



## Estimation of herbaceous biomass from species composition and cover

Irena Axmanová, Lubomír Tichý, Zuzana Fajmonová, Petra Hájková, Eva Hettenbergerová, Ching-Feng Li, Kristina Merunková, Martina Nejezchlebová, Zdenka Otýpková, Marie Vymazalová & David Zelený

### Keywords

Ellenberg indicator values; plant cover; plant height; productivity; species richness–productivity relationship

### Abbreviations

EIVs = Ellenberg indicator values

Received 7 December 2011

Accepted 7 February 2012

Co-ordinating Editor: Rasmus Ejrnaes

**Axmanová, I.** (Corresponding author, axmanova@sci.muni.cz), **Tichý, L.** (tichy@sci.muni.cz), **Hettenbergerová, E.** (eva.hette@seznam.cz), **Li, C.-F.** (woody@sci.muni.cz), **Merunková, K.** (merunkova@sci.muni.cz), **Nejezchlebová, M.** (malvinka@seznam.cz), **Otýpková, Z.** (zdenkao@sci.muni.cz), **Vymazalová, M.** (meri@seznam.cz) & **Zelený, D.** (zeleny@sci.muni.cz): Department of Botany and Zoology, Masaryk University, Kotlářská 2, CZ-611 37 Brno, Czech Republic  
**Fajmonová, Z.** (zuzkaroz@sci.muni.cz), **Hájková, P.** (buriana@sci.muni.cz): Department of Vegetation Ecology, Institute of Botany, Academy of Sciences of the Czech Republic, Lidická 25/27, CZ-602 00 Brno, Czech Republic

### Abstract

**Questions:** Biomass is an important ecological property, but its measurement is destructive and time-consuming and therefore generally missing for historical vegetation plots. Here we propose and test indirect estimation of herbaceous biomass using models based on easily obtainable variables, namely plant height and cover. We compare these models with Ellenberg indicator values for nutrients (*EIVs Nutrients*), which are sometimes used as an alternative measure of productivity.

**Location:** Czech Republic, western Slovakia.

**Methods:** Above-ground biomass (dry weight;  $\text{g m}^{-2}$ ) was regressed against the following explanatory variables: (1) *Cover  $E_1$* , total percentage cover of the herb layer visually estimated in the field; (2) *Biomass estimate-raw*, -*adjusted* and -*median*, calculated from plant covers and heights (according to a local flora); and (3) mean *EIVs Nutrients* calculated per plot. For the analyses, we used four data sets containing a total of 469 plots from different vegetation types: ‘Wet meadows’, ‘Dry grasslands’, ‘Fen–dry grassland transects’ and ‘Forest herb layer’. To test the applicability of different biomass estimates we chose an example of a species richness–productivity relationship in the ‘Wet meadows’ data set and describe differences in resulting patterns.

**Results:** Both cover of herb layer and calculated ‘biomass volumes’ were more accurate in predicting biomass dry weight than *EIVs Nutrients*. The best results were obtained from the *Biomass estimate-median* model that combines median stand height and total cover of the herb layer. *Cover  $E_1$*  showed relatively tight correlations with biomass, particularly in sparse vegetation, but was a rather poor predictor when cover values were high. This was especially noticeable in application of the *Cover  $E_1$*  model in analysis of the species richness–productivity relationship.

**Conclusions:** In contrast to biomass, cover of the herb layer has a fixed upper limit (100%), which may lead to misinterpretations in dense, structurally diverse vegetation. Most promising is the *Biomass estimate-median* method, which can be applied both to already sampled plots by calculating median height from average species heights according to local floras and to newly sampled plots using the median of plant heights measured in the field. Therefore, we propose it as a rapid, non-destructive alternative to biomass harvest.

### Introduction

Habitat productivity is one of the key factors determining species richness and composition of plant communities

(Grime 1979; Grace 1999). In temperate herbaceous vegetation, where the plants regrow new shoots every year, the annual productivity is reflected in the peak above-ground biomass. However, biomass harvesting is time demanding

and not always applicable due to its destructive nature. Therefore, it has often been replaced with various techniques of indirect biomass estimation (Catchpole & Wheeler 1992).

An indirect biomass estimation method is the point-intercept (Jonasson 1988), originally developed for plant cover assessment (Goodall 1952). The method is advantageous for repeatable measurements, but is extremely tedious and time consuming. Santillan et al. (1979) and Castle (1976) recommended the so-called rising-plate, a technique popular in forage research owing to relatively low cost and effort. However, it is negatively influenced by rain or trampling (Castle 1976) and not applicable on steeper slopes or in structurally diverse vegetation. Another device, an electrical capacitance meter (Fletcher & Robinson 1956; Vickery et al. 1980), has received strong criticism because the actual moisture content influences the obtained values (Catchpole & Wheeler 1992). Biomass estimates based on comparative analysis of light above the vegetation stand and light transmitted through the canopy are measured with more costly devices and expressed as the leaf area index (e.g. Walker et al. 1995) or the normalized difference vegetation index (e.g. Shippert et al. 1995).

Several studies reported a tight linear correlation between biomass and plant cover of individual species (e.g. Yarie 1980; Röttgermann et al. 2000) or biomass and cover of whole herbaceous communities (e.g. Hermy 1988; Gilliam & Turrill 1993). Therefore, one of the simplest and cheapest biomass estimates is the herb layer cover (Löbel et al. 2006; Muukkonen et al. 2006; Ewald 2008). However, the relationship between percentage cover and biomass is still not fully examined (Chiarucci et al. 1999). Especially in structurally diverse vegetation, it is inappropriate to ignore stand height, but there have been only a few attempts to create biomass estimations combining both plant cover and stand height (e.g. in boreal vegetation; Matilla 1981; Kuusipalo 1983).

