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SHORT COMMUNICATION

Allometric equations for biomass assessment of subalpine dwarf shrubs

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Abstract Shrubs are an important component of mountain ecosystems in terms of productivity and diversity. The estimate of shrub biomass via allometric equations represents a non-destructive alternative to obtain quantitative data. We propose allometric equations to estimate aboveground biomass from easily acquirable descriptive parameters of plant height and cover using linear models for five of the most abundant subalpine shrub species in European mountain or boreal ecosystems: *Rhododendron ferrugineum*, *Vaccinium myrtillus*, *V. uliginosum*, *V. vitis-idaea* and *Juniperus sibirica*. Samples used for the establishment of the equations are from non-disturbed *Pinus cembra–Larix decidua* stands, and from adjacent stands frequently disturbed by snow avalanches. The equations adequately predict shrub biomass for all species except *V. uliginosum*. They thus provide a useful and non-destructive method for estimating aboveground shrub biomass in subalpine ecosystems.

Keywords Method · Mountain · Ecosystem · Disturbance · Avalanche · Forest

Introduction

Forest biomass assessment via allometric equations represents a useful tool in the study of terrestrial ecosystems as it offers a non-destructive and time-affordable method (Case and Hall 2008; Liu and Westman 2009). Most applications of this approach in Europe have focused on the estimation of tree biomass (e.g. Muukkonen 2007) because it is the principal sink of carbon sequestration in forests (Beedlow et al. 2004). Shrubs have been neglected but are key drivers of forest productivity and diversity, notably in the cold ecosystems like the subalpine or boreal types (Ponge et al. 1998; Nilsson and Wardle 2005; MacKenzie and DeLuca 2006). Mountain forests are largely subjected to global changes and are facing severe land-use abandonment (Tasser and Tappeiner 2002; Motta and Lingua 2005; Chauchard et al. 2010), which can alter the shrubs' dynamics and biomass (Tappeiner et al. 2008; Rammig et al. 2010) and thus the forest productivity and functioning. Indeed, a clear relationship has been observed between the cover of dwarf shrubs and the course of the secondary succession in subalpine forest after land-use abandonment, which is also linked to the elevation status of the community, whether close to the forest limit or not (Tasser and Tappeiner 2002). When the shrub density is much too high, the tree recruitment is impacted (Tasser et al. 2007). Finally, dwarf shrubs play an important role in increasing the probability of avalanche release (Viglietti et al. 2010). For these reasons, the measurement of the shrub biomass offers valuable data that complement the forest tree biomass data, and should help to decipher the functional role of this ecosystem compartment.

Here, we test allometric equations based on descriptive parameters (plant height and plant cover) for subalpine dwarf shrubs of the European Alps, assuming that these parameters are convenient enough to model specific

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biomass. Measurements were carried out in two different ecological contexts: non-disturbed forest stands and stands disturbed by snow avalanches. Avalanches constitute a key disturbance process of subalpine ecosystems, altering the biomass and composition at the community and the landscape scale (Malanson and Butler 1984; Bebi et al. 2009). Data used to establish the equations were gathered from three sites, each composed of a non-disturbed forest stand and its adjacent avalanche path. This ecological variability offers a range of conditions adequate for the establishment of specific allometric equations that will be valid for most of the situations met in the subalpine ecosystems in European mountains. The paper does not aim to discuss the ecological function of avalanches on dwarf shrubs of subalpine ecosystems, but aims to propose allometric equations to estimate their aboveground biomass.

Materials and methods

Study area

The study area is located in the inner western Alps on the commune of Orelle (45°11′15″N–6°32′16″E, 2,000–2,100 m a.s.l.) situated in the Maurienne valley, one of the driest in the Alps. Mean annual precipitation of 925 ± 233 mm and mean annual temperatures of 3.5 ± 0.6°C (−5.6 ± 1.2°C for January, 12.5 ± 0.7°C for July) were recorded at 2,025 m a.s.l. (Bessans meteorological station, years 1984–1999).

Each of the three sites is a pair made up of a non-disturbed forest stand and its adjacent snow avalanche path. The forest stands have been mixed overstoreys for ca. 8,000 years (Blarquez et al. 2010) and are dominated by arolla pine (*Pinus cembra* L.) and larch (*Larix decidua* Mill.), with scattered spruces (*Picea abies* (L.) H. Karst.), green alders (*Alnus viridis* Chaix.) and mountain ashes (*Sorbus aucuparia* L.). The woody understorey is essentially composed of *Rhododendron ferrugineum* L., *Vaccinium myrtillus* L., *V. uliginosum* L., *V. vitis-idaea* L., and *Juniperus sibirica* Lodd. ex Burgsd. The soils of this subalpine forest are podzols (Mourier et al. 2008).

Sampling methods

Twenty sampling units per stand were selected on a grid between 2,000 and 2,100 m a.s.l., with 10 sampling units within each of three avalanche paths (OR102, OR107 and OR112; mean avalanche interval since 1911 is 7.5, 8.8 and 10.5 years, respectively), and 10 within each adjacent forest stand. Each sampling unit size was 4 m^2. The cumulated sampling surface is therefore 240 m^2 (i.e. 4 m^2 × 60 sample units).

In each sampling unit, all the aboveground biomass (AGB) was collected using clippers per shrub species. The biomass (wood and leaves) was then dried and weighed in the laboratory and expressed in dry weight per area (in kilograms per hectare). We measured five heights per shrub species (one near each corner and one in the centre of the 4-m^2 quadrat) per unit to obtain a mean height value (MH in centimetres). The shrub cover percentage (C) per species was consensually estimated on a continuous scale by the four or five observers.

Analytical methods

Specific allometric equations were obtained by ordinary least-squares multiple linear regressions of AGB on MH, C and their interaction. All variables were log-transformed (base e) prior to parameter estimation in order to make the distributions symmetric. Normality and homoscedasticity of residuals were assessed with the Shapiro–Wilk and Breusch–Pagan test, respectively. For significant overall models (i.e. models with the two independent variables and their interaction $\ln C \times \ln \mathrm{MH}$), a forward selection of explanatory variables was performed following the procedure described in Blanchet et al. (2008) in order to reduce their complexity. This method uses both the usual alpha significance level and the overall coefficient of multiple determination as stopping criteria. To further illustrate our model selection, we used a permutation test for Pearson's correlation coefficient (Legendre and Legendre 1998) to explore the relationship between the two explanatory variables C and MH.

Leave-one-out cross-validation was performed on these reduced models in order to evaluate their prediction error (root mean square error, RMSE; