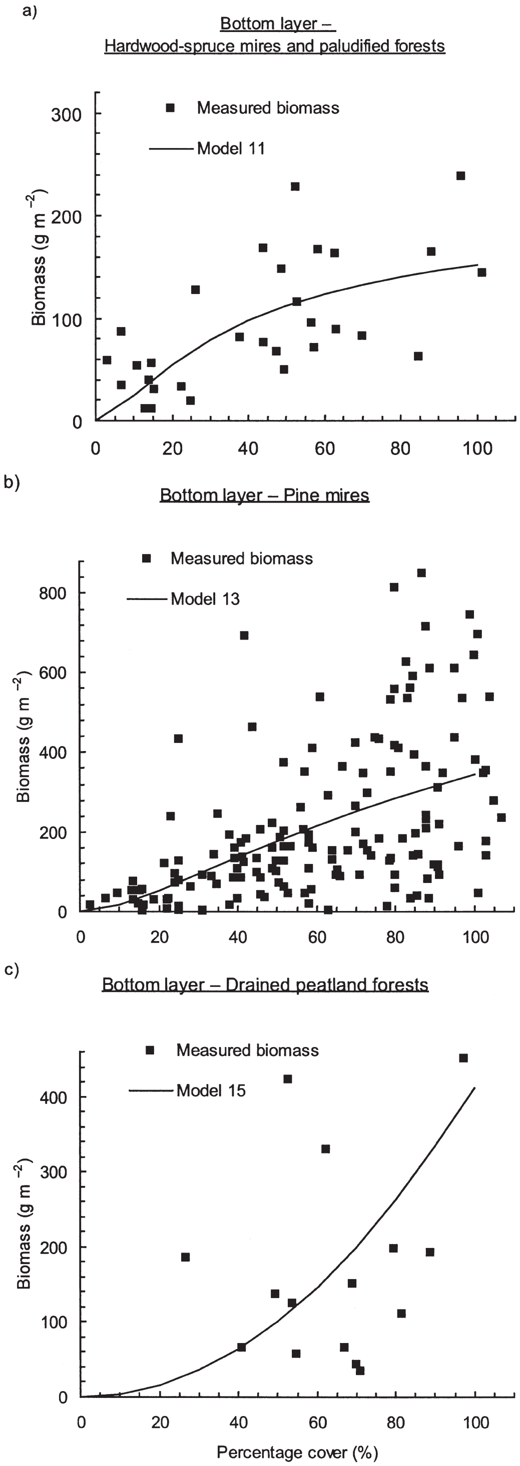


Fig. 4. Residuals of the models for predicting the aboveground biomass of understorey vegetation in upland soils.



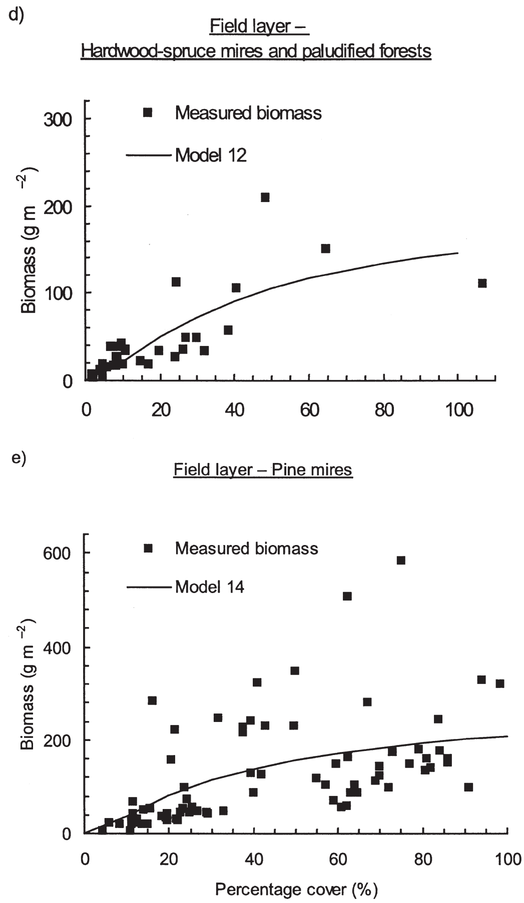
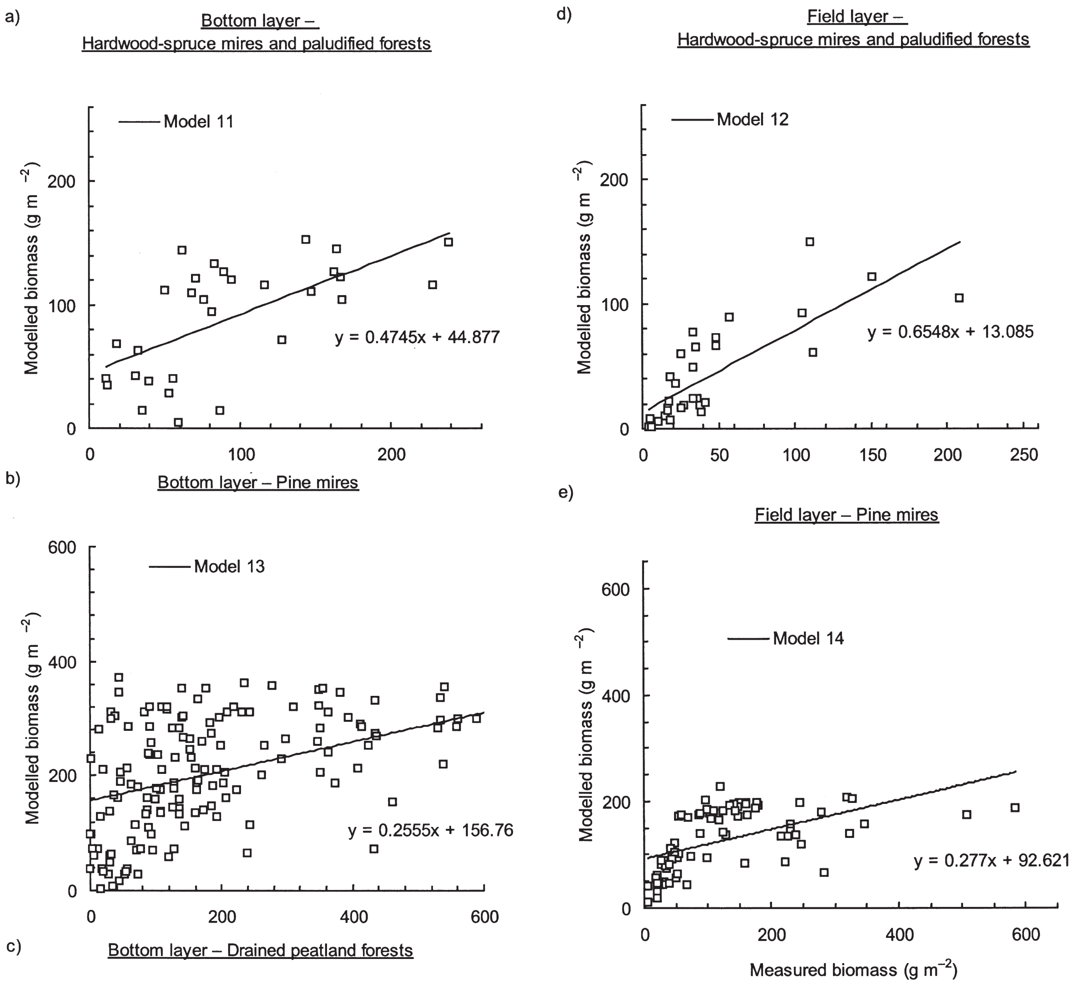


Fig. 5. Aboveground biomass of peatland understorey vegetation according to the percentage cover.



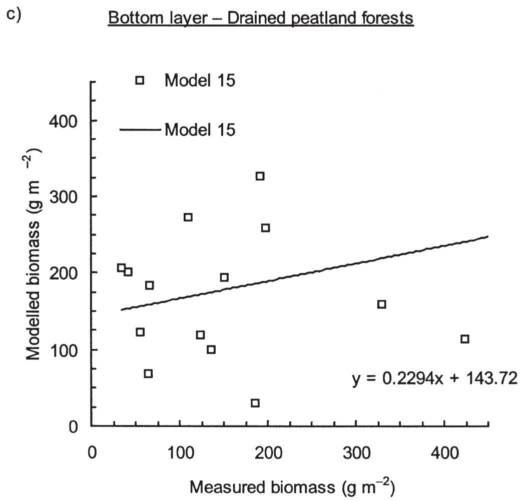


Fig. 6. Measured and modelled aboveground biomass of the peatland understorey vegetation.

