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The estimation of aboveground biomass and nutrient pools of understorey plants in closed Norway spruce forests and on clearcuts

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Abstract The estimation model PhytoCalc allows a non-destructive quantification of dry weight and nutrient pools of understorey plants in forests by using the relationship between species biomass, cover and mean shoot length. The model has been validated with independent samples in several German forest types and can be a useful tool in forest monitoring. However, in open areas within forests (e.g. clearcuts), the current model version underestimates biomass and produces unreliable nutrient pool estimations. Thus, tissue density, as approximated by leaf dry matter content (LDMC), is systematically higher under high light compared to low light conditions. We demonstrate that the ratio of LDMC under clearcut conditions to LDMC under forest conditions can be used to adjust the PhytoCalc model to clearcut conditions. We investigated the LDMC ratio of five exemplary species commonly occurring on clearcuts. Integrating the square of the ratio as a correction factor improved estimates of biomass to more than 70% fit between observations and predictions. Results also suggest this ratio can be used to correct nutrient concentrations modelled in PhytoCalc, which tend to be overestimated in clearcuts. As morphological groups of plant species exhibit significantly different ratios, we advise using group-specific correction factors for clearcut adjustments in the future.

Keywords PhytoCalc · Leaf dry matter content (LDMC) · Nutrient concentration · Plant morphological groups

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Introduction

With 1–2%, the contribution of the understorey vegetation to aboveground biomass in forest ecosystems is relatively low compared to the tree layer (Bolte et al. 2004; Gilliam 2007). However, as herbaceous plants have up to threefold higher nutrient concentrations than trees, the importance of the understorey vegetation for nutrient cycling is overproportionate to its biomass (Blank et al. 1980; Yarie 1980; Rodenkirchen 1995; Mrotzek 1998; Bolte et al. 2004; Muller 2003). Its importance even increases in disturbed systems such as clearcuts or windthrows, where the understorey vegetation becomes the most important ecosystem component in terms of primary production and nutrient uptake. Through changes in species composition, nutrient concentration and growth, the understorey vegetation can function as an important nutrient sink (Marks and Bormann 1972; Boring et al. 1981; Outcalt and White 1981; Fahey et al. 1991; Mellert et al. 1998; Bartsch 2000). However, the quantification of biomass and nutrient pools is very time-consuming and cost-intensive, as mainly destructive

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harvesting methods with many replicates are used. Furthermore, this approach cannot be used in protected areas and is not repeatable on the same plot, making such methods unfeasible for biomonitoring and permanent plot studies. Non-destructive estimation methods that use relationships between biomass and vegetation cover have been devised for several vegetation types (Siccama et al. 1970; Röttgermann et al. 2000; Muukkonen et al. 2006), but do not regard nutrient pools. Thus, intensive monitoring programs such as the European Level-II-network (Schulze et al. 2000; De Vries et al. 2003; Seidling 2005) have so far considered understorey vegetation only in terms of its indicator quality and contribution to forest biodiversity.

Enhancing an earlier approach by Kellomäki (1974), the PhytoCalc model was developed (Bolte 1999, 2006; Bolte et al. 2002) to estimate aboveground biomass and nutrient pools of the forest understorey based on cover and mean shoot length of plant species. Data from biomass harvests of 46 widespread species of beech, oak and Scots pine forests of north-eastern Germany and the low mountain ranges provided the basis for this model. Species data were aggregated into 13 morphological growth groups (main groups: herbs, graminoids, ferns, small shrubs, dwarf shrubs, mosses). For each growth group, non-linear regressions were developed to describe the relationship between aboveground biomass, species coverage and mean shoot length. In addition, during the model development species were joined to different element groups; these groups are characterised by similar nutrient concentrations within the aboveground plant organs, and consider as well the species morphology, taxonomy and site characteristics. Average nutrient concentrations of each element group were used to predict nutrient pools of plants per area by multiplicatively linking the estimated dry weight and the nutrient concentration.

PhytoCalc has been successfully validated on independent measurements in several German forest ecosystems (Mölder et al. 2008; Schulze et al. 2009). Mölder et al. (2008) found that predicted values differed by less than 10% from harvested dry weights in Hainich National Park (Thuringia), an area with broad deciduous forests rich in tree species. PhytoCalc is thus suited to measure biomass and nutrient pools of understorey vegetation in forest monitoring (Bolte et al. 2004; BMELV 2006; Bolte 2006; Schulze et al. 2009).

In disturbed areas with high irradiance levels, the model so far yielded inadequate results. Klinck and Fröhlich (2009) found that PhytoCalc strongly underestimated the aboveground biomass in small clearcuts of Norway spruce stands. This would suggest the establishment of a new model under these open field conditions which would require intensive harvesting operations. A shortcut solution could be the comprehension of tissue density. It is well known that plants in open areas form denser tissues (Meziane and Shipley 1999; Schulze et al. 2002) than in closed forests. Tissue density can be expressed by the leaf dry matter content (LDMC; Garnier and Laurent 1994; Wilson et al. 1999; Westoby et al. 2002); a plant trait easy to measure using only a small number of plant individuals (Cornelissen et al. 2003). In this study, we compare LDMC of understorey plant species under closed canopy and in 4-year-old clearcuts and demonstrate that the LMDC ratio can be used to correct the results of PhytoCalc in order to achieve reliable aboveground biomass estimations with estimation deviations close to those of the initial PhytoCalc model (Bolte 1999; Schulze et al. 2009). We investigated *Agrostis capillaris*, *Deschampsia flexuosa*, *Digitalis purpurea*, *Epilobium angustifolium* and *Rubus idaeus* as five frequent species in Norway spruce forests of Germany, that exhibit increased growth after disturbance. In particular, we focus on the following questions: (1) How reliably does PhytoCalc estimate dry weight, as well as nitrogen, phosphorus and potassium pools in the five species on clearcuts when compared to closed canopy conditions? (2) Can model predictions be improved by using the LDMC ratio as a correction factor under clearcut conditions? (3) Can specific correction factors for morphological plant groups be found?