Following Hill & Carey (1997), vegetation productivity in European studies is often expressed as the mean Ellenberg indicator values for nutrients (EIVs; Ellenberg et al. 1992). These can be easily calculated only from species composition and are therefore also applicable to already sampled data. However, EIVs have several limitations (Diekmann 2003): geographically restricted application, ordinal character, biased results if they are related to species composition (Zelený & Schaffers 2012) and, last but not least, their correlated nature (Chytrý et al. 2009). Despite all these problems, EIVs are very often used (e.g. Dzwonko 2001; Dupré et al. 2002; Cornwell & Grubb 2003), mainly because they provide simple and rapid estimates of environmental factors including productivity.

The main aim of our study is to develop simple models of indirect biomass estimation applicable to vegetation

plots already stored in existing databases (Dengler et al. 2011). At the same time, we also want to propose a fast and reasonably reliable non-destructive method of biomass estimation for new data sampling. We predict biomass dry weight using the following models: cover of herb layer (*Cover E<sub>1</sub>*), biomass volumes calculated from plant heights and their covers in the plot (*Biomass estimate-raw*, *-adjusted* and *-median* model) and Ellenberg indicator values for nutrients (*EIVs Nutrients*). The models are tested on four data sets from different vegetation types: 'Wet meadows', 'Dry grasslands', 'Fen-dry grassland transects' and 'Forest herb layer' (temperate deciduous forest). To demonstrate the applicability of our biomass surrogates, we chose an example of a species richness-productivity relationship in the 'Wet meadows' data set and describe differences in results obtained using different methods.

## Methods

### Data sampling

We compiled four data sets containing in total 469 vegetation plots from the Czech Republic and adjacent western Slovakia (Table 1), which include the main vegetation types of the Central European temperate zone: 'Wet meadows', 'Dry grasslands', 'Fen-dry grassland' transects and 'Forest herb layer'. All plots were sampled in homogeneous natural or semi-natural vegetation. The grassland vegetation was regularly mown except for extremely poor fens and low productive dry grasslands on shallow soils, the forest herb layer vegetation was unmanaged. Sites with recent disturbances or over-exploited sites were avoided.

The cover of all vascular species in the plots was originally estimated with the nine degree Braun-Blanquet scale (Westhoff & van der Maarel 1978). For the analyses we used the corresponding mean percentage values based on TURBOVEG (Hennekens & Schaminee 2001) and JUICE (Tichý 2002) default settings, but with decreased covers of *r* and *+* to obtain more realistic values: 0.1, 0.5, 3, 4, 8, 18, 38, 63 and 88%. Additionally, the total cover of the herb layer was visually estimated. In each plot, above-ground herbaceous biomass was harvested at the peak season of the particular vegetation type. Dry grasslands, wet meadows and fens were sampled in June–July, the forest herb layer from July to early August. To reflect actual productivity we sampled only biomass produced in that particular year, while woody parts of perennial species, standing dead biomass and litter were excluded. Biomass was sampled in one or more representative subplots within each vegetation plot; only in the case of the 'Fen-dry grassland transects' data set was the biomass clipped from the whole plot. Harvested biomass was oven-dried to a constant weight at 60–70 °C and weighed. As the subplot size differed among data sets, we used standardized dry weight (g) per 1 m<sup>2</sup> in the analyses.

**Table 1.** Data sets.

Data set (plot size), vegetation type, authors	Source	Biomass dry weight [g·m <sup>-2</sup> ]: min–max	Cover of herb layer [%]	No. of plots
Wet meadows (3 × 3 m) (spring fens, wet meadows) – Z. Fajmonová, P. Hájková	Rozbrojová & Hájek 2008; Hájková & Hájek 2003	47.0–1061.0	20–100	119
Dry grasslands (10 × 10 m and 4 × 4 m) (both basic and acidic types) – Z. Otýpková, K. Merunková, M. Nejezchlebová	Merunková K. & Otýpková Z. unpubl.; Nejezchlebová M. unpubl.	2.0–553.6	7–95	154
Fen–dry grassland transects (0.25 × 0.25 m) (transects from spring fens to dry grasslands) – E. Hettenbergerová	Schamp et al. 2011	92.8–833.6	20–100	131
Forest herb layer (10 × 10 m) (oak, oak–hornbeam, ravine and alluvial forests) – I. Axmanová, D. Zelený, C.-F. Li, M. Vymazalová	Axmanová et al. 2011, 2012	3.3–286.8	7–95	65

### Data analysis – biomass models

Above-ground biomass (dry weight, g·m<sup>-2</sup>) was related by linear regression (ordinary least squares regression) to the following explanatory variables:

1. *Cover E<sub>i</sub>*: Total percentage cover of herb layer visually estimated in the field.
2. Calculated ‘biomass volumes’ based on plant heights and their percentage cover in the plot. Mean heights were assigned to each species from the local flora (Kubát et al. 2002), calculated from minimum to maximum range of plant heights.

*Biomass estimate-raw*: Sum of species heights multiplied by their covers in the plot; *n* denotes number of species in the plot. This model does not consider the overlap of species covers.

$$\sum_{i=1}^n \text{Species height}_i * \text{Cover}_i$$

*Biomass estimate-adjusted*: Sum of species heights multiplied by their cover in the plot, additionally adjusted for total estimated herb layer cover per plot. The correction was used to reduce the problem of biomass overestimation when neglecting the species overlap.

$$\left( \sum_{i=1}^n \text{Species height}_i * \text{Cover}_i \right) * \left( \text{Cover of herb layer} / \sum_{i=1}^n \text{Cover}_i \right)$$

*Biomass estimate-median*: Median of plant heights multiplied by total estimated herb layer cover per plot. We used median instead of mean to minimize the effect of the outlier values.

Stand median height \* Cover of herb layer

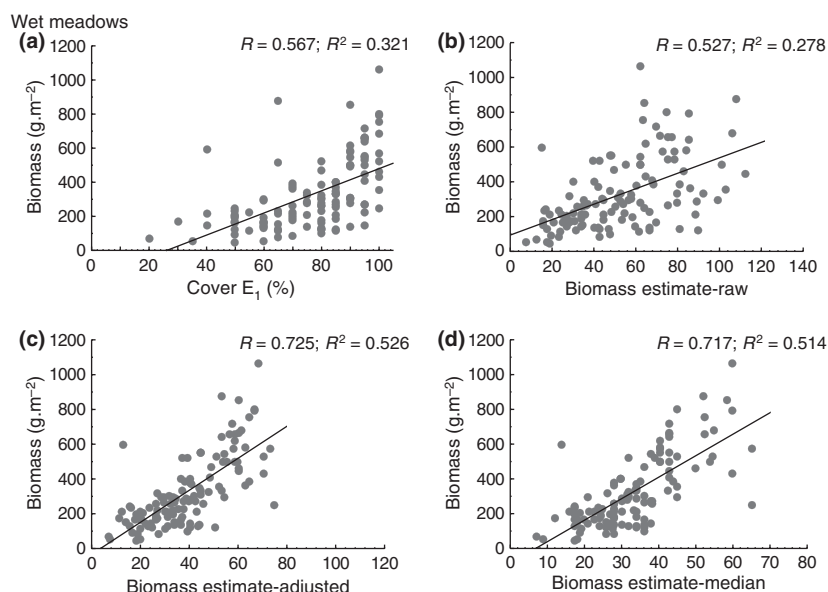
3. *EIVs Nutrients*: Unweighted mean Ellenberg indicator values for nutrients calculated per plot (Ellenberg et al. 1992).

The goodness of fit in regression models was expressed as coefficient of determination ( $R^2$ ), which can be interpreted as explained variation. Note that  $R^2$  might be affected by gradient length (see Davies & Fearn 2006), therefore, we compare  $R^2$  only among different models within a single data set, because direct comparisons among data sets might lead to misinterpretations. ‘Biomass volumes’ (*Biomass estimate-raw*, *-adjusted* and *-median*) and mean Ellenberg indicator values (*EIVs Nutrients*) were calculated using the JUICE 7.0 software (Tichý 2002). Linear regression models and Pearson’s correlations were computed using the STATISTICA 9.1 software (<http://www.statsoft.com>).

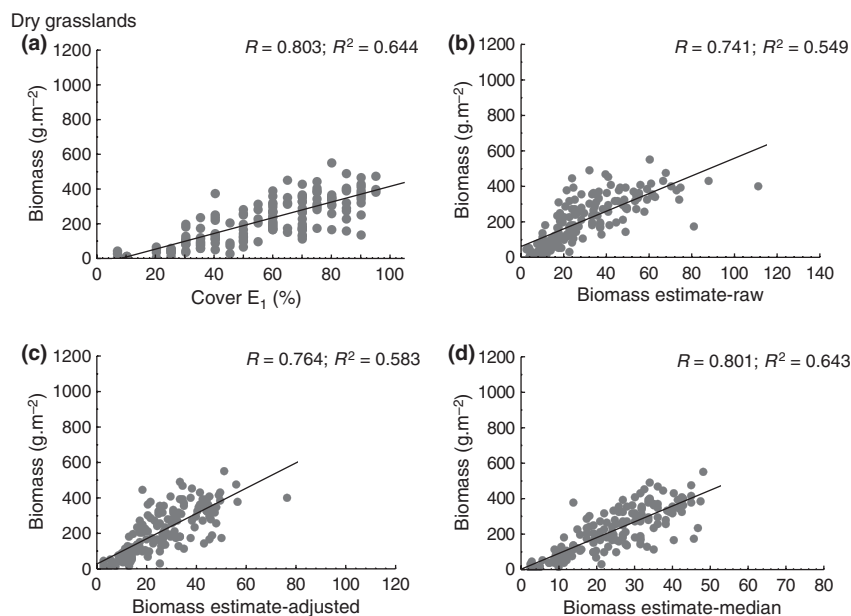
To elucidate the advantages and disadvantages of different biomass estimates, we applied them to express the species richness–productivity relationship in the ‘Wet meadows’ data set, which covered the longest productivity gradient among our data sets (Table 1), spanning from nutrient-poor fens to highly productive wet meadows. The species richness was expressed as the number of species in the herb layer. Although species richness might be co-determined by other factors apart from productivity (see e.g. Grace 1999), our intention was only to test whether the pattern found for biomass itself would be the same when using biomass models (*Cover E<sub>i</sub>*; *Biomass estimate-raw*, *-adjusted* and *-median*; *EIVs Nutrients*). We tested both the linear and quadratic model in each case and compared the results with the patterns found for biomass dry weight. The unimodal model was considered appropriate when the inclusion of a quadratic term into the model significantly increased the amount of explained variation compared to the linear model (details not shown).

### Results

All models showed a significant linear relationship with harvested biomass (Figs 1–4). Cover of the herb layer (*Cover*



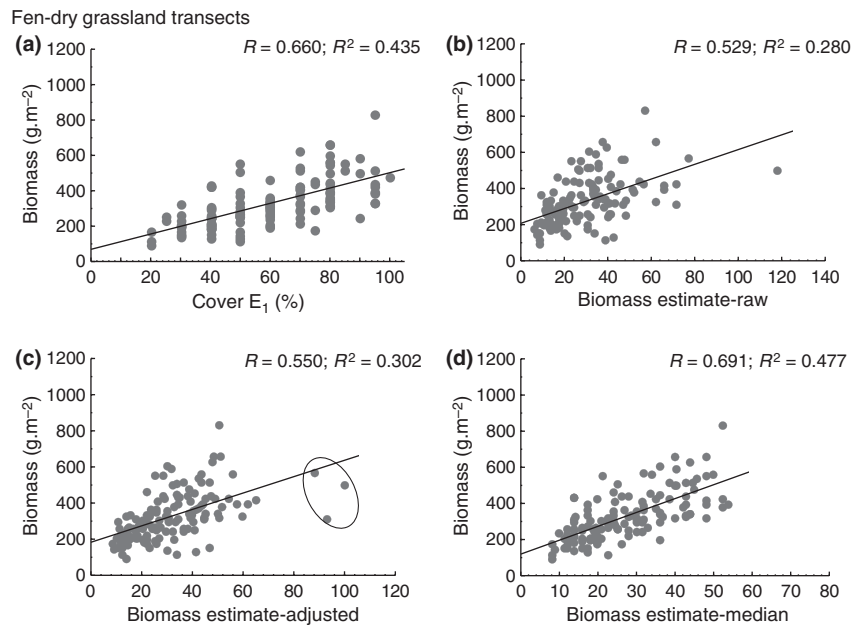
**Fig. 1.** Relationship between biomass dry weight (Biomass,  $\text{g}\cdot\text{m}^{-2}$ ) and biomass models: percentage cover of herb layer (*Cover E<sub>1</sub>*, %) and calculated 'biomass volumes' *Biomass estimate-raw*, *Biomass estimate-adjusted* and *Biomass estimate-median*, in the 'Wet meadows' data set. Pearson's correlations ( $R$ ) and regression coefficients of determination ( $R^2$ ) are indicated. All regression slopes in Figs 1–4 are significant at  $P < 0.001$ .



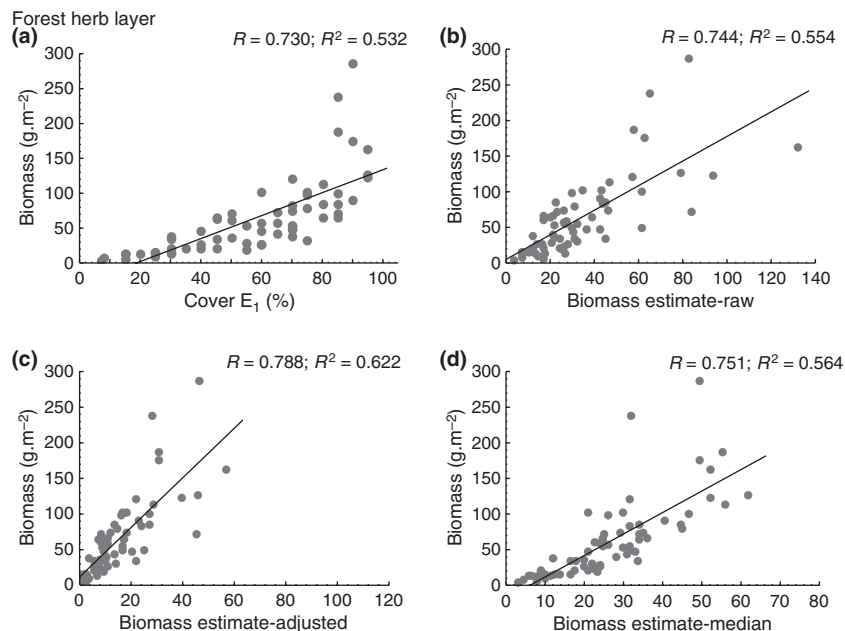
**Fig. 2.** Relationship between biomass dry weight (Biomass,  $\text{g}\cdot\text{m}^{-2}$ ) and biomass models in the 'Dry grasslands' data set. See Fig. 1 for details.

$E_1$ ) showed a rather tight correlation with herbaceous biomass in all data sets (correlation coefficients 0.567–0.803; Figs 1–4a). In the case of the 'Dry grasslands' data set, the amount of explained variation by *Cover E<sub>1</sub>* was surprisingly high and this simple model performed even better than the others. In contrast, in the 'Wet meadows'

data set, the prediction ability of the *Cover E<sub>1</sub>* model was rather low. In the 'Forest herb layer', the relationship between cover and biomass was strong up to about 80% of herb layer cover, while within higher cover values there were sites with both relatively low and high biomass. A similar but weaker trend was observed in the 'Wet meadows'.



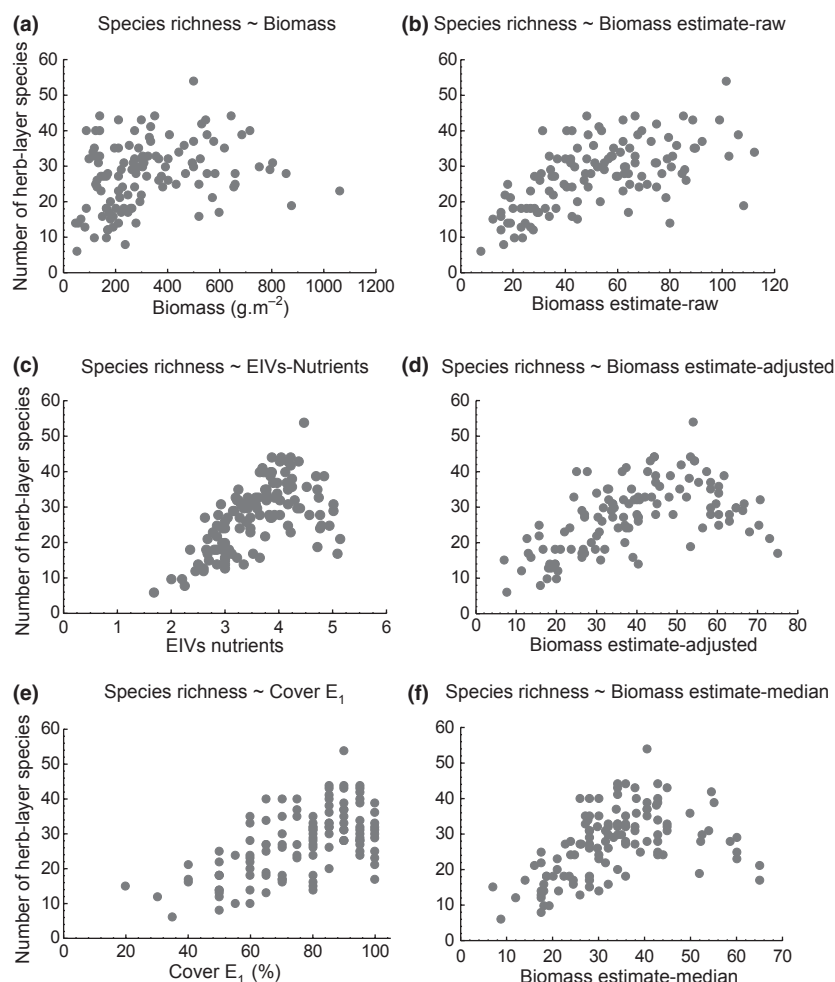
**Fig. 3.** Relationship between biomass dry weight (Biomass,  $\text{g}\cdot\text{m}^{-2}$ ) and biomass models in the ‘Fen-dry grassland transects’ data set. The plots considered outliers are marked with an ellipse. See Fig. 1 for details.