Table 5. Aboveground biomass (y) (g m^{-1}) of peatland understorey vegetation predicted as a function of the percentage cover of species (x): Equation 1. The percentage cover used is the sum of the percentage covers for every species in each group.

Biomass of	n	β_0	S.E. of β_0	β_1	S.E. of β_1	
Hardwood-spruce mires and paludified forests						
Bottom layer	31	1.3322	2.9466	0.0677	0.0543	(Model 11)
Field layer	31	1.4817	1.7847	0.0678	0.0450	(Model 12)
Pine mires						
Bottom layer	155	2.1018	6.1126	0.0329	0.0796	(Model 13)
Field layer	76	1.0416	2.5221	0.0590	0.0490	(Model 14)
Drained peatland forests						
Bottom layer	16	5.0054	15.7592	–0.0008	0.1939	(Model 15)

Mattila (1981, 1988) developed several models to predict the aboveground biomass of some lichen and grass species in northern Finland, according to percentage cover and height. In addition, Kuusipalo (1983) produced models with different forms for estimating the aboveground biomass of *Vaccinium myrtillus* L. according to percentage cover and height. Kuusipalo (1983) reported that the percentage cover alone accounted for approximately 70% of the variation in aboveground biomass of *V. myrtillus*, while percentage cover and mean height together accounted for 80%. Kuusipalo (1983) concluded that increased growth with larger leaves, a greater amount of branches and thicker stems resulted in a mean increase in height that showed a curvilinear relationship with biomass. Although Mattila (1981) and Kuusipalo (1983) developed models with two factors, percentage cover and height, their results also indicated that percentage cover alone accounted for a substantial proportion of the variation in aboveground biomass. The applicability of their models is, however, limited since height is not a typically measured variable.

No models have previously been used to estimate the aboveground biomass of peatland understorey vegetation according to percentage cover. However, Reinikainen et al. (1984) estimated the proportion of the understorey biomass according to the total living aboveground biomass. In the present study, the use of stand variables (such as stand volume, basal area, stand age, fertility level) did not improve the models.

Although the results are based on a comparatively small dataset, they present clear evidence for the existence of relationships between plant cover and aboveground biomass within upland and peatland vegetation. The bottom layer on upland soils and understorey vegetation on peatlands showed curvilinear forms, at least partly because the species composition may change according to the total percentage cover (see Fig. 3). When the total percentage cover of such groups was low, species were small. In contrast, when the total percentage cover was higher, the major pleurocarpous species *P. schreberi* and *H. splendens* predominated in the higher total percentage cover, where they formed dense bryophyte layers. For the field layer of upland soils the equations are linear, since no clear change occurred in species composition as in the earlier case. The relationship between cover and biomass of single plant species is always constantly linear (e.g. Mattila and Helle 1978, Kuusipalo 1983, Alaback 1986, Alaback 1987, Mattila 1988, Röttgermann et al. 2000).

Specieswise analysis was not possible due to the limitations of the data. The data were compiled from different sources and the definitions for the surveying units varied widely; in one study the biomass was measured as a single species, while in an other it was measured separately only for the bottom and field layers.

When the percentage cover and the amount of biomass in the understorey vegetation are examined, the estimation is based on the results of a single sampling and thus shows the situation at that particular time. Changes in the biomass of woodland ecosystems occur both within the year and over the extended periods. Here we presented the situation during the last part of the growing season when both the species cover and biomass were assumed to be maximal.

4.2 Applicability of the Results

The relationships obtained can be used for rapid nondestructive determination of the aboveground biomass when direct biomass measurements are not available but the percentage cover of different plant species is recorded or can be recorded. Vegetation analyses that are based on estimation of the percentage cover of different species are widely available. In Finland, nationwide data with specieswise observation of percentage cover are available for understorey vegetation. Such data were collected in 1951–1953, 1985–1986 and 1995 from systematic networks of sample plots, covering the whole of Finland, that were established by the Finnish National Forest Inventory (Reinikainen et al. 2001, Mäkipää and Heikkinen 2003). Furthermore, the abundance of plant species can be estimated using nondestructive determination of cover by image-based analysis, as presented by Röttgermann et al. (2000).

The models developed can be applied to the conditions corresponding to those in the Boreal vegetation zone in Fenno-Scandia and Karelia. We modelled biomass as a function of species cover based on data that do not include very young or very old forest stands. The relationship between percentage cover and biomass is not, however, especially dependent on stand age, but instead on the morphology and growth characteristics of plant species and, most importantly, the specieswise dimensions of the plant and species composition, as discussed by Frank and McNaughton (1990).

In any season, the biomass of the belowground parts of the vegetation is substantially higher than that of the aboveground parts (Zavitkovski 1976, Kubícek and Simonovic 1982, Kubícek et al. 1994). The amount of belowground biomass of grasses, herbs and dwarf shrubs in coniferous forests was estimated to be twice as large as the maximum biomass of the aboveground parts during the growing season (Mälkönen 1974, Perina and Kvet 1975, Kubícek and Simonovic 1982, Havas and Kubin 1983, Kubícek et al. 1994).

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References

Alaback, P.B. 1986. Biomass regression equations for understory plants in coastal Alaska: effects of species and sampling design on estimates. Northwest Science 60(2): 90–103.

— 1987. Biomass-dimension relationships of understory vegetation in relation to site and stand age. In: Wharton, E. & Cunia, T. (eds.). Estimating tree biomass regressions and their error. Proceedings of the workshop. May 26–30, 1986. General Technical Report NE-117. USDA Forest Service, Syracuse, NY. p. 141–148.

Bonan, G.B., Pollard, D. & Thompson, S.L. 1992. Effects of boreal forest vegetation on global climate. Nature 359: 716–718.

Bråkenhielm, S. & Liu, Q. 1998. Long-term effects of clear-felling on vegetation dynamics and species diversity in a boreal pine forest. Biodiversity and Conservation 7: 207–220.

Cajander, A.K. 1949. Forest types and their significance. Acta Forestalia Fennica 56. 71 p.

Chapin, I.F.S. 1983. Nitrogen and phosphorus nutrition and nutrient cycling by evergreen and deciduous understory shrubs in an Alaskan black spruce forest. Canadian Journal of Forest Research 13: 773–781.

Chiarucci, A., Wilson, J.B., Anderson, B.J. & De Dominicis, V. 1999. Cover versus biomass as an estimate of species abundance: does it make a difference to the conclusions? Journal of Vegetation Science 10: 35–42.

Finér, L. 1989. Biomass and nutrient cycle in fertilized and unfertilized pine, mixed birch and pine and spruce stands on a drained mire. Acta Forestalia