Materials and methods

Study site

This study is part of a long-term forest conversion experiment (see Heinrichs and Schmidt 2009) and was carried out on four 1-ha clearcuts and in adjacent Norway spruce forest stands in the Solling hills, a low mountain range (up to 528 m above sea level) in the north-western part of Central Germany. Two clearcuts each were located at the study sites Otterbach (300 m a.s.l., mean annual precipitation 900 mm, mean annual temperature of 7.7°C) and Neuhaus (509 m, 1,050 mm, 6.5°C; Gauer and Aldinger 2005). The Solling is formed of Triassic sandstone covered with loess. Predominant are podzolic brown soils (Dystric Cambisols) with a low base saturation and a good water supply. C/N ratios are ca. 20 and the predominant humus form is humimor (Ellenberg et al. 1986; Scheffer and Schachtschabel 2002; Table 1). Amelioration liming containing magnesium was applied to both study sites in 1990, at Neuhaus also in 2001.

The clearcutting was conducted in the autumn of 2003. Four years after clearcutting, the plots received ca. 90% of the photosynthetic active radiation (PAR) above the herb layer, and were, among other species, covered by *R. idaeus*, *E. angustifolium*, *D. flexuosa* and *A. capillaris* (Heinrichs

Table 1 Mean soil parameters (±SE; 0–10 cm mineral soil) and the relative photosynthetic active radiation (PAR) measured above the herb layer on clearcuts and in surrounding closed forests at the study sites Neuhaus and Otterbach in the Solling hills

	pH	C/N ratio	N (mg g^{-1})	P (mg g^{-1})	K (mg g^{-1})	PAR (%)
Neuhaus						
Clearcut	3.48 (± 0.09)	19.16 (± 1.05)	2.56 (± 0.38)	0.60 (± 0.04)	0.06 (± 0.01)	95.20 (± 2.70)
Closed forest	3.37 (± 0.08)	19.80 (± 0.77)	2.87 (± 0.31)	0.62 (± 0.04)	0.06 (± 0.00)	11.10 (± 1.98)
Otterbach						
Clearcut	3.51 (± 0.07)	20.18 (± 1.05)	1.86 (± 0.36)	0.37 (± 0.04)	0.06 (± 0.01)	88.92 (± 3.62)
Closed forest	3.21 (± 0.05)	20.33 (± 0.50)	2.10 (± 0.29)	0.38 (± 0.02)	0.10 (± 0.02)	12.86 (± 3.34)

On each clearcut and forest plot soil values were obtained on four subplots à 100 m^2, PAR (in % of open field conditions) was measured on 20 subplots with LI-190 Quantum Sensors (Licor, Nebraska, USA) on overcast days with diffuse light conditions from July to September 2007; for each study site, two clearcuts and four forest plots were available

and Schmidt 2009; Table 1). The adjacent, around 100-year-old, Norway spruce plantations (Galio harcynici-Culto-Piceetum; Zerbe 1993) with a PAR of around 10% had an understorey dominated by *Dryopteris dilatata*, *Oxalis acetosella* and *Vaccinium myrtillus*, but *A. capillaris* and *D. flexuosa* were also frequent (Table 1).

Vegetation measurements, biomass harvest and nutrient analyses

Data for *D. purpurea* and *R. idaeus* were obtained from Klinck and Fröhlich (2009), a study conducted in the same study area. Data for *A. capillaris*, *D. flexuosa* and *E. angustifolium* were sampled as follows: On the clearcuts, 20 × 0.25-m^2 plots were chosen for the harvest of *A. capillaris* and *D. flexuosa*. For *E. angustifolium*, which had higher shoot lengths than the grasses, 20 × 1-m^2 plots were chosen for harvesting (Donita 1972). Plots were selected in order to achieve a wide range of cover values for each species, ranging from below 10% to more than 95%. In addition, for both grass species, 20 × 0.25-m^2 plots were chosen under closed canopy conditions. On each plot, the species mean shoot length was derived from the measurement of the elongated shoot length of 20 randomly chosen individuals. Extremely large or small individuals that did not represent the majority of plants on the plots were omitted, when more than 20 individuals were available, to avoid outlier effects. As *D. purpurea* was present mostly in flowering stems on all plots, mean shoot length measured on taller flowering individuals was used, to avoid underestimation (Klinck and Fröhlich 2009). Species cover was measured by applying image processing software (Adobe Photoshop CS3 10.0, Adobe Systems Inc.) to perpendicular photographs. The number of screen pixels occupied by a plant species was counted using the magic wand tool and related to the reference area marked by the wooden frame included in each image (Dietz and Steinlein 1996).

From 28 June 2007 to 8 August 2007, the aboveground biomass was harvested close to the soil surface, oven dried for at least 48 h at 60°C, and weighed. For nutrient analyses, an aliquot of the dried material was finely milled and analysed for total nitrogen (N, combustion in Carlo Erba Elemental Analyser), potassium (K, atomic absorption spectrometer) and phosphorus (P, colorimeter, Schlichting et al. 1995), the latter elements extracted by pressure digestion in 65% nitric acid. Due to the different liming regimes at both study sites, calcium and magnesium were not regarded in this study.

