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1 **Title : Non-destructive biomass estimation of herbaceous plant individuals: a**
2 **transferable method between contrasted environments.**

3

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10

11

12 **Abstract**

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

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

37 **1. Introduction**

38 Monitoring plant growth in arrays of environmental conditions is critical for understanding
39 plant functioning with strong implications for ecophysiology, population biology and
40 community ecology. Tree growth monitoring is naturally performed at the individual level
41 (Peacock *et al.* 2007), and refined allometric models have been developed to deduce tree and
42 shrub biomass from non-destructive biometric measurements (Henry *et al.* 2013; Chave *et al.*
43 2014; Zhang *et al.* 2016). In contrast, the growth monitoring of herbaceous plants has been
44 mostly performed at the population (Hooper *et al.* 2005) or community levels (Sala *et al.*
45 1988). Consequently, non-destructive methods of herbaceous plant biomass estimation have
46 been mainly developed at these organization levels (Catchpole & Wheelert 1992; Harmoney
47 *et al.* 1997; Brathen & Hagberg 2004; Barkaoui *et al.* 2013).

48 This focus of plant ecologists on population and community levels for herbaceous plants can
49 be explained by the huge number of herbaceous individuals, even in small-sized monitoring
50 plots, and by the uncertainty surrounding the definition of herbaceous individuals due to the
51 varying levels of physiological integration between plant ramets (Harper 1977). Still, clearer
52 understanding of herbaceous plant demographical processes requires conducting studies at the
53 individual level because plant responses to abiotic factors and plant-plant interactions are
54 processes operating at the level of plant individuals (Damgaard *et al.* 2002; Purves & Law
55 2002; Kraft *et al.* 2015).

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

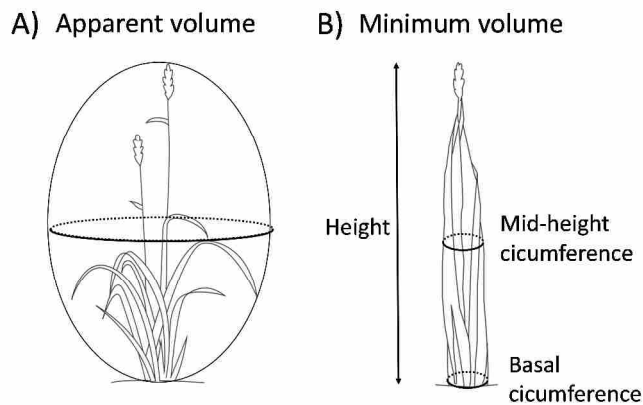
61 but rather average trajectories of populations of individuals. Non-destructive methods are
62 therefore required for repeated estimates of individual plant biomass in time.

63 A review of the literature (appendix A, see methods) reveals 15 studies that have developed
64 non-destructive methods for individual herbs. These studies generally rely on the use of
65 allometric equations relating various biometric plant measures to individual biomass (but see
66 Tackenberg 2007). The most widely used biometric measure is plant height (e.g. Guevara et
67 al. 2002), but other measures have also been used in isolation or in combination with plant
68 height, including plant cover (Röttgermann *et al.* 2000), basal area (Guevara *et al.* 2002),
69 canopy width (Assaeed 1997), or various volume formulations (Johnson *et al.* 1988;
70 Damgaard *et al.* 2002). These studies report overall good fits of allometric equations ($R^2 =$
71 0.82 ± 0.12). However, the universality of this approach remains to be evaluated for
72 herbaceous species since i) mostly (semi-)arid or artificial systems (i.e. pot experiments like
73 Damgaard et al. 2002) have been considered in which plant individuals are strongly spatially
74 segregated; ii) the dependence of allometric relationships on environmental conditions and
75 plant life stages have not been thoroughly investigated, so that the transferability of calibrated
76 allometric equations across study sites is to be demonstrated and iii) the influence of plant
77 architecture on the usefulness of the different biometric measures remains poorly
78 documented.

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

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

91



92

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

100

101 2. Material and Methods

102 2.1. Literature review

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

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*, *Arrhenatherum 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).

