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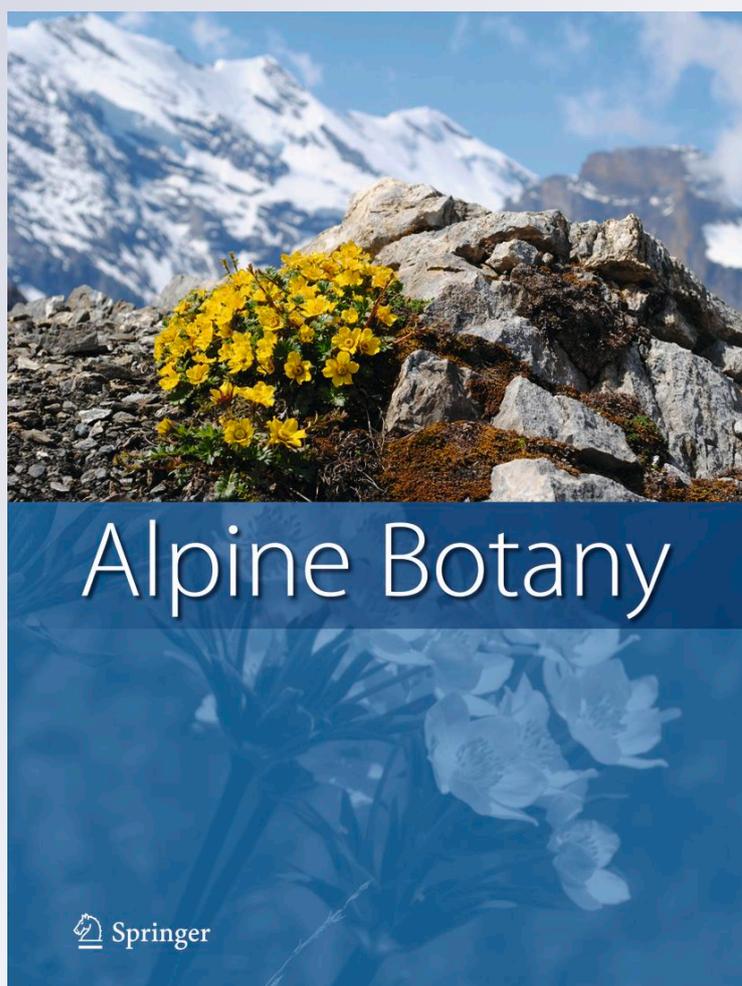
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Estimating herbaceous plant biomass in mountain grasslands: a comparative study using three different methods

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Abstract It is a challenge to find effective methods to estimate biomass over a large range of biomass values in diverse plant communities, such as typically found in mountain grasslands. We compared the performance of three non-destructive methods for estimating plant biomass (3D quadrat: a point quadrat method, plate meter: a measure of physical volume, and visual estimation: a component of

the BOTANAL method) in mountain grasslands. We tested whether: (1) all methods performed equally in terms of linearity of estimations over a large range of biomass and (2) under and over-estimations of biomass were related to specific plant compositions. We estimated plant biomass in 30 plots, for which real plant biomass was measured by destructive sampling. We accounted for the significant effect of heteroscedasticity (which was significant for all three methods) when testing for the linearity of the relationship between real biomass and biomass estimates. The plate meter displayed non-linearity, being insensitive to variation of biomass at low biomass values. BOTANAL and the 3D quadrat yielded linear relationships, with BOTANAL providing better estimates of real biomass (greater R^2). Specific floristic compositions (e.g. presence of *Deschampsia cespitosa*, *Chaerophyllum sp.*, and abundant small forbs) explained underestimation and overestimation of biomass estimates for the plate meter and 3D quadrat while BOTANAL was insensitive to floristic composition. In heterogeneous grasslands, BOTANAL appeared to be the most appropriate method, given its linear relationship with real biomass over the whole range of biomass and its low residual variation.

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Introduction

Although aboveground biomass is one of the primary characteristics of ecosystems measured in ecological, agricultural and forestry studies (Catchpole and Wheeler 1992), there is no universal method to estimate biomass valid across all plant communities and landscapes (Catchpole and

Wheeler 1992). This can limit comparisons of aboveground biomass within heterogeneous study sites, such as typically found in mountainous environments. Indeed, variation in slope, ecotones between forest and pastures and high variability in expected biomass (for example from scattered plant cover found in screes to lush alpine grassland) could lead to poor performance of methods typically developed for more homogeneous terrain or for specific growth forms. Requirements for a method to be useful in ecological studies performed in heterogeneous landscapes demand that it should be at least (1) un-biased estimator over the range of biomass studied, (2) be non-destructive, and if possible (3) quick, easy to implement and cheap (Catchpole and Wheeler 1992; Harmoney et al. 1997; t'Mannetje and Jones 2000).