Fennica 208. 63 p.
— , Mannerkoski, H., Piirainen, S. & Starr, M. 2003. Carbon and nitrogen pools in an old-growth, Norway spruce mixed forest in eastern Finland and changes associated with clear-cutting. Forest Ecology and Management 174: 51–63.
Fox, J.C., Ades, P.K. & Bi, H. 2001. Stochastic structure and individual tree growth models. Forest Ecology and Management 154: 261–276.
Frank, D.A. & McNaughton, S.J. 1990. Aboveground biomass estimations with the canopy intercept method: a plant growth form caveat. Oikos 57(1): 57–60.
Håland, B. 1994. Vegetasjon, biomasse mineralnæring og sirkulasjon i furuskog på myr. Botanical Institute, University of Bergen. Bergen. 37 p.
— & Brække, F.H. 1989. Distribution of root biomass in a low-shrub pine bog. Scandinavian Journal of Forest Research 4: 307–316.
Havas, P. & Kubin, E. 1983. Structure, growth and organic matter content in the vegetation cover of an old spruce forest in northern Finland. Annales Botanici Fennici 20: 115–149.
Helmisaari, H. & Helmisaari, H.-S. 1992. Long-term forest fertilization experiments in Finland and Sweden. Swedish Environmental Protection Agency. 123 p.
Hermy, M. 1988. Accuracy of visual cover assessments in predicting standing crop and environmental correlation in deciduous forests. Vegetatio 75: 57–64.
Hughes, M.K. 1970. Ground vegetation and forest litter production. In: Phillipson, J. (ed.). Methods of study in soil ecology: proceedings of the Paris symposium. Ecology and Conservation. UNESCO, Paris. p. 145–149.
Jonasson, S. 1988. Evaluation of the point intercept method for the estimation of plant biomass. Oikos 52: 10–106.
Kellomäki, S. 1973. Tallaamisen vaikutus mustikkatyypin kuusikon pintakasvillisuuteen. Silva Fennica 7(2): 96–113. (In Finnish).
— 1974. Metsän aluskasvillisuuden biomassan ja peittävyyden välisestä suhteesta. Silva Fennica 8(1): 20–46. (In Finnish).
— 1975. Havaintoja metsän aluskasvillisuuden biomassan ja peittävyyden välisestä suhteesta. Silva Fennica 9(1): 1–14. (In Finnish).
— & Väisänen, H. 1991. Application of a gap model for the simulation of forest ground vegetation in boreal conditions. Forest Ecology and Management 42: 35–47.
Kosonen, R. 1976. Ojituksen ja lannoituksen vaikutus isovarpuisen rämeen kasvibiomassaan, perustuotantoon ja kasvillisuuteen Jaakkoinsuon ojitusalueella Vilppulassa (PH). Metsäntutkimuslaitoksen suontutkimusosaston tiedonantoja 3/1976. 45 p. (In Finnish).
— 1981. Isovarpuisen rämeen kasvibiomassa ja tuotos. Suo 32(4–5): 95–97.
Kubícek, F. & Simonovic, V. 1982. Production analyses of the herbaceous layer in several fir communities, Spisska Magura mountains. Ekológia (CSSR) 1(4): 369–380.
— , Simonovic, V. & Somsák, L. 1994. Production-ecological parameters of the herb layer in coniferous forests. Ekológia (Bratislava) 13(2): 145–153.
Kuusipalo, J. 1983. Mustikan varvuston biomassamäärän vaihtelusta erilaisissa metsiköissä. Silva Fennica 17(3): 245–257. (In Finnish).
Laiho, R. 1996. Changes in understorey biomass and species composition after water level drawdown on pine mires in southern Finland. Suo 47(2): 59–69.
— & Laine, J. 1994. Nitrogen and phosphorus stores in peatlands drained for forestry in Finland. Scandinavian Journal of Forest Research 9: 251–260.
Laine, J. & Vasander, H. 1990. Suotyypit. Kirjayhtymä Oy, Helsinki. 80 p.
— & Vasander, H. 1996. Ecology and vegetation gradients of peatlands. In: Vasander, H. (ed.). Peatlands in Finland. Finnish Peatland Society, Helsinki. p. 10–20.
— , Vasander, H. & Laiho, R. 1995. Long-term effects of water level drawdown on the vegetation of drained pine mires in southern Finland. Journal of Applied Ecology 32: 785–802.
Lappalainen, E. & Hänninen, P. 1993. Suomen turvevarat. Geological Survey of Finland Report of Investigation 117: 1–118. (In Finnish).
Lindholm, T. 1981. Suppasuon kasviyhdyskuntien perustuotanto-ominaisuudet. Suo 32(4–5): 104–109. (In Finnish).
Mäkipää, R. 1994. Effects of nitrogen fertilization on the humus layer and ground vegetation under closed canopy in boreal coniferous stands. Silva Fennica 28(2): 81–94.
— 1998. Sensitivity of understorey vegetation to nitrogen and sulphur deposition in a spruce stand.