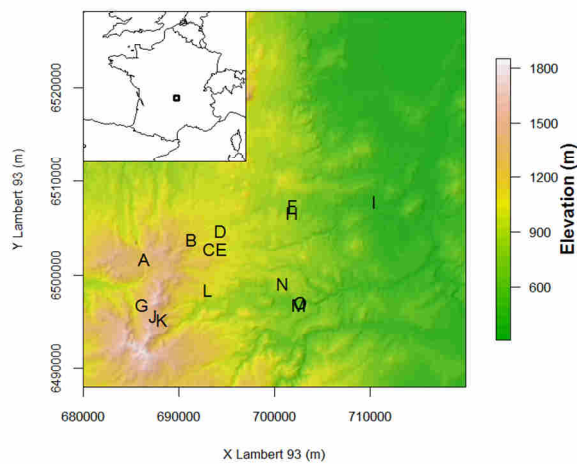
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Species	Height (mm)	LDMC (mg/g)	SLA (mm ² /mg)	SeedMass (mg)	Leaf distribution	Shoot growth form
<i>Achillea millefolium</i>	472	194.4	12.02	0.132	Semi-rosette	Stem erect
<i>Agrostis capillaris</i>	669	266.3	31.28	0.064	Regular distribution along the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

123

124 **Table 1.** Study species characteristics. Trait values are extracted from the LEDA trait
125 database (Kleyer *et al.* 2008).
126 We aimed at calibrating allometric equations that would hold for an array of environments,
127 plant size and phenological stages. To do so, we applied a double sampling procedure on plant
128 individuals collected in contrasted habitats. This procedure involved measuring and
129 harvesting ten individuals in four different sites for each of the twelve species studied
130 (resulting in a total of 40 individuals per species). We selected plants covering a wide range of
131 plant sizes and phenological stages. Since all species were not present at each site, we
132 collected data in a total of 15 sites located in the Sancy massif in Central France with
133 contrasted characteristics in terms of altitude, climate, topography, soil type and agricultural
134 use (Table 2). Field sampling was performed from early June to late July 2015 (Appendix C).
135 Sampling ten individuals of twelve species in four sites resulted in biometric measurements,
136 harvesting and weighing of 480 individual plants.
137

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	Abandoned
C	1454	840	1038	Volcanic	Mown
D	1384	915	1012	Plutonic	Grazed
E	1179	1134	934	Volcanic	Abandoned
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



138

139 **Table 2.** Site characteristics and locations. Temperature and precipitation are derived from
 140 100 m raster maps downscaled from the 1km Worldclim grids (Hijmans et al 2005) following
 141 the procedure of Dullinger et al (2012). DDEG5 stands for the annual sum of degree days
 142 above 5 °C. Soil data are derived from the European Soil Data Base V2.0 (2004).
 143 Agricultural use is deduced from field observations.

144

145 *2.3. Biometric measurements and allometric equations*

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










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

164 We considered three simple biometric measurements to estimate the minimum volume of
165 each plant: the maximum height, the basal circumference and the circumference at mid height
166 (Figure 1-B). Both circumferences were measured with a graduated tape by tightening organs
167 until first signs of resistance in order to avoid plant tissue damages. This procedure
168 minimizes measurement error by reducing inter-individual variations in standing volume
169 linked to neighbourhood conditions (Fig. 1). Furthermore, there is very little potential
170 variation in circumference measurement linked to the tightening force exerted by the
171 observer, since large tightening forces are avoided to preserve the plant from tissue damage.

172 These biometric measurements were recorded in the field for the 480 plant individuals
173 considered. The plants were then clipped to ground level. In the lab, we sorted dead material,

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

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

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	$B = d_1 \frac{H}{6} \left(A_{basal} + A_{half} + \sqrt{A_{basal}A_{half}} \right) + d_2 \frac{H}{6} A_{half}$	$B = \left[d_1 \frac{H}{6} \left(A_{basal} + A_{half} + \sqrt{A_{basal}A_{half}} \right) + d_2 \frac{H}{6} A_{half} \right]^z$
	Ellipsoid	$B = d \frac{4}{3} \pi H r_{half}^2$	$B = d \left(\frac{4}{3} \pi H r_{half}^2 \right)^z$