Two categories of methods are commonly used. The first one, which is mostly conducted when calibrating other indices, is to harvest, hand-sort and weigh samples of vegetation from a number of quadrats (clip and weigh method, Catchpole and Wheeler 1992). This method is certainly accurate, but is destructive and time consuming. The second category of methods relies on indirect indices that are assumed to relate to biomass, if possible linearly. This includes several pasture plate or disk meter (Bransby et al. 1977, Schneider and Bell 1985), and methods such as point counting of various sorts: including the point-quadrat (Goodall 1952), canopy intercept (Frank and McNaughton 1990), point intercept (Jonasson 1988), point contact (Catchpole and Wheeler 1992) and 3D quadrat methods (Said et al. 2005). These methods are non-destructive, but are not always quick nor cheap. In addition, they are usually fine-tuned to estimate biomass of specific growth forms (e.g. 3D quadrat for leaf biomass in woodland, disk meter for grassland). Alternatively, another indirect method has been developed based on the calibrated visual assessment of biomass (e.g. as used in the visual estimation component of the BOTANAL method, Tothill et al. 1992). The latter is typically quick (after preliminary training sessions) and has been proven to perform well in mountain grassland and tropical rangeland situations (Coser et al. 1991, Dall'Agnol et al. 2005, Lavorel et al. 2008, Lopez-Guerrero et al. 1999, Mellors 1991, t'Mannetje and Jones 2000).

Here, we compare the performance of three non-destructive methods (3D quadrat, plate meter and BOTANAL visual estimation—hereafter BOTANAL) for estimating herbaceous aboveground biomass (with real values measured by harvesting and weighing) in forest understory and alpine grassland (excluding trees and shrubs) in a mountain environment. Given the heterogeneity in both biomass and floristic composition across a typical mountain landscape, effective methods should fill two criteria: (1) provide linear relationships across a wide range of biomass values to ease inverse-prediction and extrapolation (Osborne 1991), and (2) be robust to variation in floristic composition. For each

method, we, therefore, (1) tested linearity over the whole range of biomass values, (2) explored whether under or overestimation of biomass estimates occurred because of specific floristic compositions.

Materials and methods

Study site

The study was conducted from July 2nd to 8th 2008, immediately after the peak of biomass (Duparc et al. unpublished data), in the Bauges mountain massif located in the Northern French Alps (45°41'N, 6°08'E). The area is a sub-alpine calcareous massif where elevation ranges from 700 to 2,217 m, with only 2% of the area above 2,000 m (Loison et al. 1999). The tree line varies between 1,400 and 1,500 m. Most of the forest is composed of coniferous and deciduous trees dominated by beech (*Fagus sylvatica*) and fir groves (*Abies alba*). We selected herbaceous communities in clearings or pasture areas, encompassing a mosaic of plant communities (mainly Alpenrose heaths, Blue moor-grass-evergreen sedge swards, Matgrass swards, Mountain hay meadows, Rusty sedge grassland, Screes, Tall herb community, according to the CORINE biotope manual; European Community Commission 1991). Plots were located at two different sites of our study area (Armène 45°33'22.4"N 6°13'36.6"E; Bellevaux: 45°37'41.3"N 6°12'34.8"E).

Sampling design

We focused on estimating aboveground biomass of herbaceous vegetation over a large range of biomass. We chose 30 fixed plots (50 × 50 cm), with visually contrasting amounts of biomass (confirmed by the distribution of aboveground dried biomass, Fig. 1). Distribution of the plots was purely driven by a coarse of visual assessment of standing biomass. Each plot was measured successively with three non-destructive methods: plate meter, BOTANAL and 3D quadrat (see below for details). Afterwards, all aboveground biomass of each plot was harvested, dried at 55°C during 48 h and weighed to measure the real biomass. In addition, the plant composition of all plots was estimated by recording all plant species present in each plot to obtain a species list in presence/absence for each plot. Our protocol allowed us to explore the performance of the three tested methods tested to estimate biomass in a diversity of grasslands types.