Estimation of LDMC

Leaf dry matter content (LDMC) was measured following the procedure proposed by Wilson et al. (1999): We calculated the ratio of dry weight divided by saturated wet weight (fresh plant material) on leaf samples from five individuals per species and stand type. In total, 15 species were regarded including the five harvested ones, whereby the leaf material was collected independently of biomass harvests. The investigated species were assigned to the following morphological growth groups: Small herbs (*Galium saxatile*, *Maianthemum bifolium*, *Trientalis europaea*), tall herbs (*D. purpurea*, *E. angustifolium*), grasses (*A. capillaris*, *Calamagrostis epigejos*, *D. flexuosa*, *Holcus mollis*), sedges and rushes (*Carex pilulifera*, *Juncus effusus*, *Luzula luzuloides*), small shrubs/dwarf shrubs (*Rubus fruticosus*, *R. idaeus*, *V. myrtillus*). In general, five leaves per individual were collected (except *M. bifolium*). For the small statured *G. saxatile*, with thin and small leaves, the whole aboveground plant material was considered.

For each species, the ratio of LDMC under clearcut to LDMC under forest condition was calculated. Out of these species-specific ratios, a mean ratio per growth group was calculated.

Biomass and nutrient pool estimation with PhytoCalc

The current calibration of the PhytoCalc model is based on biomass harvests of 46 forest species of Germany's north-eastern lowlands and low mountain ranges. As shown in formula (1), the aboveground dry weight ($DW_{predicted}$) of a species is modelled as a function of percentage cover (C) and mean shoot length (SL):

$$DW_{predicted} = aC^{b}\,SL^{c} \quad (1)$$

Based on 1,700 data records of 46 species, Bolte (2006) fitted regression coefficients *a*, *b* and *c* for 13 different morphological growth groups. Iteratively, the combination of coefficients was determined representing the least residual sum of squares and the highest non-linear coefficient of determination (R^2; Table A1; Supplementary material).

Based on measured element concentrations, the 46 species were assigned to 11 element groups with similar nutrient concentrations in aboveground organs (Bolte et al. 2002). For each element group, average nutrient concentrations were determined (NC_{EG}), which are the basis for nutrient pool estimations (Table A2; Supplementary material). Multiplying these average values by predicted dry weight determined for the constituent species (2) yields an estimate of the standing nutrient pool ($NP_{predicted}$):

$$NP_{predicted} = DW_{predicted}\,NC_{EG}\,10^{-3} \quad (2)$$

To compute dry weights and nutrient pools in this study, we applied the parameters for the growth groups small grasses (*D. flexuosa*), middle grasses (*A. capillaris*), tall herbs (*D. purpurea*, *E. angustifolium*) and small shrubs (*R. idaeus*), and for the element groups nutrient-poor grasses (*A. capillaris, D. flexuosa*), nutrient-poor herbs (*D. purpurea*, *E. angustifolium*) and *Rubus*-shrubs (*R. idaeus*).

PhytoCalc under clearcut situations

We computed separate regressions of the dependent variable aboveground dry weight of *A. capillaris* and *D. flexuosa* against the independent variables cover and mean shoot length in closed Norway spruce forests and on clearcuts, respectively. The influence of shoot length on biomass is adequately modelled by one power function across forests and clearcuts, whereas regressions of species cover against dry weights resulted in quite similar powers (but see *D. flexuosa*) across stand types but in higher slopes under clearcut conditions (Fig. 1). This implies a poor performance of PhytoCalc with parameters calibrated in forests under clearcut conditions. Thus, the performance was tested by contrasting observed and predicted dry weights.

Above-mentioned regressions suggest that the linear integration of one factor, which can account for the steeper

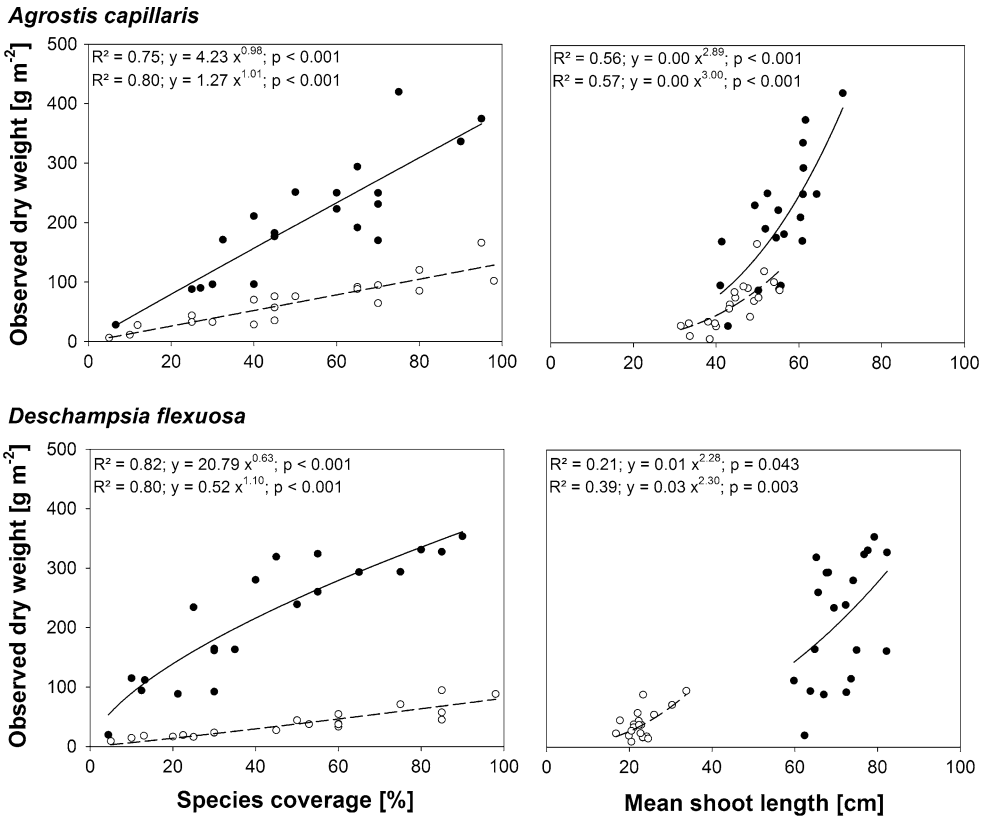

Fig. 1 Bivariate regressions of observed aboveground dry weight against cover and mean shoot length of *A. capillaris* and *D. flexuosa*, sampled on plots in closed Norway spruce forests (*open circle*) and on clearcuts (*filled circle*)