**Fig. 4.** Relationship between biomass dry weight (Biomass,  $\text{g}\cdot\text{m}^{-2}$ ) and biomass models in the ‘Forest herb layer’ data set. See Fig. 1 for details.

Regression models with the *Biomass estimate-raw* model (sum of species heights multiplied by their individual cover) explained less variation than the *Cover E<sub>1</sub>* model in the ‘Wet meadows’ and ‘Fen-dry grassland transects’,

while the results were more or less comparable in the other two data sets (Figs 1–4b). The *Biomass estimate-adjusted* model (raw model corrected by total herb layer cover) resulted in improved goodness of fit (Figs 1–4c), with the



**Fig. 5.** Comparison of methods of biomass estimation as an example of the species richness–productivity relationship in the ‘Wet meadows’ data set. The ‘productivity’ is expressed as the following variables: biomass dry weight (Biomass;  $\text{g}\cdot\text{m}^{-2}$ ), mean *EIVs Nutrients*, percentage cover of herb layer (*Cover  $E_1$* ) and calculated biomass volumes based on species heights and cover (*Biomass estimate-raw*, *-adjusted* and *-median*).

exception of the ‘Fen–dry grassland transects’, where we found distinct outlier values (Fig. 3c, marked by an ellipse). The *Biomass estimate-median* model (median stand height multiplied by total cover) showed high amounts of explained variation in all data sets (Figs 1–4d), and the improvement was most pronounced in the ‘Fen–dry grassland transects’ (Fig. 3d).

The prediction ability of regression models with Ellenberg indicator values for nutrients were the least accurate compared to both cover of herb layer or calculated biomass volumes (Table 2), with one exception in the ‘Wet meadows’ data set, where the *EIVs Nutrients* explained more variation than the *Biomass estimate-raw* and *Cover  $E_1$*  models.

The species richness–productivity relationship in the ‘Wet meadows’ data set as an application of our models is presented in Fig. 5. Species richness (number of species in the herb layer) related to biomass dry weight (annual

above-ground biomass as a rough surrogate for productivity) showed a unimodal pattern (Fig. 5a). This was confirmed by the mean *EIVs Nutrients*, *Biomass estimate-adjusted* and *Biomass estimate-median* models (significant quadratic regression, results not shown; Fig. 5c, d, f). In contrast, the herb layer cover (*Cover  $E_1$* ; Fig. 5e) did not show the declining part of the unimodal curve, and only the linear model was significant. In the case of *Biomass estimate-raw*, although the quadratic regression was significant, a decrease in species richness within higher productivity values was not evident (Fig. 5b).

## Discussion

While analyses of macro-scale patterns are usually based on low accuracy, indirect productivity estimates, such as satellite-based normalized difference vegetation index

**Table 2.** Overall comparison of regression models of herbaceous biomass (linear regressions;  $R^2$ ) in different data sets. Biomass dry weight ( $\text{g}\cdot\text{m}^{-2}$ ) was predicted from cover of the herb layer, calculated ‘biomass volumes’ and mean Ellenberg indicator values for nutrients (EIVs); for details see Methods. The significance was in all cases at  $P < 0.001$ .

Biomass ~	Wet meadows	Dry grasslands	Fen–dry grassland transects	Forest herb layer
	$R^2$	$R^2$	$R^2$	$R^2$
Cover $E_1$	0.321	0.644	0.435	0.532
Biomass estimate-raw	0.278	0.549	0.280	0.554
Biomass estimate-adjusted	0.526	0.583	0.302	0.622
Biomass estimate-median	0.514	0.643	0.477	0.564
EIVs Nutrients	0.412	0.230	0.178	0.380

(NDVI) or indices connected with energy (e.g. Šímová et al. 2011), local-scale studies need more reliable data. However, due to various constraints, relatively precise destructive measurements of biomass are not always possible, and most historical data sets do not contain them at all. Therefore, Ellenberg indicator values are considered one of the most valuable tools for biomass production estimates in Europe (Hill & Carey 1997; Schaffers & Sýkora 2000), especially because of their applicability to already sampled phytosociological databases. However, problems and limits of EIVs (Diekmann 2003; Zelený & Schaffers 2012) indicate that we should also consider other indirect methods of biomass estimation.