Tested methods

The plate meter (Bransby et al. 1977; Rayburn and Lozier 2003) relates actual biomass to height resistance of the

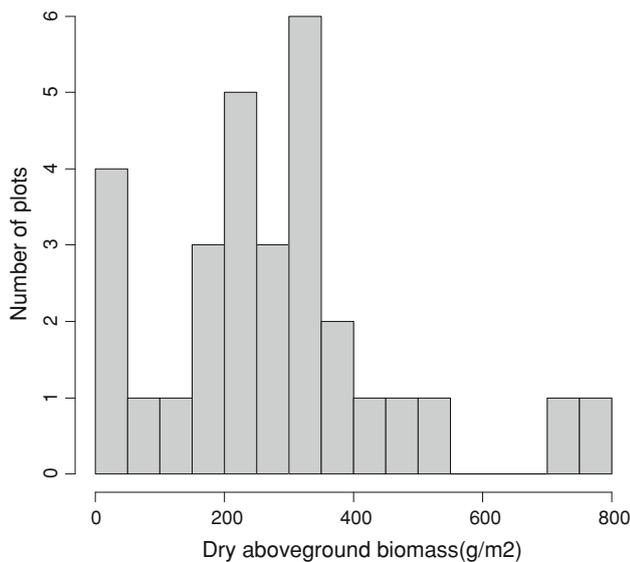


Fig. 1 Distribution of aboveground biomass values (in g/m²) estimated after cutting, harvesting and drying standing biomass of 30 plots (50 × 50 cm)

grassland. The plate meter consists of a plexiglass plate (50 × 50 cm; Rayburn and Lozier 2003) which slides along a graduated measurement scale. Height of the aboveground biomass is measured when the plate stops with vegetation canopy resistance.

BOTANAL (Tothill et al. 1992) combines visual estimates of biomass with the dry-weight rank method (Haydock and Shaw 1975). Here, we used only the visual estimation component of the BOTANAL method to estimate above-ground biomass. When using this method in the field, each observer estimates herbage mass in each quadrat which is then corrected by regression using a subset of quadrats which are estimated, harvested, dried and weighed (Lavorel et al. 2008, Tothill et al. 1992). In this study, we did not use the calibration equation to produce biomass estimates, but rather tested the accuracy of this calibration technique by confronting the observers visual estimates with real biomass over a large range of biomass (see Statistical analysis below). We first performed a training session (Lavorel et al.

2008, for details see Appendix) during which the biomass of 20 quadrats separate from the main experiment were harvested, dried and weighed, after the individual observer (C. Redjadj) had recorded visual estimates. This training involved learning to assess the amount of biomass present based on its volume, density, ground cover and the differing dry weights of various vegetation types (see Appendix for details on the training sessions). Following this preliminary training session, the observer visually estimated above-ground herbage mass (in g/m²) in each of the sampled 30 50 × 50 cm quadrats.

The 3D quadrat method (Said et al. 2005) is based on the principle of the point-contact method (Catchpole and Wheeler 1992) applied in a vertical 3-Dimensional quadrat (25 × 25 cm base, 165 cm height). This method is based on a linear relationship between the number of leaf contacts and leaf biomass (square root transformed), established for each species or plant category with similar leaf shapes (Said et al. 2005). As part of our study, we set up the 3D quadrat in the center of the plot. We recorded the number of contacts for each plant species on the five pins of the 3D quadrat in the 0–85 cm height stratum. We then converted the number of contacts into biomass (g/m²) for each plant species or plant category, based on Said et al. (2005) and our own calibrations.

Statistical analysis

For each method, we fitted a set of models to test for linearity of the relationship between real biomass and estimates from the three methods (estimated biomass for BOTANAL and 3D quadrat, and height for the plate meter). We checked for linearity by testing for a quadratic term (Table 1). Due to possible heteroscedasticity, we chose to use Generalized Least Square regression (GLS, Pinheiro and Bates 2000), whereby we modeled heteroscedasticity by specifying that the residual variance varied exponentially with increasing real biomass. Heteroscedasticity can be tested for by comparing the GLS regression with and without the variance function in the error term. Models without variance function

Table 1 Models fitted to test for the linearity of the relationship between dry aboveground biomass and indices or estimates of biomass obtained from three different methods, BOTANAL, plate meter, and 3D quadrat