relationship between cover and biomass on clearcuts, into PhytoCalc might be sufficient in order to achieve reliable dry weight estimations. Such step could make a refitting of allometric functions used by PhytoCalc unnecessary. Thus, the calculated LDMC ratios between clearcut and forest conditions were established as correction factors (CF) for the five species investigated exemplarily.

To optimise the integration of CF in PhytoCalc, we multiplicatively linked the CF to Eq. (1) and performed a non-linear regression, which determined the β value that resulted in the least residual sum of squares. A regression coefficient of $\beta = 1$ would offer a simple multiplication of $DW_{predicted}$ with CF as shown in formula (3). A $\beta \neq 1$ would point to the need for further adaptations of formula (3) to achieve reliable dry weight predictions.

$$DW_{observed} = aC^{b}\,SL^{c} = DW_{predicted}\,CF^{\beta} \quad (3)$$

According to formula (2), reliable nutrient pool estimations depend, beside reliable dry weight estimations, also on adequate element group concentrations used by PhytoCalc, which should reflect observed nutrient concentrations in the field. Thus, we compared nutrient concentrations observed in closed forests and on clearcuts with nutrient concentrations of the element groups using a one-sample *t*-test. In addition, to analyse whether the integration of the CF into nutrient pool estimations would improve estimation results, a non-linear regression using CF as covariable was calculated between observed and predicted nutrient pools ($NP_{observed} = NP_{predicted}\ CF^{\beta} = DW_{predicted}\ NC_{EGpredicted}\ 10^{-3}\ CF^{\beta}$). A regression coefficient of $\beta = 0$ would make a correction of the used nutrient concentration unnecessary. A $\beta \neq 0$ would indicate a further correction of the used nutrient concentrations for the different element groups in PhytoCalc.

All observed values and their corresponding predicted values were compared calculating R^2 out of the variation around unity, which marks total identity of observed and predicted values.

Differences between group-specific CFs were analysed by the Kruskal–Wallis test. As the sample size for the growth groups was too small no post hoc test was performed.

All statistical analyses were conducted using R 2.8.1 (R Development Core Team 2008). Results were assumed to be significant at $P < 0.05$.

Results

Influence of the study site

Among the studied species only *E. angustifolium* had been harvested at both study sites. The fact that there were no significant differences in nutrient concentrations between the sites (N: $t = -0.84$, $P = 0.41$; P: $t = 1.97$; $P = 0.07$; K: $t = 2.09$, $P = 0.06$) indicates that pooling nutrient measurements was justified.

Performance of PhytoCalc on clearcuts: dry weight

PhytoCalc had been calibrated under closed canopy conditions; consequently, the usage of the growth group-specific functions resulted in close fits between predicted and observed dry weights (middle grass: *A. capillaris*, $R^2 = 0.79$; small grass: *D. flexuosa*. $R^2 = 0.89$). The maximum measured dry weights were 94.4 g m^{-2} for *D. flexuosa* and 165.8 g m^{-2} for *A. capillaris* compared to a maximum estimated value of 78.6 g m^{-2} and 139.0 g m^{-2}.

In contrast to this, the steeper allometric relations between dry weight and the cover value on clearcuts produced large underestimations of the dry weight when using the same functions for both species (Table A1; Fig. A1; Supplementary material).

For both grass species, as well as for *D. purpurea*, *E. angustifolium* and *R. idaeus*, the LDMC differed significantly between closed canopy and clearcut conditions (Table 2). The ratio between both LDMC values was therefore derived to function as a correction factor for PhytoCalc predictions on clearcuts. The CF was lowest for

Table 2 Mean $LDMC_{clearcut}$ and mean $LDMC_{forest}$ based on five individuals per species and stand type, results of the Student's *t*-test comparing both values, and the calculated correction factor (CF)

	$LDMC_{clearcut}$	$LDMC_{forest}$	*t*	*P* value	CF
Agrostis capillaris	0.37	0.23	10.67	<0.001	1.61
Deschampsia flexuosa	0.37	0.24	10.39	<0.001	1.54
Digitalis purpurea	0.29	0.17	6.77	<0.001	1.71
Epilobium angustifolium	0.35	0.15	20.42	<0.001	2.33
Rubus idaeus	0.46	0.34	7.10	<0.001	1.35

CF was calculated as the ratio of $LDMC_{clearcut}$ to $LDMC_{forest}$

Table 3 Estimated β coefficients, their standard error (SE) and *P* value from non-linear regressions of observed against predicted dry weights on clearcuts using the CF as a covariable based on 20 studied plots per species

	β	SE	*P* value
Agrostis capillaris	1.96	0.08	<0.001
Deschampsia flexuosa	2.48	0.18	<0.001
Digitalis purpurea	2.42	0.11	<0.001
Epilobium angustifolium	1.78	0.07	<0.001
Rubus idaeus	2.40	0.18	<0.001

Table 4 Coefficients of determination resulting from contrasting observed dry weights with either uncorrected predicted values obtained from PhytoCalc or with predicted values corrected by multiplication with CF^2

	Morphological group	Predicted dry weight	
		Uncorrected	Corrected with CF^2
Agrostis capillaris	Middle grass	0.00	0.88***
Deschampsia flexuosa	Small grass	0.00	0.93***
Digitalis purpurea	Tall herb	0.00	0.63***
Epilobium angustifolium	Tall herb	0.00	0.76***
Rubus idaeus	Small shrub	0.35**	0.89***

The morphological group to which each species is assigned to indicates the applied regression function according to Table A1 (Supplementary material)

*** $P \leq 0.001$; ** $P \leq 0.01$, $n = 20$ plots per species

the small shrub *R. idaeus* and highest for *D. purpurea* and *E. angustifolium*. The two grass species showed intermediate values.

