Non-destructive biomass estimation of herbaceous plant individuals: A transferable method between contrasted environments

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Abstract

Monitoring plant growth at the individual level in arrays of environmental conditions is key to understanding plant functioning with strong implications for ecophysiology, population biology and community ecology. This requires non-destructive methods for repeated estimates of individual plant biomass in time. Although allometric equations have been widely used for trees and shrubs, there is currently no general approach for herbaceous species that can be applied across habitats, plant architecture, life stage and leading to transferable equations between contrasted environments. Here we propose a method based on three biometric measurements of the minimum volume occupied by aboveground plant organs. A total of 36 equations were fitted and compared for twelve species of temperate grasslands, corresponding to various volume shapes, scaling functions (linear or power) and including (or not) a life stage effect. The accuracy of the selected equations was compared to similar attempts reported in the literature. We further assessed the across-site transferability of the best allometric equations. The goodness-of-fit of the best equations selected for each species was high ($\overline{R}^2$ = 0.83). The type of selected equations was species-specific, emphasising the benefits of considering a wide range of plant volume shapes and both linear and power functions. Using a comprehensive assessment of allometric equation transferability, we found that site effects could be neglected for eleven out of twelve species. Biomass equations based on the minimum volume proved accurate. The proposed method is easy to implement in any type of habitat, copes with various plant architectures and reduces risks of error measurement compared to previously developed approaches. The method further allows, for the first time, to use a single equation for monitoring the growth trajectory of herbaceous plant individuals in contrasted environments.

Keywords: Grasslands; allometry; canopy volume; individual-based monitoring; plant biomass; growth trajectory.

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1. Introduction

Monitoring plant growth in arrays of environmental conditions is critical for understanding plant functioning with strong implications for ecophysiology, population biology and community ecology. Tree growth monitoring is naturally performed at the individual level (Peacock *et al.* 2007), and refined allometric models have been developed to deduce tree and shrub biomass from non-destructive biometric measurements (Henry *et al.* 2013; Chave *et al.* 2014; Zhang *et al.* 2016). In contrast, the growth monitoring of herbaceous plants has been mostly performed at the population (Hooper *et al.* 2005) or community levels (Sala *et al.* 1988). Consequently, non-destructive methods of herbaceous plant biomass estimation have been mainly developed at these organization levels (Catchpole & Wheelert 1992; Harmoney *et al.* 1997; Brathen & Hagberg 2004; Barkaoui *et al.* 2013).

This focus of plant ecologists on population and community levels for herbaceous plants can be explained by the huge number of herbaceous individuals, even in small-sized monitoring plots, and by the uncertainty surrounding the definition of herbaceous individuals due to the varying levels of physiological integration between plant ramets (Harper 1977). Still, clearer understanding of herbaceous plant demographical processes requires conducting studies at the individual level because plant responses to abiotic factors and plant-plant interactions are processes operating at the level of plant individuals (Damgaard *et al.* 2002; Purves & Law 2002; Kraft *et al.* 2015).

The dynamics of individual plant biomass has traditionally been assessed through destructive sampling of replicates (e.g. Shipley & Meziane 2002). This approach has several drawbacks. First, it is time consuming and costly, which represents a strong limitation for collecting data of suitable frequency and/or number of replicates. Second, and most importantly, such a destructive method does not allow the monitoring of growth trajectories of single individuals

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but rather average trajectories of populations of individuals. Non-destructive methods are therefore required for repeated estimates of individual plant biomass in time.

A review of the literature (appendix A, see methods) reveals 15 studies that have developed non-destructive methods for individual herbs. These studies generally rely on the use of allometric equations relating various biometric plant measures to individual biomass (but see Tackenberg 2007). The most widely used biometric measure is plant height (e.g. Guevara et al. 2002), but other measures have also been used in isolation or in combination with plant height, including plant cover (Röttgermann *et al.* 2000), basal area (Guevara *et al.* 2002), canopy width (Assaeed 1997), or various volume formulations (Johnson *et al.* 1988; Damgaard *et al.* 2002). These studies report overall good fits of allometric equations (R^2 = 0.82 ± 0.12). However, the universality of this approach remains to be evaluated for herbaceous species since i) mostly (semi-)arid or artificial systems (i.e. pot experiments like Damgaard et al. 2002) have been considered in which plant individuals are strongly spatially segregated; ii) the dependence of allometric relationships on environmental conditions and plant life stages have not been thoroughly investigated, so that the transferability of calibrated allometric equations across study sites is to be demonstrated and iii) the influence of plant architecture on the usefulness of the different biometric measures remains poorly documented.

Here, we calibrate a set of allometric equations for estimating the biomass of individual plants for twelve typical species of temperate grasslands of various architectural types and sizes. Our primary objective is to compare alternative allometric equations regarding their across sites transferability. We also compare the gain in accuracy associated with the use of three biometric measurements (instead of simply one or two), and with the inclusion of phenological stage and site effects in the allometric equations. To do so, a set of allometric equations were calibrated using destructive samples collected in contrasted environments.

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Before destruction the samples were first measured according to three biometric measurements: plant height, basal and mid-height circumferences (Fig. 1). Based on the reported results, we provide some guidelines for optimising the predictive accuracy and transferability of the proposed non-destructive method of biomass estimation of herbaceous plant individuals.