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

192

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

197

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

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

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

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

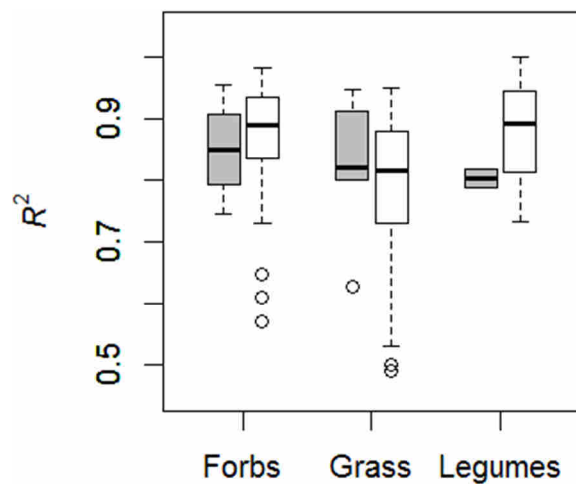
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222 **3. Results**

223 Among the 54 allometric equations, the most transferable one was selected for each of the 12
224 investigated species. The normalized errors reported for model transferability ranged between
225 0.11 and 0.35 with $\overline{NRMSE}_{transf} = 0.20$ (Table 4). Differences in predictive accuracy
226 between the most accurate and the selected models were low ($\Delta NRMSE$ ranging between 0

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

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



243

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

246

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

255 Models including life stage effects were selected for seven out of twelve species (Figure 3-C).

256 Although inclusion of life stage resulted in strong improvement for linear models (increase in
257 R^2 up to 40%), it did not improve power models by more than 7.2% except for *Lolium*

258 *perenne*, which showed an increase of 17%. Power functions were selected for seven out of

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*).
278
279

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

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

283

284 **Discussion**

285 The method proposed here is accurate, easy to implement and leads to equations that are
286 generally transferable between contrasted environments. The selected allometric equations
287 for each species showed high prediction accuracy and goodness of fit, similar to the results
288 reported in the literature (Appendix A). The main difference is that our method relies on the
289 minimum volume whereas other studies have used the apparent volume (e.g. Johnson et al.
290 1988, see Appendix A). The apparent volume can be easily estimated in systems where plants
291 are spatially segregated such as in arid habitats where all previous studies have been
292 conducted. However, in intricate vegetation, such as in temperate grasslands, the plant canopy
293 cannot clearly be delineated at the individual level. We here demonstrated that biomass
294 estimations based on the minimum volume efficiently circumvent this problem, making the
295 proposed method relevant to any herbaceous community.

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

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

309 consequence of allometric biomass allocation between stems, leaves and reproductive organs
310 during plant ontogeny that do not have the same bulk densities (Niklas 2004; Weiner 2004;
311 Poorter *et al.* 2015). Although the power function is biologically justified by the allometric
312 scaling theory, it was not always associated with significant fit improvements in our study.
313 Four out of twelve studied species exhibited linear relationships and several studies reported
314 good estimations of individual herb biomass from linear models (Gutierrez & Aguilera 1989;
315 Assaeed 1997; Röttgermann *et al.* 2000; Guevara *et al.* 2002; Hirata *et al.* 2007; van der
316 Eynden 2011). Isometric scaling between plant organs has been reported for small plants
317 (Enquist & Niklas 2002; Enquist *et al.* 2007; Poorter *et al.* 2015), and is consistent with
318 optimal biomass partitioning theory (Lohier *et al.* 2014). Our contrasted findings emphasize
319 the need to systematically consider linear and non-linear functions when fitting biomass
320 equations from biometric measurements of herbaceous individual plants, as currently
321 recommended for other plant groups (Chave *et al.* 2014).
322 Most importantly, we found that a single equation can reasonably be used to successfully
323 predict the biomass of individual plants in different habitats for the large majority of the
324 investigated species, at least within the range of environmental conditions investigated here,
325 which was already wide (Table 2). A notable exception was the perennial ryegrass (*Lolium*
326 *perenne*). It is possible that we sampled different selected ryegrass genotypes with contrasted
327 ecophysiological and morphological characteristics since different varieties of ryegrass are
328 used for hay production and pasture (Beecher *et al.* 2015). The strong site effect for this
329 species may therefore have been confounded with a genotype effect. To our knowledge this
330 study is the most comprehensive assessment of the transferability of biomass equations
331 between different environments for herbaceous species. A few previous studies have
332 compared allometric equations fitted for different disturbance regimes, including fire (van der
333 Eynden 2011) and grazing (Tausch *et al.* 1994; Nafus *et al.* 2009, but all were within

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

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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