Regression analyses of observed against predicted dry weights using the CF as covariable resulted in coefficients β differing all significantly from 0, and ranging from 1.78 for *E. angustifolium* to 2.48 for *D. flexuosa* (Table 3). This indicated to include the CFs in its quadratic term into PhytoCalc by a simple multiplication when used on clearcuts. Such CF integration resulted in significant determination coefficients of 0.63 for *D. purpurea* to 0.89 for *R. idaeus* when contrasting observed and predicted dry weight values and brought the regression slope of each species close to unity, whereas the usage of uncorrected values did not allow the calculation of determination coefficients around unity in most cases (Table 4; Fig. 2a vs. b).

Considering all species together, a comparison between predicted dry weights corrected using CF^2 and observed dry weights resulted in a significant R^2 of 0.77. The linear regression equation of this comparison forced through the origin was $DW_{observed} = 0.995\ DW_{predicted}$ with a residual standard error of 0.027. The slope was not significantly different from unity ($t = -0.180$, $P = 0.857$).

Performance of PhytoCalc on clearcuts: nutrient pools

Beside adequately predicted dry weights, reliable nutrient concentrations of element groups used within PhytoCalc are necessary for nutrient pool predictions. N concentrations of *A. capillaris* and *D. flexuosa* observed under closed canopy were higher than the according element group concentration. For *D. flexuosa*, this was also the case for K (Fig. 3). However, determination coefficients, when contrasting observed nutrient pools and predicted nutrient pools, were all significant and ranged from 0.66 for the nitrogen pool of *A. capillaris* to 0.82 for the phosphorus pool of *D. flexuosa* (Table 5). On clearcuts, though, nutrient concentrations of harvested plants were significantly lower for all species (except for the K- and P-concentrations of *Rubus idaeus*) than PhytoCalc concentrations (Fig. 3). Consequently, when contrasting observations and

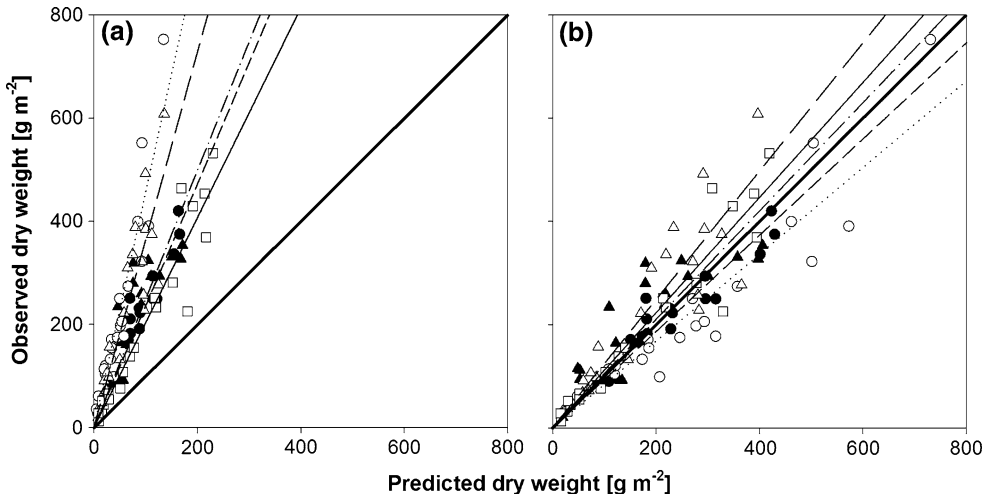

Fig. 2 Modelled vs. observed dry weights on clearcuts for (*filled circle*) *A. capillaris*, (*filled triangle*) *D. flexuosa*, (*open triangle*) *D. purpurea*, (*open circle*) *E. angustifolium* and (*open square*) *R. idaeus*; **a** using the uncorrected PhytoCalc model, **b** using the model corrected by multiplication with CF^2; Regression lines are given for each species (*A. capillaris*: *short dash*; *D. flexuosa*: *dash dot*; *D. purpurea*: *long dash*; *E. angustifolium*: *dotted*; *R. idaeus*: *solid line*). The *thick solid line* represents unity; the degree of tilting from unity in **a** is proportional to LDMC ratios (*A. capillaris*: 1.61; *D. flexuosa*: 1.54; *D. purpurea*: 1.71; *E. angustifolium*: 2.33; *R. idaeus*: 1.35); R^2 values out of the variation around unity are given in Table 4