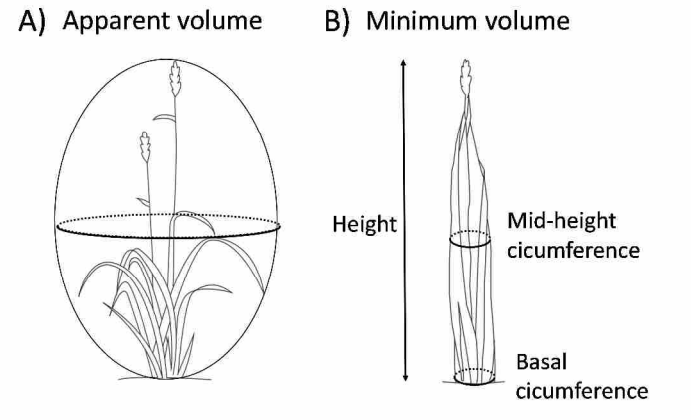

Figure 1 The biometric measurements being considered. The apparent volume (left panel) is difficult to estimate accurately because the spatial arrangement of organs of herbaceous species, especially leaves, strongly depends on external factors. The minimum volume (right panel) corresponds to the volume that an individual plant occupies when all aboveground organs are joined together and uncoiled along the plant longitudinal axis. We consider height, basal circumference and circumference at mid height to estimate the minimum volume (see Table 3 for formulations).

2. Material and Methods

2.1. Literature review

A search was conducted in ISI® Web of Science with the timespan 1950 to 2015 using the keywords “non-destructive” AND “biomass” AND “plants”. This resulted in 430 references.

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105 Articles focusing on trees, shrubs and aquatic species were excluded. Finally, we considered
106 only the minority of studies, and associated references, estimating biomass of plant
107 individuals and not stand or population levels in open habitats. This evaluation resulted in a
108 set of 15 references reporting allometric equations for a total of 76 species. These studies
109 were either located in arid habitats or were pot experiments (Appendix A).

110 *2.2. Site and species characteristics*

111 We selected twelve species that are typical of temperate grasslands of Western Europe: six
112 grass species (*Dactylis glomerata*, *Arrhenaterum elatius*, *Poa pratensis*, *Agrostis capillaris*,
113 *Elymus repens*, *Lolium perenne*), four forbs (*Plantago lanceolata*, *Taraxacum officinale*,
114 *Achillea millefolium*, *Veronica chamaedrys*) and two legumes (*Trifolium pratensis*, *Lotus*
115 *corniculatus*). The selection of species was based on their plant traits and aimed at testing our
116 method over a large variety of plant growth strategy and morphology (Table 1). We thus
117 considered fast growing exploitative species like *Arrhenatherum elatius*, slower growing and
118 more conservative species like *Achillea millefolium* and species of various canopy
119 architecture and size. Indeed, we sampled all shoot growth forms, types of leaf distribution,
120 and a large proportion of the plant height distribution referenced in the LEDA trait database
121 for herbaceous plants (Kleyer *et al.* 2008; Appendix B).

122

Species	Height (mm)	LDMC (mg/g)	SLA (mm^2/mg)	SeedMass (mg)	Leaf distribution	Shoot growth form
Achillea millefolium	472	194.4	12.02	0.132	Semi-rosette	Stem erect
Agrostis capillaris	669	266.3	31.28	0.064	Regular distribution along the stem	Stem ascending to prostrate
Arrhenatherum elatius	1177	255.1	29.18	3.079	Semi-rosette	Stem erect
Dactylis glomerata	1075	258.8	22.80	0.911	Regular distribution along the stem	Stem erect
Elymus repens	746	273.5	25.08	2.375	Regular distribution along the stem	Stem erect
Lolium perenne	801	207.7	24.68	1.975	Semi-rosette	Stem erect
Lotus corniculatus	286	206.0	27.67	1.403	Regular distribution along the stem	Stem ascending to prostrate
Plantago lanceolata	567	181.5	17.32	1.617	Rosette	Stem erect
Poa pratensis	608	288.0	16.25	0.273	Semi-rosette	Stem ascending to prostrate
Taraxacum officinale	489	159.7	23.40	0.532	Rosette	Stem erect
Trifolium pratense	667	205.0	23.33	1.581	Regular distribution along the stem	Stem erect
Veronica chamaedrys	250	312.1	20.39	0.206	Regular distribution along the stem	Stem ascending to prostrate

123

Table 1. Study species characteristics. Trait values are extracted from the LEDA trait database (Kleyer *et al.* 2008).

We aimed at calibrating allometric equations that would hold for an array of environments, plant size and phenological stages. To do so, we applied a double sampling procedure on plant individuals collected in contrasted habitats. This procedure involved measuring and harvesting ten individuals in four different sites for each of the twelve species studied (resulting in a total of 40 individuals per species). We selected plants covering a wide range of plant sizes and phenological stages. Since all species were not present at each site, we collected data in a total of 15 sites located in the Sancy massif in Central France with contrasted characteristics in terms of altitude, climate, topography, soil type and agricultural use (Table 2). Field sampling was performed from early June to late July 2015 (Appendix C). Sampling ten individuals of twelve species in four sites resulted in biometric measurements, harvesting and weighing of 480 individual plants.

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Sites	Elevation (m a.s.l)	Sum DDEG5 (°C)	Annual precipitation (mm)	Parent material	Agricultural use
A	1358	942	1000	Volcanic	Grazed
B	1254	1051	964	Volcanic	Abandonned
C	1454	840	1038	Volcanic	Mown
D	1384	915	1012	Plutonic	Grazed
E	1179	1134	934	Volcanic	Abandonned
F	1088	1250	890	Volcanic	Mown
G	1056	1283	881	Volcanic	Grazed
H	1000	1350	859	Volcanic	Mown
I	1059	1279	880	Volcanic	Mown
J	858	1552	791	Volcanic	Grazed
K	629	1894	700	Marl	Mown
L	730	1720	749	Basalt	Grazed
M	765	1668	763	Basalt	Grazed
N	606	1929	691	Marl	Mown
O	389	2247	625	Marly limestone	Mown

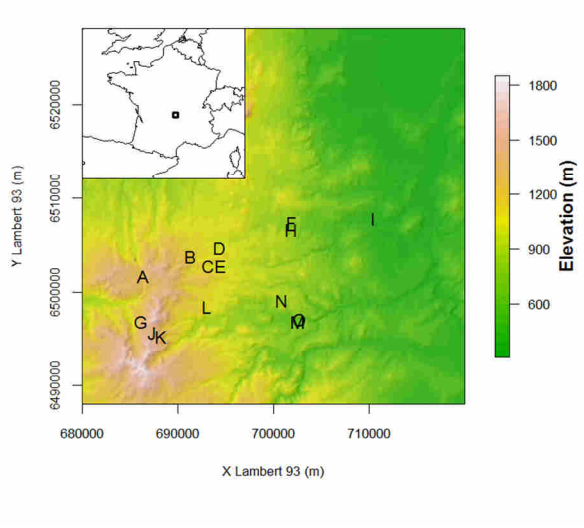

Table 2. Site characteristics and locations. Temperature and precipitation are derived from 100 m raster maps downscaled from the 1km Worldclim grids (Hijmans et al 2005) following the procedure of Dullinger et al (2012). DDEG5 stands for the annual sum of degree days above 5 °C. Soil data are derived from the European Soil Data Base V2.0 (2004). Agricultural use is deduced from field observations.

2.3. Biometric measurements and allometric equations

In this study, we define an individual plant as a ramet or collection of clumped ramets with the highest degree of physiological integration. Following this definition, an individual of a grass species may be represented by a single tiller or several adjacent and physiologically

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integrated tillers forming a tussock. The mass *B* of a plant individual can be estimated from its volume *V* following $B = V \times D$ where *D* is the bulk density. The apparent volume of a plant is a combination of plant tissue and void. Bulk density is therefore a complex quantity that depends both on tissue characteristics and plant architecture (Figure 1-A). The void component of the plant apparent volume is an important source of inter-individual variability in estimated biomass. The spatial arrangement of leaves, stems and reproductive organs is highly dependent on external factors such as wind and neighbouring plants because of tissue flexibility. This makes any measurement of the apparent volume highly uncertain. Previous studies using measures of a plant apparent volume have mostly been located in arid habitats where plants are spatially segregated, thereby decreasing this nuisance variability (see e.g. Johnson et al. 1988). To avoid difficulties of intertwined plants in the field, we consider the minimum volume of the canopy, rather than its apparent volume (Figure 1-B). We define the minimum volume as the volume that an individual plant occupies when all aboveground organs are joined together and uncoiled along the plant longitudinal axis. This requires hand manipulation of plants but does not alter their tissues nor their future growth.

We considered three simple biometric measurements to estimate the minimum volume of each plant: the maximum height, the basal circumference and the circumference at mid height (Figure 1-B). Both circumferences were measured with a graduated tape by tightening organs until first signs of resistance in order to avoid plant tissue damages. This procedure minimizes measurement error by reducing inter-individual variations in standing volume linked to neighbourhood conditions (Fig. 1). Furthermore, there is very little potential variation in circumference measurement linked to the tightening force exerted by the observer, since large tightening forces are avoided to preserve the plant from tissue damage. These biometric measurements were recorded in the field for the 480 plant individuals considered. The plants were then clipped to ground level. In the lab, we sorted dead material,

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green tissues and reproductive organs. All plant samples were oven-dried at 60°C during 48 hours and weighed. The total plant biomass including dead material was used for subsequent analyses.

Based on the three basic measurements introduced above, we formulated allometric equations for nine possible shapes of the minimum volume (Table 3). Shapes like cylinder, double cylinder, cone, double cone or ellipsoid were first considered as having a unique value of bulk density. We further considered the possibility that the lower and upper parts of shapes like double cylinder and double cone may show different bulk density. This was justified by the uneven distribution of different organs (leaves, stems, reproductive organs) along the longitudinal axis of plants. Finally, we also considered basic allometric models where the plant biomass is a simple function of height (stick) or height and basal circumference (reversed nail) or height and circumference at mid-height (spinning-top). We considered both linear and power relationships between the measured plant biomass and the patterns presented above. Both types of relationship correspond to two distinct hypotheses. The linear model assumes that the bulk density of plant individuals does not vary with plant size. Conversely, the power model assumes bulk density to vary with plant size as a result of non-isometric allocation between organs of different density during plant ontogeny (Weiner 2004; Poorter *et al.* 2015).

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Shape	Name	Formula	
		linear	power
	Stick	$B = dH$	$B = dH^z$
	Reversed nail	$B = d_1H + d_2C_{basal}$	$B = d_1H^{z_1} + d_2C_{basal}^{z_2}$
	Spinning-top	$B = d_1H + d_2C_{half}$	$B = d_1H^{z_1} + d_2C_{half}^{z_2}$
	Homogeneous double cylinder	$B = d\frac{H}{2}(A_{basal} + A_{half})$	$B = d\left[\frac{H}{2}(A_{basal} + A_{half})\right]^z$
	Inhomogeneous double cylinder	$B = \frac{H}{2}(d_1A_{basal} + d_2A_{half})$	$B = \left[\frac{H}{2}(d_1A_{basal} + d_2A_{half})\right]^z$
	Simple cone	$B = d\frac{H}{3}A_{basal}$	$B = d\left(\frac{H}{3}A_{basal}\right)^z$
	Homogeneous double cone	$B = d\frac{H}{6}\left(A_{basal} + 2A_{half} + \sqrt{A_{basal}A_{half}}\right)$	$B = d\left[\frac{H}{6}\left(A_{basal} + 2A_{half} + \sqrt{A_{basal}A_{half}}\right)\right]^z$
	Inhomogeneous double cone	$B = d_1\frac{H}{6}\left(A_{basal} + A_{half} + \sqrt{A_{basal}A_{half}}\right) + d_2\frac{H}{6}A_{half}$	$B = \left[d_1\frac{H}{6}\left(A_{basal} + A_{half} + \sqrt{A_{basal}A_{half}}\right) + d_2\frac{H}{6}A_{half}\right]^z$
	Ellispoid	$B = d\frac{4}{3}\pi Hr_{half}^2$	$B = d\left(\frac{4}{3}\pi Hr_{half}^2\right)^z$

with $A_{basal} = C_{basal}^2/4\pi$
$A_{half} = C_{half}^2/4\pi$
$r_{half} = C_{half}/2\pi$

Table 3. Allometric equations based on various volume shapes. These equations make use of a plant's maximum height (H), basal circumference (C_{basal}) and circumference at mid-height (C_{half}). B indicates total dry biomass of aboveground organs. Volumes with both white and gray parts indicate that two different bulk densities (d) are estimated.