### Cover of herb layer

We found that herb layer cover (*Cover  $E_1$*  model) was a relatively good predictor of biomass, especially in the ‘Dry grasslands’ and ‘Forest herb layer’, if cover was below ca. 80%. This is in agreement with previous studies that reported linear correlations between biomass and cover, mostly from open, rather simply structured vegetation types, such as oligotrophic grasslands, open garigue (Chiarucci et al. 1999) or forest herb layer (Hermy 1988; Muukkonen et al. 2006; Ewald 2008). In these habitats, biomass production is limited primarily by environmental stress (e.g. water, nutrients or light availability) and only secondarily by competition. In contrast, competition becomes more important in productive vegetation such as wet meadows, where stands are of various heights and usually have a multi-layered structure. In that case, we should be aware of two serious problems associated with cover as a potential biomass surrogate.

First, percentage cover does not take into account the stand height: low and high stands with different amounts of biomass may have the same cover. Second, while the herb layer cover is estimated on a constrained scale (maximum of 100%), the biomass production does not have any arbitrary scale limit. Therefore, using herb layer cover as a surrogate for biomass might affect the analysed results, which was also confirmed in the demonstration analysis of

species richness–productivity relationship in the ‘Wet meadows’ data set (Fig. 5e). The relationship between species richness and productivity in non-forest vegetation is usually described by a unimodal (humped-back) model, which predicts highest species number within intermediate productivity levels (Grime 1979). In contrast to the other tested biomass surrogates, we did not find the expected declining part of the unimodal curve with *Cover  $E_1$* , because the plots with 80–100% cover strongly varied in biomass dry weight (see also Löbel et al. 2006). Nevertheless, we conclude that in data sets with sparse vegetation and more or less comparable stand heights, the herb layer cover presents reasonably reliable and easily obtainable estimates of biomass.

### Biomass estimates based on plant heights and covers

In contrast to herb layer cover, calculated ‘biomass volumes’ based on plant heights and covers do not have any fixed upper limit; therefore, they are mathematically more comparable to real biomass values. However, their computation is based on values of species heights listed in local floras, which are in some cases rather unrealistic for specific data sets (e.g. decumbent species, climbers, rosette species or stunted species growing outside their ecological optimum) or for specific plots (e.g. juvenile species). Of the methods tested here, *Biomass estimate-raw* and *-adjusted* are very sensitive to these problematic species, while *Biomass estimate-median* proved to be more robust. This can be seen in the outlier plots of the ‘Fen–dry grassland’ transects (Fig. 3c). In these plots, the mean height of the dominant grass, *Molinia arundinacea*, was overestimated, because the height in the flora was related to fully developed plants including inflorescences (1.6 m; Kubát et al. 2002), while the biomass was formed mainly from lower leaf tussocks. In general, we see further improvement in the biomass estimates using so-called canopy heights, which are probably more relevant species traits (e.g. LEDA-Traitbase, Kleyer et al. 2008).

The *Biomass estimate-raw* model was a relatively poor predictor, mainly because it does not consider overlap of

species covers and is sensitive to heights of problematic species. However, despite the above-mentioned problems, we proved that *Biomass estimate-raw* can explain more variation in biomass than EIVs. If there is no possibility to correct the computation using a total estimate of herb layer cover (e.g. if the estimate is missing in historical data), *Biomass estimate-raw* can be used as a biomass surrogate; otherwise the *Biomass estimate-adjusted* and *-median* are preferable. The need for an adjustment to total cover also arises from the fact that different authors tend to either over- or underestimate individual species covers (Lepš & Hadincová 1992; Klimeš 2003). Therefore, the higher the number of subjective estimates that go into the calculation, the higher the amount of noise in the data. *Biomass estimate-median* is advantageous because it uses only one estimated variable – total cover. This method can be applied both to already sampled plots, by calculating the median of the average species heights according to the local flora, and to newly sampled plots using the real median of plant height measured or estimated directly in the field. Therefore, we propose this method as a rapid, non-destructive alternative to biomass harvest.

### Ellenberg indicator values

In contrast to other surrogate variables used in our study, *EIVs Nutrients* was the worst predictor of herbaceous biomass (correlation coefficients  $R = 0.42\text{--}0.64$ ). This contradicts the conclusions of earlier studies (Hill & Carey 1997; Schaffers & Sýkora 2000), which reported relatively tight relationships between site-based EIVs for nutrients and the above-ground biomass. In our less heterogeneous data sets, the change in species composition along the productivity gradient was not as fast, and the limited biomass range (especially in the ‘Forest herb layer’ and ‘Dry grasslands’ data sets) probably resulted in lower amounts of explained variability (see Davies & Fearn 2006).

We revealed relatively high correlations for the *EIVs* *Nutrients*, especially with the EIVs for Moisture (in all data sets except ‘Fen–dry grassland transects’; see also Cornwell & Grubb 2003) and in the ‘Forest herb layer’ also with Reaction (results not shown). This might also be an explanation of why the *EIVs Nutrients* model showed such low predictive ability of biomass. Due to the correlated nature of EIVs, a change in one environmental factor can lead to changes in EIVs for a different factor, even though the latter factor did not change (Chytrý et al. 2009). Moreover, the low correlation between biomass and *EIVs Nutrients* in the ‘Forest herb layer’ might also be partly explained by the fact that herb layer biomass production is limited not only by

nutrient availability but even more by light availability (see e.g. Axmanová et al. 2011).