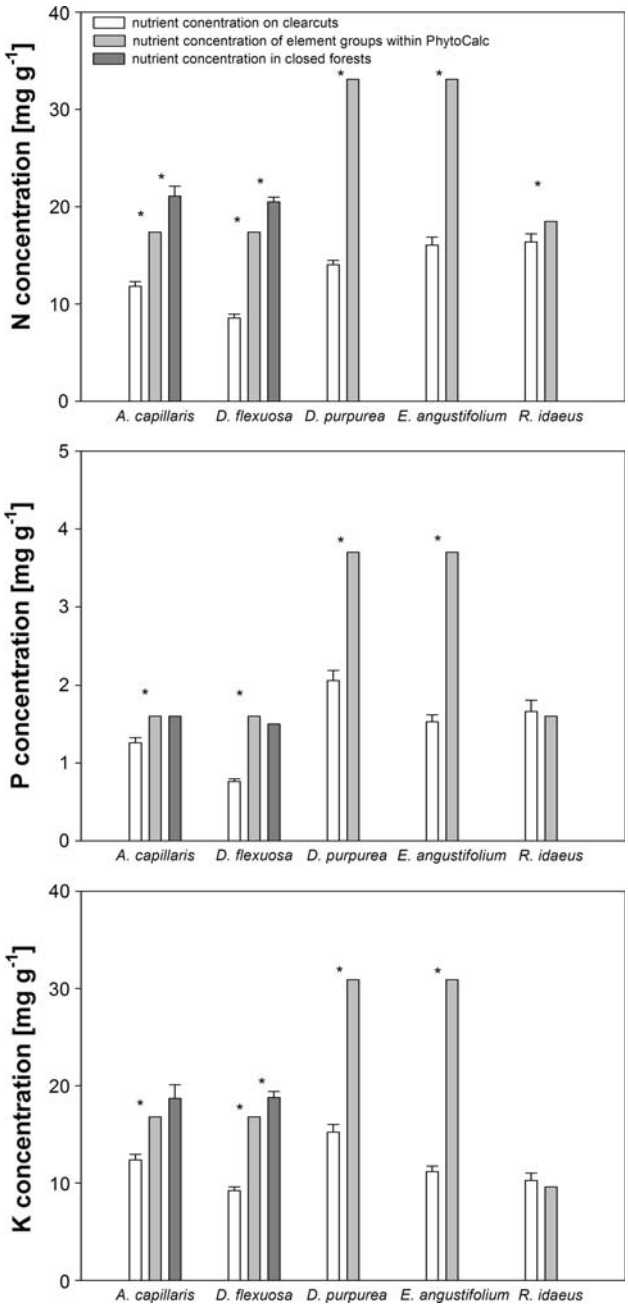

Fig. 3 Observed nutrient concentrations in closed Norway spruce stands for *A. capillaris* and *D. flexuosa* and on clearcuts for both grasses, *D. purpurea*, *E. angustifolium* and *R. idaeus* in comparison with element group concentrations applied by PhytoCalc for these species; * indicates significant differences between observed nutrient concentration determined on 20 plots and element group concentration based on one-sample *t*-test; observe the different vertical axis scale for the P concentration

predictions, determination coefficients were low in most cases (Table 5). A regression analysis of observed against predicted nutrient pools using the CF as covariable resulted in β coefficients significantly different from 0 for *A. capillaris*, *D. flexuosa*, *D. purpurea*, and *E. angustifolium* (Table 6). The results indicate to correct the nutrient concentration implemented within PhytoCalc by multiplication with CF^{-1}. This correction resulted in higher determination coefficients for all species (except *R. idaeus*) than the usage of uncorrected concentrations (Table 5). The determination coefficients ranged from 0.65 to 0.88 for N, 0.48–0.80 for K, and 0.58–0.77 for P. *D. flexuosa*, however, showed lower values.

Morphological group-specific correction factors

The tall herbs, *D. purpurea* and *E. angustifolium*, disclosed in general larger differences between observed nutrient concentrations and element group concentrations than the other species (Fig. 3). This is in accordance with the highest CF found for the growth group of tall herbs. Small herbs, as well as sedges and rushes showed the smallest values, whilst the group of small and dwarf shrubs depicted an intermediate value (Table 7). The importance of growth group-specific CFs was verified by the Kruskal–Wallis test ($\chi^2 = 10.38$, $df = 4$, P value $= 0.034$), which showed a significant difference between growth groups despite the small sample size.

Discussion

PhytoCalc performance under closed canopy conditions

In closed Norway spruce forests of the Solling the model PhytoCalc estimated reliable aboveground dry weights for *A. capillaris* and *D. flexuosa*, consistent with results of Höhne (1962), Höhne et al. (1981) and Bolte (1999) in temperate coniferous and deciduous forests. A good fit was also found when contrasting observed and predicted N-, P- and K-pools, although observed N and K concentrations were higher than concentrations applied by PhytoCalc. *A. capillaris* and *D. flexuosa* are typical species of infertile sites with low nitrogen concentrations (1–2% N) compared to other grasses colonising more nutrient rich sites (e.g. *Brachypodium sylvaticum*, *Melica uniflora*: 2.5–3.3% N) or compared to herbs having in general higher nutrient concentrations (Höhne 1962). In the Solling, though, the soils show a better nitrogen supply than soils in Germany's north-east, where the main part of datasets used for the PhytoCalc calibration was sampled. This is to some extent caused by higher nitrogen depositions in the Solling compared to north-east Germany (Gauger et al. 2001). Nevertheless, the measured concentrations are in accordance with other studies (Höhne 1962, 1963; Bennert 1980; Chapin 1980; Höhne et al. 1981). In general, nutrient concentrations of species are species traits (however, traits with a

Table 5 Coefficients of determination of the comparisons of observed against predicted nutrient pools under closed forests and on clearcuts for each species