Eighteen allometric models were initially tested for each species (i.e. total plant biomass regressed against nine patterns following either a linear or power function). We further tested the robustness of these allometric equations against environmental or life stage effects. To do so, we fitted 36 additional models where life stage or life stage and site were added as

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independent variables. Sites were considered as factors with four levels. Plant developmental stage was considered as a binary factor representing the presence or absence of reproductive organs. We assessed model performance following three criteria. First, we quantified the model goodness-of-fit to the full dataset (n = 40 for each species) using the coefficient of determination. Second, we computed model predictive accuracy using a repeated split-sample procedure (100 iterations). Seventy five per cent of the full dataset were used for model calibration (n = 30) and 25% for model evaluation. The splitting procedure aimed at uniformly sample evaluation data within the range of species total biomass. We then calculated the average Normalized Root Mean Square Error of predictions (NRMSE) across the 100 iterations. Third, we assessed the across-site transferability using a 4-fold cross-validation procedure where sites were used for data splitting. Therefore, the models were calibrated for all but one site (n = 30) and evaluated on the remaining site. We then calculated the average Normalized Root Mean Square Error of predictions (NRMSE) across the 4 possible iterations (one per site).

We compared the 54 models based on these three criteria (i.e. goodness-of-fit, predictive accuracy and between-site transferability), but selected the best equation for each species as the one showing the best between-site transferability.

All statistical analyses were performed under the R environment (R Core Team 2015). Scripts and basic data are provided in Appendices C-D.

3. Results

Among the 54 allometric equations, the most transferable one was selected for each of the 12 investigated species. The normalized errors reported for model transferability ranged between 0.11 and 0.35 with $\overline{NRMSE_{transf}}$ = 0.20 (Table 4). Differences in predictive accuracy between the most accurate and the selected models were low (ΔNRMSE ranging between 0

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and 0.09), meaning that most transferable models were also the most accurate or close to the most accurate (Table 4). Overall, the selected equations showed high goodness-of-fit with R^2 ranging from 0.63 to 0.95 and $\overline{R}^2 = 0.83$ (Figure 2) and good predictive accuracy with NRMSE ranging from 0.10 to 0.23 and $\overline{NRMSE} = 0.16$ (Table 4). These good performances are in line with the results retrieved from the few previous studies having documented allometric equations for herbaceous species in open habitats (Figure 2). Goodness-of-fit and predictive accuracy did not differ between plant functional groups and was not significantly correlated with the plant traits considered here (Table 1).

The selected model was very variable among species in terms of shape, type of function and importance of stage effect. The shapes of the selected models had non-evident relationships with species traits. Reversed nail was selected as the best shape for *Trifolium pratensis* only, simple cone for *Plantago lanceolata*, spinning-top for three species (*Achillea millefolium*, *Elymus repens*, *Lotus corniculatus* and *Veronica chamaedrys*), homogenous double cone for *Poa pratensis*, homogeneous double cylinder for three species (*Agrostis capillaris*, *Lolium perenne* and *Taraxacum officinale*), homogeneous ellipsoid for *Arrhenatherum elatius*, and inhomogeneous double cylinder for *Dactylis glomerata*.

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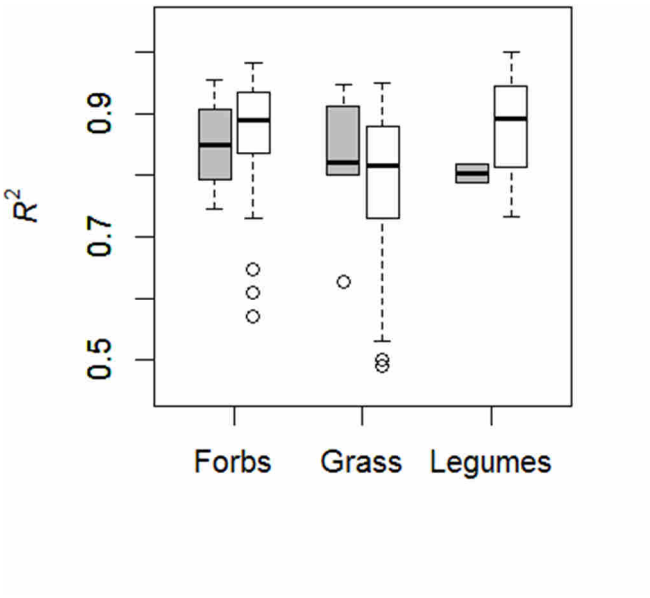

Figure 2. Goodness-of-fit of the allometric equation selected for each species from this study (gray boxes) and results extracted from the literature (white boxes; Appendix A).

The stick model based solely on plant height was never selected as the most transferable model (Table 4, Figure 3-A). It was further found to be the worst model for all species except *Veronica chamaedrys*. Shapes relying on basal circumference and height (reversed nail and simple cone) were selected for two out of twelve species. Shapes further including mid-height circumference were selected for the ten remaining species. The improvement in goodness-of-fit provided by this third biometric measure ranged between 0 and 18% (Figure 3-B). These results highlight that the complementary biometric measurements proposed in this study make a critical contribution to the predictive ability of the allometric equations.

Models including life stage effects were selected for seven out of twelve species (Figure 3-C). Although inclusion of life stage resulted in strong improvement for linear models (increase in R^2 up to 40%), it did not improve power models by more than 7.2% except for *Lolium perenne*, which showed an increase of 17%. Power functions were selected for seven out of

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twelve species. These results highlight that power functions are useful, but not essential, for predicting the biomass of temperate individual herbs at various stages of their life cycle. Finally, we calibrated allometric equations including site effects. Although one may expect elevation to show a unidirectional influence, we did not find a clear pattern of site effects among the twelve species (Appendix E). We further assessed the gain in goodness-of-fit associated with the use of a site effect in the allometric equation, and found that this gain was limited for all species except *Lolium perenne* (Figure 3-D). For this peculiar species our results encourage to devise site specific allometric equations to recover a good predictive accuracy.

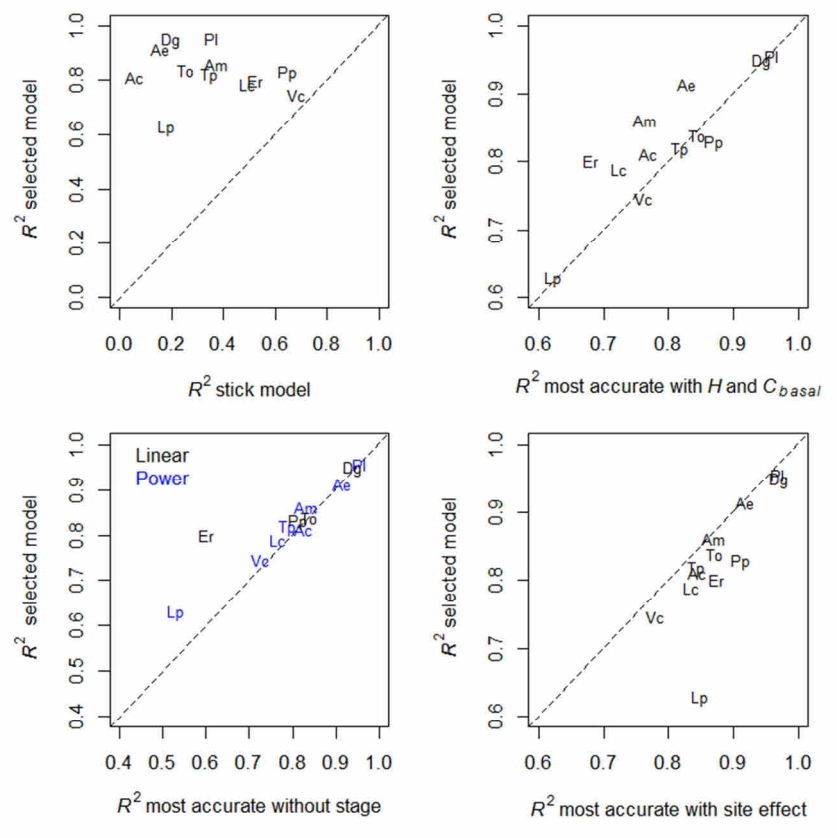

Figure 3. Goodness-of-fit of the selected models compared to A) the most accurate stick model without site effect, B) the most accurate model that relies on plant height (H) and basal circumference (C_{basal}) without site effect, C) the most accurate model without stage effect and D) the most accurate model including site effects. Letters indicate the species : Am (*Achillea*

274 *millefolium*); Ac (*Agrostis capillaris*); Ae (*Arrhenaterum elatius*); Dg (*Dactylis glomerata*);
275 Er (*Elymus repens*); Lp (*Lolium perenne*); Lc (*Lotus corniculatus*); Pl (*Plantago lanceolata*);
276 Pp (*Poa pratensis*); To (*Taraxacum officinale*); Tp (*Trifolium pratensis*); Vc (*Veronica*
277 *chamaedrys*).
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				Fit with full dataset								**Predictive accuracy**		**Between site Transferability**
Species	**Shape**	**Function**	**Stage**	R^2	d	d_1	d_2	z	z_1	z_2	ΔR^2	**NRMSE**	**ΔNRMSE**	**$NRMSE_{transf}$**
Achillea millefolium	Spinning top	Power	yes	0.86	-	2E-08	0.75	-	4.06	2.26	0.008	0.15	0	0.15
Agrostis capillaris	Homogeneous double cylinder	Power	no	0.81	5.95	-	-	0.53	-	-	0.029	0.16	-0.012	0.24
Arrhenaterum elatius	Homogenous ellipsoid	Power	no	0.91	2.27	-	-	0.76	-	-	0.004	0.1	0	0.14
Dactylis glomerata	Inhomogeneous double cylinder	Power	no	0.95	-	0.03	0.16	0.92	-	-	0.021	0.12	-0.035	0.15
Elymus repens	Spinning top	Linear	yes	0.8	-	1.96	230.64	-	-	-	0.074	0.17	-0.027	0.17
Lolium perenne	Homogeneous double cylinder	Power	yes	0.63	0.44	-	-	0.81	-	-	0.176	0.23	-0.094	0.35
Lotus corniculatus	Spinning top	Linear	yes	0.79	-	1.31	31.20	-	-	-	0.070	0.18	-0.019	0.30
Plantago lanceolata	Simple cone	Power	no	0.96	2.85	-	-	0.72	-	-	0.006	0.1	-0.011	0.11
Poa pratensis	Homogeneous double cone	Linear	yes	0.83	0.11	-	-	-	-	-	0.035	0.18	-0.035	0.29
Taraxacum officinale	Homogeneous double cylinder	Linear	no	0.84	0.03	-	-	-	-	-	0.040	0.16	-0.004	0.17
Trifolium pratensis	Reversed nail	Linear	yes	0.82	-	5.3	60.17	-	-	-	0.025	0.15	0	0.17
Veronica chamaedrys	Spinning top	Power	yes	0.75	-	0.03	3E-07	-	1.55	13.4	0.007	0.19	-0.017	0.20

Table 4. Selected allometric equations for each species. The selection procedure is based on the lowest Normalized Root Mean Square Error of the between-site transferability analysis ($NRMSE_{transf}$) among models that do not account for potential site effects. The selected models were compared to the most accurate ones with ΔR^2 depicting the difference of goodness-of-fit and ΔNRMSE the difference of predictive accuracy.