Model			Method					
Dry biomass	Method	df	BOTANAL		Plate meter		Q3D	
			ΔAIC	R ²	ΔAIC	R ²	ΔAIC	R ²
Testing for linearity			ΔAIC	R ²	ΔAIC	R ²	ΔAIC	R ²
1. Linear	Ols	3	20.12	0.649	29.65	0.400	26.30	0.181
2. Quadratic	Ols	4	15.32	0.720	31.47	0.403	24.66	0.275
3. Linear	Gls	4	0	0.823	1.81	0.330	0	0.602
4. Quadratic	Gls	5	1.51	0.825	0	0.410	0.99	0.615

Lowest AIC values indicating the selected overall model are in bold

in the error term correspond to Ordinary Least Square (OLS) regressions. Estimates from the GLS regressions were calculated based on restricted likelihood methods. We re-fitted GLS models with a maximum likelihood method (Pinheiro and Bates 2000) and performed model selection using an information theoretic approach (AIC, Burnham and Anderson 2002). The model with the lowest AIC was selected as the best model. If models differed by less than 2 points in AIC, we selected the model with the lowest number of parameters. We calculated the generalized coefficient of determination (Nagelkerke 1991) to estimate the percentage of variability in the observed biomass explained by the best model.

Finally, we explored whether under- or over-estimation by each method was related to the floristic composition of each plot. We considered the residual values of the best model (linear or quadratic) and split these residuals into three groups (strongly negative, strongly positive, and close to 0 residuals) based on quartiles (respectively, lower to 1st quartile, upper to 3rd quartile, and between 1st and 3rd quartile). We then performed a Between-Class PCA (Dolédec and Chessel 1987) based on the plant composition of each plot (presence/absence of plant species per plot), contrasting the three categories of residuals. A permutation procedure (Dolédec and Chessel 1987) examined whether the plots belonging to the three categories of residuals significantly differed in terms of plant composition. Lastly, we identified those plant species contributing most in explaining the deviance of each plot's index value compared to the expected value.

Results

Linearity of the relationship between indices and aboveground biomass

The height measured with the plate meter was the only index to display non-linearity with aboveground biomass: for this method the quadratic model was better supported than the linear one (Table 1, $R^2 = 0.410$). This quadratic relationship shows that measures of height barely increase with dry biomass for low values of biomass (Fig. 2b). For BOTANAL and 3D quadrat, the linear model fit was better than the quadratic one (Table 1). The relationship between estimated biomass and real biomass was, however, better with the BOTANAL than with the 3D quadrat (BOTANAL: $R^2 = 0.823$, 3D quadrat: $R^2 = 0.602$, Fig. 2).

For all indices, there was evidence of heteroscedasticity, as models with generalized least squares always performed better than models with ordinary least squares (in terms of AIC values, Table 1). There was indeed an increase in the variance in the error with increasing biomass. As