### Conclusions

We tested our models in four data sets that substantially differed in their species composition and ecological characteristics. Moreover, our data sets were sampled both in one broadly defined vegetation type and across many vegetation types, which indicates that our results are relatively robust. Of course, our models were proposed only for herbaceous vegetation, and the estimates would not be appropriate in vegetation types that have a high proportion of perennial biomass (e.g. shrubs, see for example field method suggested in Radloff & Mucina 2007). We might expect that the application of our models could be problematic in recently disturbed or strongly affected vegetation, where species heights are significantly lower or higher compared to their mean values according to the flora. However, data from such habitats are not very common in the databases, and in new data sampling this problem might be avoided by estimating stand median height directly in the field. We are also aware that the biomass estimates are values calculated from species composition data, which should be considered in analyses that relate them to other variables derived from species composition (e.g. species richness, sample scores along ordination axes or results of numerical classifications). In these analyses, the importance of biomass estimates may be biased toward more optimistic values than is in fact warranted from the values themselves. This issue is similar to the problem of mean EIVs, and the extent of the bias can be checked using the permutation tests proposed for EIVs in Zelený & Schaffers (2012).

To conclude, we developed models that could be successfully applied to historical vegetation data as well as in new data sampling to estimate herbaceous biomass. EIVs, which are despite their problems (see e.g. Diekmann 2003; Zelený & Schaffers 2012) often used in vegetation studies, performed worse than our other models. Even simple cover of the herb layer might be a relatively good biomass surrogate, but it is not suitable for closed or structurally diverse stands. Among the tested models, the most promising is the *Biomass estimate-median* model, which is calculated from median stand height and estimated cover of the herb layer.

### Acknowledgements

We thank to Milan Chytrý for his comments on this paper. This study was funded by the Ministry of Education, Youth and Sports of the Czech Republic (MSM0021622416)



and the Czech Science Foundation (526/09/H025 and 505/11/0732).

## Author contributions

LT & IA conceived the idea and analysed the data, IA led the writing, IA, ZF, PH, EH, C-FL, KM, MN, ZO, MV and DZ collected data in the field, processed material and commented on the manuscript.

## References

- Axmanová, I., Zelený, D., Li, C.-F. & Chytrý, M. 2011. Environmental factors influencing herb layer productivity in Central European oak forests: insights from soil and biomass analyses and a phytometer experiment. *Plant and Soil* 342: 183–194.
- Axmanová, I., Chytrý, M., Zelený, D., Li, C.-F., Vymazalová, M., Danihelka, J., Horsák, M., Kočí, M., Kubešová, S., Lososová, Z., Otýpková, Z., Tichý, L., Martynenko, V.B., Baisheva, E.Z., Schuster, B. & Diekmann, M. 2012. The species richness–productivity relationship in the herb layer of European deciduous forests. *Global Ecology and Biogeography*. DOI: 10.1111/j.1466-8238.2011.00707.x.
- Castle, M.E. 1976. A simple disk instrument for estimating herb-age yield. *Grass and Forage Science* 31: 37–40.
- Catchpole, W.R. & Wheeler, C.J. 1992. Estimating plant biomass: a review of techniques. *Australian Journal of Ecology* 17: 121–131.
- 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 conclusions? *Journal of Vegetation Science* 10: 35–42.
- Chytrý, M., Hejman, M., Hennekens, S.M. & Schellberg, J. 2009. Changes in vegetation types and Ellenberg indicator values after 65 years of fertilizer application in the rengen grassland experiment, Germany. *Applied Vegetation Science* 12: 167–176.
- Cornwell, W.K. & Grubb, P.J. 2003. Regional and local patterns in plant species richness with respect to resource availability. *Oikos* 100: 417–428.
- Davies, A.M.C. & Fearn, T. 2006. Back to basics: calibration statistics. *Spectroscopy Europe* 18: 31–32.
- Dengler, J., Jansen, F., Glöckler, F., Peet, R.K., De Cáceres, M., Chytrý, M., Ewald, J., Oldeland, J., Lopez-Gonzalez, G., Finckh, M., Mucina, L., Rodwell, J.S., Schaminée, J.H.J. & Spencer, N. 2011. The global index of vegetation-plot databases (GIVD): a new resource for vegetation science. *Journal of Vegetation Science* 22: 582–597.
- Diekmann, M. 2003. Species indicator values as an important tool in applied plant ecology – a review. *Basic and Applied Ecology* 4: 493–506.
- Dupré, C., Wessberg, C. & Diekmann, M. 2002. Species richness in deciduous forests: effects of species pools and environmental variables. *Journal of Vegetation Science* 13: 505–516.
- Dzwonko, Z. 2001. Assessment of light and soil conditions in ancient and recent woodlands by Ellenberg indicator values. *Journal of Applied Ecology* 38: 942–951.
- Ellenberg, H., Weber, H.E., Düll, R., Wirth, W., Werner, W. & Paulißen, D. 1992. Zeigerwerte von Pflanzen in Mitteleuropa Ed. 2.. *Scripta Geobotanica* 18: 1–258.
- Ewald, J. 2008. Plant species richness in mountain forests of the Bavarian Alps. *Plant Biosystems* 142: 594–603.
- Fletcher, J.E. & Robinson, M.E. 1956. A capacitance meter for estimating forage weight. *Journal of Range Management* 9: 96–97.
- Gilliam, F.S. & Turrill, N.L. 1993. Herbaceous layer cover and biomass in a young versus a mature stand of a central Appalachian hardwood forest. *Bulletin of the Torrey Botanical Club* 120: 445–450.
- Goodall, D.W. 1952. Some considerations in the use of point quadrats for the analysis of vegetation. *Australian Journal of Biological Sciences* 5: 1–41.
- Grace, J.B. 1999. The factors controlling species density in herbaceous plant communities: an assessment. *Perspectives in Plant Ecology, Evolution and Systematics* 2: 1–28.
- Grime, J.P. 1979. *Plant strategies and vegetation processes*. John Wiley, Chichester, UK.
- Hájková, P. & Hájek, M. 2003. Species richness and above-ground biomass of poor and calcareous spring fens in the flysch West Carpathians, and their relationships to water and soil chemistry. *Preslia* 75: 271–287.
- Hennekens, S.M. & Schaminée, J.H.J. 2001. TURBOVEG, a comprehensive database management system for vegetation data. *Journal of Vegetation Science* 12: 589–591.
- Hermý, M. 1988. Accuracy of visual cover assessments in predicting standing crop and environmental correlation in deciduous forests. *Vegetatio* 75: 57–64.
- Hill, M.O. & Carey, P.D. 1997. Prediction of yield in the Rothamsted Park Grass Experiment by Ellenberg indicator values. *Journal of Vegetation Science* 8: 579–586.
- Jonasson, S. 1988. Evaluation of the point intercept method for the estimation of plant biomass. *Oikos* 52: 101–106.
- Kleyer, M., Bekker, R.M., Knevel, I.C., Bakker, J.P., Thompson, K., Sonnenschein, M., Poschlod, P., van Groenendael, J.M., Klimeš, L., Klimešová, J., Klotz, S., Rusch, G.M., Hermý, M., Adriaens, D., Boedeltje, G., Bossuyt, B., Dannemann, A., Endels, P., Götzenberger, L., Hodgson, J.G., Jackel, A.-K., Kühn, I., Kunzmann, D., Ozinga, W.A., Römermann, C., Stadler, M., Schlegelmilch, J., Steendam, H.J., Tackenberg, O., Wilmann, B., Cornelissen, J.H.C., Eriksson, O., Garnier, E. & Peco, B. 2008. The LEDA Traitbase: a database of life-history traits of the Northwest European flora. *Journal of Ecology* 96: 1266–1274.
- Klimeš, L. 2003. Scale-dependent variation in visual estimates of grassland plant cover. *Journal of Vegetation Science* 14: 815–821.
- Kubát, K., Hroudá, L., Chrtek, J. Jr, Kaplan, Z., Kirschner, J. & Štěpánek, J. (eds) 2002. *Klíč ke květeně České republiky (Key to the flora of the Czech Republic)*. Academia, Praha, CZ.