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Discussion

The method proposed here is accurate, easy to implement and leads to equations that are generally transferable between contrasted environments. The selected allometric equations for each species showed high prediction accuracy and goodness of fit, similar to the results reported in the literature (Appendix A). The main difference is that our method relies on the minimum volume whereas other studies have used the apparent volume (e.g. Johnson et al. 1988, see Appendix A). The apparent volume can be easily estimated in systems where plants are spatially segregated such as in arid habitats where all previous studies have been conducted. However, in intricate vegetation, such as in temperate grasslands, the plant canopy cannot clearly be delineated at the individual level. We here demonstrated that biomass estimations based on the minimum volume efficiently circumvent this problem, making the proposed method relevant to any herbaceous community.

Results from the present study show that the three investigated biometric measurements (height, basal circumference and mid-height circumference) are complementary (Fig. 3A-B). They allow to select for the best shape among nine possible formulation of the minimum volume. Our investigation was based on a modest number of species but covered a large range of canopy architecture, size and leaf traits of the Western European flora. Six out of nine shapes, which made use of two to three biometric measurements were selected as the best formulations (Table 4). These results provide evidence of the flexibility of the method, which can cope with different plant architectures and grassland types.

In the present work, power functions often resulted in greater predictive power than linear functions, indicating significant variations of plant bulk density with plant size. This is consistent with the fact that power models without and with reproductive stage as independent predictor showed similar goodness-of-fit whereas linear models without stage effect were generally less accurate than models including stage effect. This can be interpreted as a

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consequence of allometric biomass allocation between stems, leaves and reproductive organs during plant ontogeny that do not have the same bulk densities (Niklas 2004; Weiner 2004; Poorter *et al.* 2015). Although the power function is biologically justified by the allometric scaling theory, it was not always associated with significant fit improvements in our study. Four out of twelve studied species exhibited linear relationships and several studies reported good estimations of individual herb biomass from linear models (Gutierrez & Aguilera 1989; Assaeed 1997; Röttgermann *et al.* 2000; Guevara *et al.* 2002; Hirata *et al.* 2007; van der Eynden 2011). Isometric scaling between plant organs has been reported for small plants (Enquist & Niklas 2002; Enquist et al. 2007; Poorter et al. 2015), and is consistent with optimal biomass partitioning theory (Lohier *et al.* 2014). Our contrasted findings emphasize the need to systematically consider linear and non-linear functions when fitting biomass equations from biometric measurements of herbaceous individual plants, as currently recommended for other plant groups (Chave *et al.* 2014).

Most importantly, we found that a single equation can reasonably be used to successfully predict the biomass of individual plants in different habitats for the large majority of the investigated species, at least within the range of environmental conditions investigated here, which was already wide (Table 2). A notable exception was the perennial ryegrass (*Lolium perenne*). It is possible that we sampled different selected ryegrass genotypes with contrasted ecophysiological and morphological characteristics since different varieties of ryegrass are used for hay production and pasture (Beecher *et al.* 2015). The strong site effect for this species may therefore have been confounded with a genotype effect. To our knowledge this study is the most comprehensive assessment of the transferability of biomass equations between different environments for herbaceous species. A few previous studies have compared allometric equations fitted for different disturbance regimes, including fire (van der Eynden 2011) and grazing (Tausch et al. 1994; Nafus et al. 2009, but all were within

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334 homogeneous abiotic conditions. Huenneke et al. (2001) and Andariese & Covington (1986)
335 compared different sites varying in abiotic conditions. The most frequent conclusion of these
336 studies is that biomass equations should be calibrated for each investigated site. Only
337 Huenneke et al. (2001) and our findings contrast with this prevailing view. Despite the good
338 across-site transferability of the allometric equations evidenced in this study, further
339 investigation is needed where both approaches would be specifically compared.
340 Based on these findings we recommend the application of this method for most herbaceous
341 species, except for very small (below 0.05 meters height) and tall species (above 2 meters
342 height) for which the proposed measurements may be unpractical. We furthermore suggest
343 the following guidelines for interested users:

344 1- Potential users should fit their own equations rather than using the reported parameters
345 for two reasons: i) to minimize potential observer biases, and ii) because prediction
346 errors when extrapolating models to distinct biogeographic areas have not yet been
347 evaluated.
348 2- Large environmental gradients should be sampled when calibrating the allometric
349 equations and equations should be used within the range of investigated environmental
350 conditions.
351 3- In order to determine the best equation for each species, all possible equations
352 reported here should be fitted; the most appropriate species-specific equations cannot
353 be selected a priori using basic knowledge of species architecture and size. As a
354 default model, we recommend using a power model for a homogenous double cone
355 which showed on average the best performances, all criteria combined.