Nutrient concentration within PhytoCalc	Element group	Closed forest			Clearcut		
		N	P	K	N	P	K
Agrostis capillaris	Nutrient-poor grass						
Uncorrected		0.66***	0.81***	0.72***	0.00	0.62***	0.37**
Corrected		ND	ND	ND	0.88***	0.67***	0.76***
Deschampsia flexuosa	Nutrient-poor grass						
Uncorrected		0.75***	0.82***	0.79***	0.00	0.00	0.00
Corrected		ND	ND	ND	0.31*	0.00	0.44**
Epilobium angustifolium	Nutrient-poor herb						
Uncorrected		ND	ND	ND	0.00	0.00	0.00
Corrected		ND	ND	ND	0.75***	0.77***	0.48**
Digitalis purpurea	Nutrient-poor herb						
Uncorrected		ND	ND	ND	0.00	0.17	0.00
Corrected		ND	ND	ND	0.65***	0.58***	0.70***
Rubus idaeus	*Rubus* shrub						
Uncorrected		ND	ND	ND	0.84***	0.84***	0.96***
Corrected		ND	ND	ND	0.80***	0.64***	0.91***

For the prediction on clearcuts, either the uncorrected nutrient concentrations implemented within PhytoCalc or the same nutrient concentrations corrected by multiplication with CF^{-1} were used. The assignment of the species to the element group indicates, which concentrations were used for prediction according to Table A2 (Supplementary material)

*** $P \leq 0.001$; ** $P \leq 0.01$; * $P \leq 0.05$, *ND* not defined, $n = 20$ plots per species

Table 6 Estimated β coefficients, their standard error (SE) and P value from non-linear regressions of observed against predicted nutrient pools using the CF as a covariable, n = 20 plots per species

	N			P			K		
	β	SE	P	β	SE	P	β	SE	P
Agrostis capillaris	−0.880	0.085	<0.001	−0.593	0.118	<0.001	−0.727	0.122	<0.001
Deschampsia flexuosa	−1.205	0.179	<0.001	−1.275	0.204	<0.001	−0.940	0.191	<0.001
Digitalis purpurea	−1.194	0.130	<0.001	−0.735	0.142	<0.001	−0.946	0.131	<0.001
Epilobium angustifolium	−1.099	0.086	<0.001	−1.298	0.077	<0.001	−1.449	0.068	<0.001
Rubus idaeus	−0.084	0.209	0.693	0.339	0.245	0.183	−0.188	0.236	0.436

relative high plasticity), leading to higher differences in nutrient storage between different species or species groups than between sites (Höhne 1962; Thompson et al. 1997).

Performance of PhytoCalc on clearcuts: dry weight

Although PhytoCalc worked well under a closed Norway spruce canopy, it gave inadequate results on small-scale clearcuts for all analysed species as already shown by Klinck and Fröhlich (2009). The application of a simple linear transformation by using the presented LDMC ratio as a correction factor resulted in predicted dry weights of *A. capillaris*, *D. flexuosa*, *D. purpurea*, *E. angustifolium* and *R. idaeus* that explained 62–93% of the variance of observations. These predictions were consistent with biomass values found by different authors under high light availability for these species (van Andel 1975; Al-Mufti et al. 1977; van Baalen and Prins 1983; Fahey et al. 1991). Differences in biomass or growth performance under different light regimes have been reported before for *D. flexuosa* (Scurfield 1954), *D. purpurea* (van Baalen and Prins 1983), *E. angustifolium* (Myerscough 1980) and *R. idaeus* (Ricard and Messier 1996), with all species showing maximum dry weights on open sites. This can be explained by a change in the leaf anatomy, as shown for the plasticity of LDMC: plants growing under high irradiance generally have a dense vascular system and a dense, often multilayered, mesophyll, leading to higher leaf dry weights compared to plants of the same species growing in shady conditions (Larcher 2001; Ricard and Messier 1996; Myerscough 1980). Meziane and Shipley (1999) and Shipley (2000) also showed that leaf traits of several

Table 7 Leaf dry matter content of understorey species on clearcuts and in closed forests assigned to different morphological groups and the calculated species-specific and morphological group-specific correction factors, LDMC values are based on five individuals per species

	Clearcut	Forest	CF
Small herbs			
Galium saxatile	0.25	0.22	1.14
Maianthemum bifolium	0.28	0.24	1.17
Trientalis europea	0.34	0.24	1.42
Growth group			1.24
Tall herbs			
Digitalis purpurea	0.29	0.17	1.71
Epilobium angustifolium	0.35	0.15	2.33
Growth group			2.02
Poaceae			
Calamagrostis epigejos	0.47	0.34	1.38
Holcus mollis	0.42	0.23	1.83
Agrostis capillaris	0.37	0.23	1.61
Deschampsia flexuosa	0.37	0.24	1.54
Growth group			1.59
Cyperaceae/Juncaceae			
Carex pilulifera	0.45	0.39	1.15
Juncus effusus	0.41	0.32	1.28
Luzula luzuloides	0.40	0.34	1.18
Growth group			1.20
Small shrubs/dwarf shrubs			
Rubus fruticosus	0.44	0.35	1.26
Rubus idaeus	0.46	0.34	1.35
Vaccinium myrtillus	0.46	0.35	1.31
Growth group			1.31

species change uniformly with irradiance: lamina and mesophyll thicknesses increased with light availability, whereas the leaf water content decreased. Garnier and Laurent (1994) presented a negative correlation of the leaf water content with the cross-sectional area occupied by vascular tissue and sclerenchyma, which increase with irradiance.

Other factors resulting in a larger dry weight under high irradiance can be a higher density of stems but with leaves covering a smaller area, a larger degree of overlaying vegetation components, or thicker stems, especially for species like *D. purpurea*. Compared to these factors, though, which can differ for each study plot or only account for distinct species groups, the LDMC can be easily recorded for a larger area by sampling leaves from 5 to 10 individuals (Cornelissen et al. 2003) under the different light regimes. The difference in this plant trait can then be a successful correction tool for differences in density and quality of the plant tissue and consequently, the aboveground dry weight with varying environmental conditions, as shown in this study.