Ecological Engineering 10: 87–95.
— & Heikkinen, J. 2003. Large-scale changes in abundance of terricolous bryophytes and macrolichens in Finland. Journal of Vegetation Science 14: 497–508.
Mälkönen, E. 1974. Annual primary production and nutrient cycle in some Scots pine stands. Communicationes Instituti Forestalis Fenniae 84(5). 87 p.
Mattila, E. 1981. Survey of reindeer winter ranches as a part of the Finnish National Inventory in 1976–1978. Communicationes Instituti Forestalis Fenniae 99(6). 78 p.
— 1988. Suomen poronhoitoalueen talvilaitumet. Folia Forestalia 713. 53 p. (In Finnish).
— & Helle, T. 1978. Keskisen poronhoitoalueen talvilaidunten inventointi. Folia Forestalia 358. 31 p. (In Finnish).
Minkkinen, K., Vasander, H., Jauhiainen, S., Karsisto, M. & Laine, J. 1999. Post-drainage changes in vegetation composition and carbon balance in Lakkasuo mire, Central Finland. Plant and Soil 207: 107–120.
Mueller-Dombois, D. & Ellenberg, H. 1974. Aims and methods of vegetation ecology. John Wiley & Sons, New York. 547 p.
Perina, V. & Kvet, J. 1975. Vliv prosvetlení horské smrciny na tvorbu biomasy prízemního patra. Lesnictví 21: 659–687. (In Czech).
Reich, P.B., Buschena, C., Tjoelker, M.G., Wrage, K., Knops, J., Tilman, D. & Machado, J.L. 2003. Variation in growth rate and ecophysiology among 34 grassland and savanna species under contrasting N supply: a test of functional group differences. New Phytologist 157: 617–631.
Reinikainen, A. 1981. Metsänparannustoimenpiteiden vaikutuksesta suoekosysteemin kasvibiomassaan ja perustuotantoon. Suo 32(4–5): 110–113. (In Finnish).
— , Vasander, H. & Lindholm, T. 1984. Plant biomass and primary production of southern boreal mire-ecosystems in Finland. Proceedings of the 7th International Peat Congress, Dublin, Ireland 4: 1–20.
— , Mäkipää, R., Vanha-Majamaa, I. & Hotanen, J.-P. (eds.). 2001. Kasvit muuttuvassa metsäluonnossa. Finnish Forest Research Institute, Helsinki. 384 p. (In Finnish).
Röttgermann, M., Steinlein, T., Beyschlag, W. & Dietz, H. 2000. Linear relationship between aboveground biomass and plant cover in low open herbaceous vegetation. Journal of Vegetation Science 11(1): 145–148.
SAS Institute 1999. SAS System. SAS Institute Inc., Cary, NC, USA.
Solmari, H. 1986. Kasvillisuus ja maanpäällinen kasvibiomassa sekä -tuotos korpinäytealoilla ja turvekankailla Hämeessä. Department of Botany, Unversity of Helsinki. Helsinki. 76 p. (In Finnish).
— & Vasander, H. 1981. Neljän korpiyhdyskunnan kasvibiomassa ja tuotos. Suo 32(4–5): 97–99. (In Finnish).
Tappeiner, J.C. & Alm, A.A. 1975. Undergrowth vegetation effects on the nutrient content of litterfall and soils in red pine and birch stands in northern Minnesota. Ecology 56: 1193–1200.
Van Cleve, K. & Alexander, V. 1981. Nitrogen cycling in tundra and boreal ecosystems. In: Clark, F.E. & Rosswall, T. (eds.). Terrestrial nitrogen cycles. Ecological Bulletin, Stockholm. p. 375–404.
Vasander, H. 1981a. Keidasrämeen kasvibiomassa ja tuotos. Suo 32(4–5): 91–94. (In Finnish).
— 1981b. Luonnontilaisen keidasrämeen sekä lannoitetun ojikon ja muuttuman ravinnevarat. Suo 32(4–5): 137–141. (In Finnish).
— 1982. Plant biomass and production in virgin, drained and fertilized sites in a raised bog in southern Finland. Annales Botanici Fennici 19: 103–125.
Vuorinen, J., Jäppinen, J. & Kuusipalo, J. 1980. Pintakasvillisuus, biomassa ja tuotos. In: Pasanen, S. (ed.). Lannoituksen vaikutus ojitetun suon metsäekosysteemiin: tutkimusraportti vuodelta 1979. Department of Biology, University of Joensuu, Joensuu. p. 11–30. (In Finnish).
Yarie, J. 1980. The role of understory vegetation in the nutrient cycle of forested ecosystems in the mountain hemlock biogeoclimatic zone. Ecology 61(6): 1498–1514.
— & Mead, B.R. 1989. Biomass regression equations for determination of vertical structure of major understory species of Southeast Alaska. Northwest Science 63(5): 221–231.
Zavitkovski, J. 1976. Ground vegetation biomass, production, and efficiency of energy utilization in some northern Wisconsin forest ecosystems. Ecology 57(4): 694–706.

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