356 This non-destructive, cross-site estimation method of individual plant biomass opens new
357 perspectives for research at the individual and community levels. At the individual level,
358 monitoring biomass trajectories of plant individuals will allow the assessment of changes in

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359 demographic rates in relation to environmental conditions. Such information can be used to
360 better tease apart the respective influences of abiotic conditions and biotic neighbourhood in
361 plant dynamics along their growth trajectories, and thus to enrich existing approaches based
362 on biomass measurements at the end of a field experiment (e.g., Wilson & Keddy 1986;
363 Goldberg et al. 1999; Freckleton & Watkinson 2001). These empirical assessments may feed
364 dynamical models of plant dynamics at the population and community levels (Lande *et al.*
365 2003; Rees & Ellner 2009). With modern developments in theoretical ecology, dynamic
366 modelling approaches have proved powerful in assessing the detailed nature of competition
367 (Damgaard *et al.* 2002) and the importance of niche differentiation and fitness differences in
368 the outcome of competition (Levine & HilleRisLambers 2009; Adler *et al.* 2010; Kraft *et al.*
369 2015). Coexistence theory of herbaceous plants has mainly be applied in arid systems where
370 parameters like reproductive output, survival, cover and density are monitored (Sears &
371 Chesson 2007; Adler *et al.* 2010; Kraft *et al.* 2015). The use of non-destructive estimates of
372 individual biomass could help test this theory with models based on biomass production,
373 which are more informative for systems like temperate grassland where population growth is
374 mostly vegetative (Benson & Hartnett 2006).
375

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380 **References**

381 Adler, P.B., Ellner, S.P. & Levine, J.M. (2010). Coexistence of perennial plants: An
382 embarrassment of niches. *Ecology Letters*, **13**, 1019–1029.

Andariese, S.W. & Covington, W.W. (1986). Biomass Estimation for Four Common Grass Species in Northern Arizona Ponderosa Pine. *Journal of Range Management*, **39**, 472–473.

Assaeed, A. (1997). Estimation of biomass and utilization of three perennial range grasses in Saudi Arabia. *Journal of arid Environments*, **36**, 103–111.

Barkaoui, K., Bernard-Verdier, M. & Navas, M.L. (2013). Questioning the Reliability of the Point Intercept Method for Assessing Community Functional Structure in Low-Productive and Highly Diverse Mediterranean Grasslands. *Folia Geobotanica*, **48**, 393–414.

Beecher, M., Hennessy, D., Boland, T.M., Mcevoy, M., O'Donovan, M. & Lewis, E. (2015). The variation in morphology of perennial ryegrass cultivars throughout the grazing season and effects on organic matter digestibility. *Grass and Forage Science*, **70**, 19–29.

Benson, E.J. & Hartnett, D.C. (2006). The Role of Seed and Vegetative Reproduction in Plant Recruitment and Demography in Tallgrass Prairie. *Plant Ecology*, **187**, 163–178.

Brathen, K.A. & Hagberg, O. (2004). More efficient estimation of plant biomass. *Journal of Vegetation Science*, **15**, 653–660.

Catchpole, W.R. & Wheelert, C.J. (1992). Estimating plant biomass : A review of techniques. *Australian Journal of Ecology*, **17**, 121–131.

Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M.S., Delitti, W.B.C., Duque, A., Eid, T., Fearnside, P.M., Goodman, R.C., Henry, M., Martínez-Yrízar, A., Mugasha, W.A., Muller-Landau, H.C., Mencuccini, M., Nelson, B.W., Ngomanda, A., Nogueira, E.M., Ortiz-Malavassi, E., Pélissier, R., Ploton, P., Ryan, C.M., Saldarriaga, J.G. & Vieilledent, G. (2014). Improved allometric models to estimate the aboveground

biomass of tropical trees. *Global Change Biology*, **20**, 3177–3190.

Damgaard, C.F., Weiner, J. & Nagashima, H. (2002). Modelling individual growth and competition in plant populations: growth curves of *Chenopodium album* at two densities. *Journal of Ecology*, **90**, 666–671.

Enquist, B.J., Allen, A.P., Brown, J.H., Gillooly, J.F., Kerkhoff, A.J., Niklas, K.J., Price, C. a & West, G.B. (2007). Biological scaling: does the exception prove the rule? *Nature*, **445**, E9–E10; discussion E10–E11.

Enquist, B.J. & Niklas, K.J. (2002). Response to Sack et al. Global allocation rules for patterns in partioning. *Science*, **296**, 4–5.

ESDB, V.. (2004). *ESDB v2.0: The European Soil Database distribution version 2.0, European Commission and the European Soil Bureau Network, CD-ROM, EUR 19945 EN*.

van der Eynden, M. (2011). *Effects of fire history on species richness and carbon stocks in a Peruvian puna grassland , and development of allometric equations for biomass estimation of common puna species*.

Freckleton, R.P. & Watkinson, a. R. (2001). Asymmetric competition between plant species. *Functional Ecology*, **15**, 615–623.

Goldberg, D.E., Rajaniemi, T.K., Gurevitch, J. & Stewart-Oaten, A. (1999). Empirical approaches to quantifying interaction intensity: competition and facilitation along productivity gradients. *Ecology*, **80**, 1118–1131.

Guevara, J.C., Gonnet, J.M. & Estevez, O.R. (2002). Biomass estimation for native perennial grasses in the plain of Mendoza, Argentina. *Journal of Arid Environments*, **50**, 613–619.

Gutierrez, J.R. & Aguilera, L.E. (1989). Size-biomass relationships for some herbaceous

plants of the Chilean arid region. *Revista Chilena de Historia Natural*, **62**, 95–98.

Harmoney, K.R., Moore, K.J., George, J.R., Brummer, E.C. & Russell, J.R. (1997). Determination of Pasture Biomass Using Four Indirect Methods. *Agron. J.*, **89**, 665–672.

Harper, J.L. (1977). *Population Biology of Plants*. Academic Press.

Henry, M., Bombelli, A., Trotta, C., Alessandrini, A., Birigazzi, L., Sola, G., Vieilledent, G., Santenoise, P., Longuetaud, F., Valentini, R., Picard, N. & Saint-André, L. (2013). GlobAllomeTree: International platform for tree allometric equations to support volume, biomass and carbon assessment. *IForest*, **6**, 326–330.