PhytoCalc performance on clearcuts: nutrient pools

Nutrient concentrations on clearcuts were lower than average element group concentrations used by PhytoCalc. This is in accordance with differences detected by Fahey et al. (1991) for *A. capillaris* and *D. flexuosa*, and by Högbom and Högberg (1991) and Palviainen et al. (2005) for *D. flexuosa* comparing clearcuts and closed forests.

As already mentioned earlier, under open site conditions leaf structure may change: high light availability increases leaf sclerophylly, which is negatively correlated with nutrient concentrations (Loveless 1961; Garnier and Laurent 1994). Furthermore, on clearcuts, plants invest more into stems; the proportion of leaves on the dry weight decreases (Scurfield 1954; van Baalen and Prins 1983). Compared to other plant organs, though, leaves store the largest amount of nutrients (mainly N, P, Ca, Mg, S; Höhne 1962; van Andel and Jager 1981; Larcher 2001). Consequently, also the nutrient concentrations used by PhytoCalc had to be adjusted to clearcut conditions. Non-linear regressions showed that the inverse of the correction factor, proposed in this study, is suited to adjust the nutrient concentration. This factor accounted for the reduced nutrient concentration due to a larger degree of sclerenchymatic tissue within leaves under high irradiance compared to low light values. However, for some species, especially *D. flexuosa*, this correction is not sufficient as predictions explained no variance of observations for P and only 31 and 44% for N and K, respectively. For this species the discrepancy regarding the existence of flowering stems between closed forest conditions and clearcuts is extremely severe (Scurfield 1954).

Besides the higher sclerophylly of leaves, other factors can as well account for lower nutrient concentrations and thus for the still unexplained variance of observed nutrient pools by corrected predictions: On clearcuts, stems can already show indications of lignification compared to forest conditions. K is preferentially stored in flowers and fruits, and not impoverished in stems; however, the leaching of this highly soluble element, due to higher amounts of rainfall reaching the plants on clearcuts, seems to be more important (Höhne 1962; Morton 1977; Larcher 2001). Furthermore, most of these species are growth-limited due to the low light availability under a closed canopy (Scurfield 1954; van Andel 1975; Al-Mufti et al. 1977; van Baalen and Prins 1983; Strengbom et al. 2004). Thus, under clearcut conditions growth is largely enhanced, although the amount of available nutrients might not increase at the same rate, despite a faster mineralisation after clearcutting. The consequence is a "dilution-effect"

within the plant biomass (Larcher 2001) characterised by a negative correlation between the nutrient concentration and the aboveground biomass as found by Mellert et al. (1998) and Steiner et al. (1998). The fact that forest residues were removed on the Solling plots after clearcutting, avoiding further release of nutrients from decomposing branches (Stevens and Hornung 1990), contributes as well to the "dilution-effect". Within *R. idaeus*, though, nutrient concentrations showed almost no difference between observations on clearcuts and concentrations of the corresponding element group. Ricard and Messier (1996) found no relative increase in stem compared to leaf biomass with increasing light intensity. Furthermore, woody species in general show a slower growth rate. The dwarf-shrub species *V. myrtillus*, for example, also showed constant nutrient concentrations when comparing clearcut and forest conditions (Altegrim and Sjöberg 1996; Palviainen et al. 2005). Thus, the plasticity of species under different environmental conditions seems to depend on specific morphological characteristics. Also CFs calculated for different morphological groups in this study were significantly different from each other. One explanation for the differences between these growth groups is generally that small plants grow in the shadow of taller plants; this is also true on clearcuts. Taller herbs, instead, are totally exposed to sun light. Grasses can dominate clearcuts and are therefore also found under full sunlight. Rushes and sedges have tougher leaves with a high sclerenchymatic content, even under forest conditions, explaining the smaller differences in LDMC between environmental conditions. The same is true for dwarf shrubs and small shrubs. Thus, it might be reasonable in the future to include one correction factor for each morphological growth group into PhytoCalc to apply this model to clearcut conditions. Thereby, some growth groups chosen in the present study differed from morphological growth groups used by Bolte (1999, 2006): we have considered all woody species together, but grasses and rushes/sedges were considered separately because of their differences in leaf physiology. However, the consideration of more species may lead to a finer differentiation than presently available.

Conclusions

PhytoCalc is an applicable model for estimating dry weight and nutrient pools of Central European forest communities. By integrating the variability of the easy determinable LDMC under different irradiance regimes as a linear correction factor, the model is also usable in open areas such as larger areas of windthrow or clearcuts. These are expected to occur more frequently in the future due to severe winter storms or during the conversion of Norway spruce stands into mixed stands. On open sites, LDMC accounts for a higher tissue density within species, as well as for lower nutrient concentrations compared to forest conditions, a consequence of the higher sclerophylly of leaves under high irradiance. Different morphological groups showed significantly different CFs, which suggests to integrate one correction factor per morphological group into PhytoCalc to adjust for open site conditions. The group-specific ratios detected here are, however, only based on a few number of species that were frequent at the Solling sites. Thus, a further integration of species being more frequent in other forest types is necessary as well as the integration of other study sites and forest types to achieve a standard correction factor that is generally applicable on clearcuts. Nevertheless, particular attention should be paid to species known to be able to become dominant during secondary succession after clearcut or windthrow as they will account for most of the biomass then.

However, here, only the extremes (closed canopy vs. full light availability) have been analysed, and the results cannot be transferred to situations in highly thinned forest stands, in forest gaps, at forest edges or on clearcuts where regenerating trees expand rapidly. Therefore, the reaction of plants to different levels of irradiance should be analysed along a gradient from low to high light availability. Thus, threshold values of light availability can be identified which indicate the necessity of a correction of estimated values. In addition, a regression function could be used as a correction factor emanating from plant reactions dependent on light availability.

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