- Kuusipalo, J. 1983. Mustikan varvuston biomassamäärän vaihtelusta erilaisissa metsiköissä (On the distribution of blueberry biomass in different forest stands). *Silva Fennica* 17: 245–257.
- Lepš, J. & Hadincová, V. 1992. How reliable are our vegetation analyses? *Journal of Vegetation Science* 3: 119–124.
- Löbel, S., Dengler, J. & Hobohm, C. 2006. Species richness of vascular plants, bryophytes and lichens in dry grasslands: the effects of environment, landscape structure and competition. *Folia Geobotanica* 41: 377–393.
- Matilla, E. 1981. Survey of reindeer winter ranges as a part of the finnish national inventory in 1976–1978. *Communications Instituti Forestalis Fenniae* 99: 1–74.
- Muukkonen, P., Mäkipää, R., Laiho, R., Minkkinen, K., Vasander, H. & Finér, L. 2006. Relationship between biomass and percentage cover in understorey vegetation of boreal coniferous forests. *Silva Fennica* 40: 231–245.
- Radloff, F.G.T. & Mucina, L. 2007. A quick and robust method for biomass estimation in structurally diverse vegetation. *Journal of Vegetation Science* 18: 719–724.
- Röttgermann, M., Steinlein, T., Beyschlag, W. & Dietz, H. 2000. Linear relationships between aboveground biomass and plant cover in low open herbaceous vegetation. *Journal of Vegetation Science* 11: 145–148.
- Rozbrojová, Z. & Hájek, M. 2008. Changes in nutrient limitation of spring fen vegetation across environmental gradients in the West Carpathians. *Journal of Vegetation Science* 19: 613–620.
- Santillan, R.A., Ocumpaugh, W.R. & Mott, G.O. 1979. Estimating forage yield with a disk meter. *Agronomy Journal* 71: 71–74.
- Schaffers, A.P. & Sýkora, K.V. 2000. Reliability of Ellenberg indicator values for moisture, nitrogen and soil reaction: a comparison with field measurements. *Journal of Vegetation Science* 11: 225–244.
- Schamp, B., Hettenbergerová, E. & Hájek, M. 2011. Testing community assembly predictions for nominal and continuous plant traits in species-rich grasslands. *Preslia* 83: 329–346.
- Shippert, M.M., Walker, D.A., Auerbach, N.A. & Lewis, B.E. 1995. Biomass and leaf-area index maps derived from SPOT images for Toolik Lake and Imnavait Creek areas, Alaska. *Polar Record* 31: 147–154.
- Šimová, I., Storch, D., Keil, P., Boyle, B., Phillips, O.L. & Enquist, B.J. 2011. Global species–energy relationship in forest plots: role of abundance, temperature and species climatic tolerances. *Global Ecology and Biogeography* 20: 842–856.
- Tichý, L. 2002. JUICE, software for vegetation classification. *Journal of Vegetation Science* 13: 451–453.
- Vickery, P.J., Bennett, I.L. & Nicol, G.R. 1980. An improved electronic capacitance meter for estimating herbage mass. *Grass and Forage Science* 35: 247–252.
- Walker, D.A., Auerbach, N.A. & Shippert, M.M. 1995. NDVI, biomass, and landscape evolution of glaciated terrain in northern Alaska. *Polar Record* 31: 169–178.
- Westhoff, V. & van der Maarel, E. 1978. The Braun-Blanquet approach. In: Whittaker, R.H. (ed.) *Classification of plant communities*. pp. 289–399. W. Junk, The Hague, NL.
- Yarie, J. 1980. The role of understory vegetation in the nutrient cycle of forested ecosystems in the mountain Hemlock biogeoclimatic zone. *Ecology* 61: 1498–1514.
- Zelený, D. & Schaffers, A.P. 2012. Too good to be true: pitfalls of using mean Ellenberg indicator values in vegetation analyses. *Journal of Vegetation Science*, DOI: 10.1111/j.1654-1103.2011.01366.x.