Hirata, M., Oishi, K., Muramatu, K., Xiong, Y., Kaihotu, I., Nishiwaki, A., Ishida, J., Hirooka, H., Hanada, M., Toukura, Y. & Hongo, A. (2007). Estimation of plant biomass and plant water mass through dimensional measurements of plant volume in the Dund-Govi Province, Mongolia. *Grassland Science*, **53**, 217–225.

Hooper, D.U., Chapin, I.F.., Ewell, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Scmid, B., Setälä, H., Symstad, A.J., Vandermeer, J. & Wardle, D.A. (2005). Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, **75**, 3–35.

Huenneke, L.F., Clason, D. & Muldavin, E. (2001). Spatial heterogeneity in Chihuahuan Desert vegetation: implications for sampling methods in semi-arid ecosystems. *Journal of Arid Environments*, **47**, 257–270.

Johnson, P., Johnson, C. & West, N. (1988). Estimation of phytomass for ungrazed crested wheatgrass plants using allometric equations. *Journal of Range Management*, **41**, 421–425.

Kleyer, M., Bekker, R.M., Knevel, I.C., Bakker, J.P., Thompson, K., Sonnenschein, M.,

452 Poschlod, P., van Groenendael, J.M., Klimeš, L., Klimešová, J., Klotz, S., Rusch, G.M.,
453 Hermy, M., Adriaens, D., Boedeltje, G., Bossuyt, B., Dannemann, A., Endels, P.,
454 Götzenberger, L., Hodgson, J.G., Jackel, A.-K., Kühn, I., Kunzmann, D., Ozinga, W.A.,
455 Römermann, C., Stadler, M., Schlegelmilch, J., Steendam, H.J., Tackenberg, O.,
456 Wilmann, B., Cornelissen, J.H.C., Eriksson, O., Garnier, E. & Peco, B. (2008). The
457 LEDA Traitbase: a database of life-history traits of the Northwest European flora.
458 *Journal of Ecology*, **96**, 1266–1274.

459 Kraft, N.J.B., Godoy, O. & Levine, J.M. (2015). Plant functional traits and the
460 multidimensional nature of species coexistence. *Procceding of the National Academy of*
461 *Sciences*, **112**, 797–802.

462 Lande, R., Engen, S. & Saether, B.E. (2003). *Stochastic population dynamics in ecology and*
463 *conservation*. Oxford University Press.

464 Levine, J.M. & HilleRisLambers, J. (2009). The importance of niches for the maintenance of
465 species diversity. *Nature*, **461**, 254–7.

466 Lohier, T., Jabot, F., Meziane, D., Shipley, B., Reich, P.B. & Deffuant, G. (2014). Explaining
467 ontogenetic shifts in root-shoot scaling with transient dynamics. *Annals of botany*, **114**,
468 513–24.

469 Nafus, A.M., McClaran, M.P., Archer, S.R. & Throop, H.L. (2009). Multispecies Allometric
470 Models Predict Grass Biomass in Semidesert Rangeland. *Rangeland Ecology &*
471 *Management*, **62**, 68–72.

472 Niklas, K.J. (2004). Plant allometry: is there a grand unifying theory? *Biological reviews of*
473 *the Cambridge Philosophical Society*, **79**, 871–89.

474 Peacock, J., Baker, T.R., Lewis, S.L., Lopez-Gonzalez, G. & Phillips, O.L. (2007). The

RAINFOR database: monitoring forest biomass and dynamics. *Journal of Vegetation Science*, **18**, 535.

Poorter, H., Jagodzinski, A.M., Ruiz-Peinado, R., Kuyah, S., Luo, Y., Oleksyn, J., Usoltsev, V. a., Buckley, T.N., Reich, P.B. & Sack, L. (2015). How does biomass distribution change with size and differ among species? An analysis for 1200 plant species from five continents. *New Phytologist*, **208**, 736–749.

Purves, D.W. & Law, R. (2002). Fine-scale spatial structure in a grassland community : quantifying the plant ' s-eye view. 121–129.

R Core Team. (2015). R: A Language and Environment for Statistical Computing.

Rees, M. & Ellner, S.P. (2009). Integral projection models for populations in temporally environments varying. *Ecological Monographs*, **79**, 575–594.

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.

Sala, O.E., Parton, W.J., Joyce, L. a. & Lauenroth, W.K. (1988). Primary production of the central grassland region of the United States. *Ecology*, **69**, 40–45.

Sears, A.L.W. & Chesson, P.L. (2007). New methods for quantifying the spatial storage effect: an illustration with desert annuals. *Ecology*, **88**, 2240–7.

Shipley, B. & Meziane, D. (2002). The balanced-growth hypothesis and the allometry of leaf and root biomass allocation. *Functional Ecology*, **16**, 326–331.

Tackenberg, O. (2007). A new method for non-destructive measurement of biomass, growth rates, vertical biomass distribution and dry matter content based on digital image analysis. *Annals of Botany*, **99**, 777–783.

Author-produced version of the article published in Ecological Indicators, 2017, 72, 769-776.
The original publication is available at http://www.sciencedirect.com/
doi : 10.1016/j.ecss.2008.08.013

Tausch, Robin J., Robert S. Nowak, Allen D. Bruner, and J.S. (1994). Effects of simulated fall and early spring grazing on cheatgrass and perennial grass in western Nevada. *Proceedings of Ecology and Management of Annual Rangelands. USDA Forest Service, Intermountain Research Station. Gen. Tech. Report INT-GTR-313*, 113–119.

Weiner, J. (2004). Allocation, plasticity and allometry in plants. *Perspectives in Plant Ecology, Evolution and Systematics*, **6**, 207–215.

Wilson, S.D. & Keddy, P.A. (1986). Measuring diffuse competition along an environmental gradient: Results from a shoreline plant community. *The American Naturalist*, **127**, 862–869.

Zhang, L., Cui, G., Shen, W. & Liu, X. (2016). Cover as a simple predictor of biomass for two shrubs in Tibet. *Ecological Indicators*, **64**, 266–271.