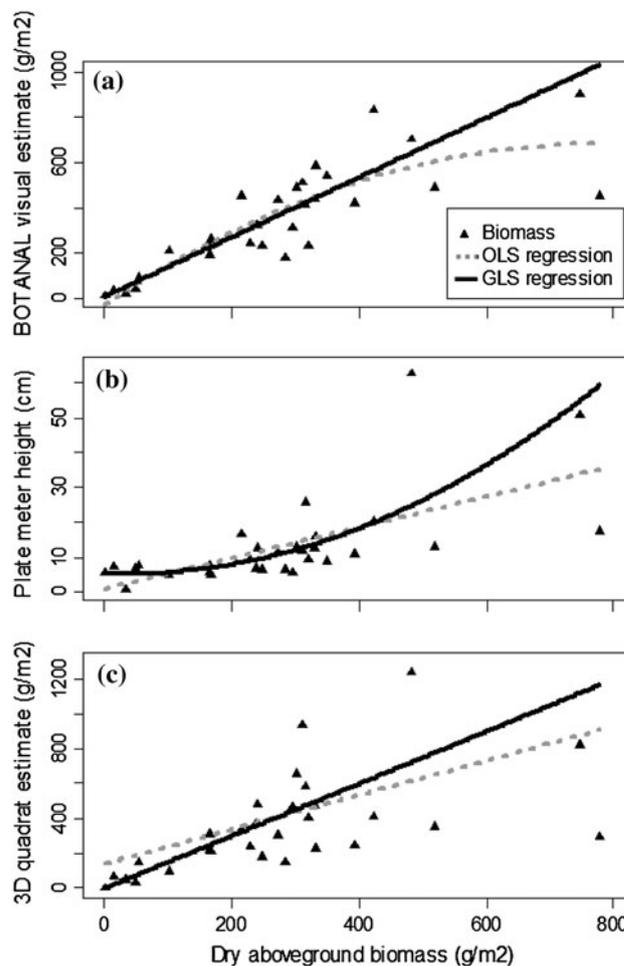


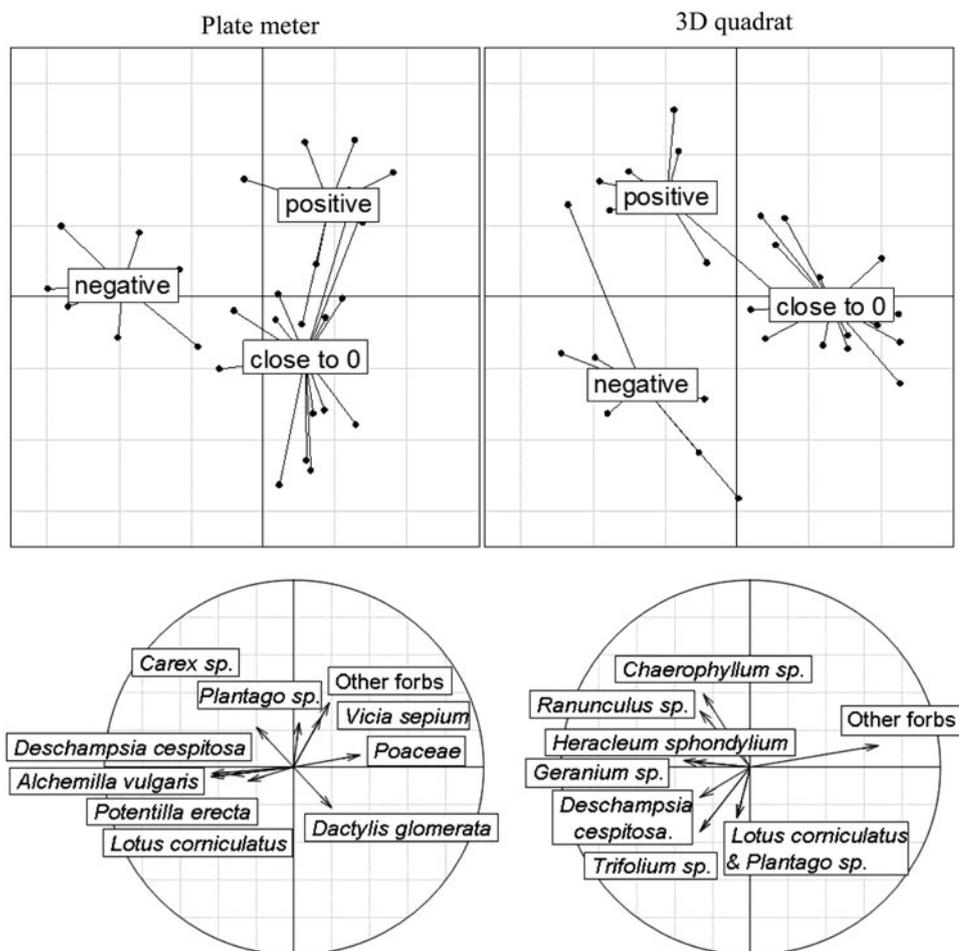
Fig. 2 Estimates of biomass plotted against dry aboveground biomass for **a** BOTANAL, **b** plate meter, and **c** 3D quadrat, using Generalized Least Square regression (plain line) and Ordinary Least Square regression (dashed line)

exemplified here, the use of ordinary least squares regression would have led us to a misleading model selection (see Table 1), with poor distribution of residuals over the range of dry biomass values (especially for 3D quadrat and plate meter, Fig. 2).

Effect of plant composition

The Between-Class PCA contrasting the different categories of residuals according to their floristic composition showed that for the plate meter and 3D quadrat underestimation and overestimation were associated with particular plant species in each plot (Fig. 3). The contrast between the three groups of residuals was significant for the plate meter ($P = 0.010$) and the 3D quadrat ($P = 0.001$), but not for BOTANAL ($P = 0.240$) and with different origin. For the plate meter, the contrast between the three groups was mainly driven by *Deschampsia cespitosa* and *Alchemilla vulgaris* which were

Fig. 3 Between-class analysis based on plant composition of plots depending on whether the plot's residual was strongly negative ("negative" category), strongly positive ("positive" category) or close to fitted values ("close to 0" category)—see text for details. *Points in the upper graphs represent each sampling quadrat, positioned according to its score value on the two first axes of the between-PCA. Lower graphs show how each plant species or plant group contribute to the first two between-PCA axes. Left box plate meter, right box 3D quadrat*



associated with “negative” residual values, by “Others forbs” (unidentifiable small forbs) which were associated with “positive” values of residuals, and finally by *Dactylis glomerata*, which was associated with residual values “close to zero” (Fig. 3). For the 3D quadrat method, the contrast between the three groups was mainly driven by six plants: “Other forbs” were associated with residual values “close to zero”, *Chaerophyllum sp.* and *Ranunculus sp.* with “positive” residual values and *Trifolium sp.*, *Deschampsia cespitosa*, *Lotus corniculatus* and *Plantago sp.* with “negative” residual values (Fig. 3).

Discussion

Our objective was to test the reliability of alternative methods for estimation of biomass in the field within landscapes containing a wide range of grassland biomass values and floristic composition, as is typical in mountains. Our results suggest that the three methods we tested estimated plant biomass differently according to the aboveground biomass and composition, over a relatively large range of biomass values. The differences among methods can be found in (1)

the linearity or non-linearity of the relationship between estimated biomass and real biomass, and in (2) the sensitivity to plant composition. In addition, whatever the method, estimates from all methods exhibited heteroscedasticity, where variance increased with increasing biomass. Not accounting for this statistical problem can lead to misleading inferences about the model best describing the index to biomass relationship (White 1980). Heteroscedasticity showed that estimates had a higher variance when a plots' dry biomass was larger. The biological causes of this large variance (higher risk of overestimating or underestimating dried biomass) appear to be due to variance in vegetation structure (vertical stratification) and in differing species tissue densities at high biomass. Acknowledging the occurrence of heteroscedasticity should also help in designing protocols in heterogeneous grasslands, allocating more sampling effort into grasslands/plots expected to have a higher biomass.

For the sake of simplicity, most calibration methods used in ecological studies are based on linear regressions. Non-linear models tend to be easy to overfit and make it more difficult to perform inverse predictions (Osborne 1991). Here, we found that the plate meter method led to a

non-linear relationship with biomass. This was mainly due to its poor performance in estimating biomass in quadrats with low aboveground biomass (<200 g/m²). In these quadrats the height measured by the plate meter was virtually insensitive to changes in biomass among plots, as the plate meter measured microtopography, such as surface rocks, rather than real aboveground biomass. Therefore, depending on the question of interest, this approach may lead to irrelevant measure of biomass. For example, in mountainous landscapes composed of heterogeneous communities and where screes are important habitats for ungulates (Calenge 2007, Darmon et al. 2012), it is of prime importance to accurately estimate the amount of resources they can find in such habitat. Using plate meter is obviously not advisable in such environments to address the question of resource availability to herbivores.

Looking more closely at the causes of the observed under- or over-estimation of biomass, we found that the accuracy of the plate meter and 3D quadrat methods was sensitive to the occurrence of a few plants or groups of plants because of their morphology or mechanical properties. For instance, *Deschampsia cespitosa* is a tough tussock Poaceae, with morphology similar to other graminoids, but with a high dry matter content in leaves. Hence, biomass in plots with high occurrence of this species tends to be underestimated, especially when using the plate meter. For the 3D Quadrat, overestimation is provided by the presence of tall herbs with a loose foliage and low tissue density such as *Chaerophyllum* sp. which produces high number of hit in relation to its dried biomass. Other forbs lead to overestimation for plate meter, but for a different reason, it was usually found in low biomass concentrated close to the ground for which height is misleading due to a measurement of micro-topography instead of biomass. In contrast, the BOTANAL method performed well over a wide range of aboveground biomass and was largely independent of plant composition due to the capacity of a trained observer to adapt their visual estimates to the nature of the floristic composition.

The visual estimation from the BOTANAL appears to be the most appropriate method to estimate aboveground biomass in a diversity of herbaceous strata, being the method with the greatest explanatory power (the largest R^2 of the three methods). The 3D quadrat method performed rather well in terms of linearity, but was more sensitive to plant composition and had a lower coefficient of determination (0.602 vs. 0.823 for 3D quadrat and BOTANAL respectively). The performance of the 3D quadrat may also be affected by the quality of the reference equations established for species or plant category. BOTANAL and the 3D quadrat share the drawback of requiring some training and calibration prior to being used. For example for BOTANAL, the observer must learn to incorporate into their visual estimates the relative dry weights of differing categories of species and

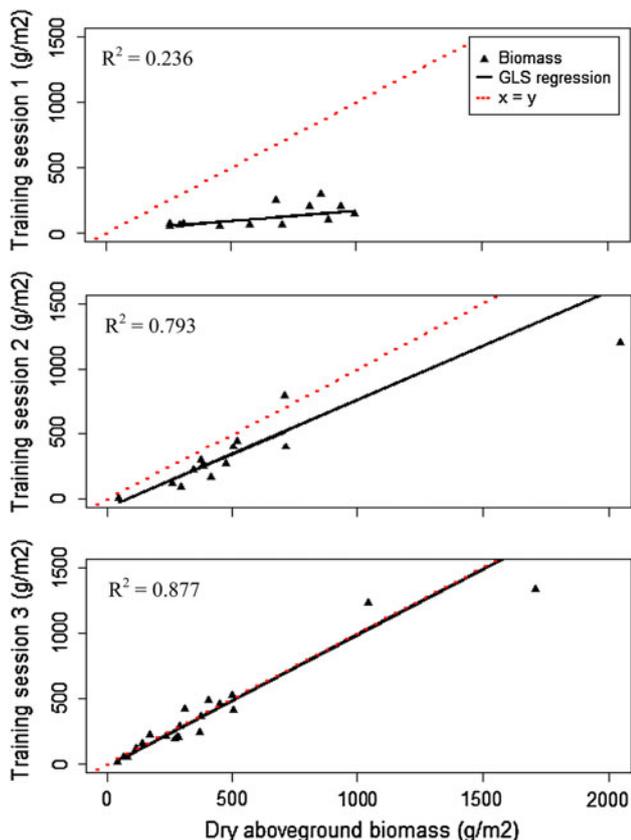
must develop an initial calibration of visual biomass estimates versus real biomass in a subset of quadrats. This BOTANAL calibration is also observer-specific where each observer needs to produce their own calibration for each measurement session (e.g. sampling campaign), adding some constraints to the execution of field work. Another issue that needs to be acknowledged in the use of visual estimations is the problem of observer bias. Each individual observer tends to have their own scale of estimates in relation to the actual biomass, and thus each observer tends to have a different correlation equation between estimated and real biomass. However, this is not a problem given that each observer visual estimates is corrected with his/her own calibration equation. In a previous study using the BOTANAL method in a mountain environment with two observers, the slopes and intercepts of the correlations between estimated and true biomass for the two observers were significantly different, but the R^2 of the two observers was comparable (Lavorel et al. 2008).

The plate meter method is not prone to the same problems. Indeed, plate meters are easy to build and can be used with hardly any prior training. Yet, we cannot advise the use of this method in heterogeneous grasslands with very low biomass. Recently Fehmi and Stevens (2009) showed that plate meters inadequately estimated biomass in semi-arid grassland because tillers dry up with senescence and plants become less flexible and more able to resist the weight of the plate, leading to overestimations of biomass. Using a plate meter when micro-topography is not an important issue should, however, not be a problem, and its otherwise ease of use certainly explains its wide success (Bransby et al. 1977). More sophisticated plates or systems of microplates have been developed (Radloff and Mucina 2007) that can be used to obtain estimates of low spatial scale variation in biomass, but these are unlikely to solve the problem of micro-topography and the estimation of biomass for plots with very low biomass. At our study site, typical of the external Alps, we would advise the use of BOTANAL, which requires a short training (see Appendix as instance) and calibration period, but is easily mastered by inexperienced operators and performs well over a wide range of biomass values while requiring only minimal equipment to be carried over rugged and steep areas. BOTANAL was the method successfully used in a study of alpine grasslands in a similar environment in the central French Alps (Lavorel et al. 2008). A consideration of the various advantages and shortcomings of each the various methods of biomass estimation, as related to the range of biomass and habitat heterogeneity of the site, is recommended as a prerequisite prior to any study estimating biomass.

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Appendix

Three successive training session for visual estimate of BOTANAL (g/m²) of a same observer (C. Redjadj), using GLS regression (number of quadrat for the three training session were respectively: $n = 13, 14, 20$). R^2 are given for each training session.



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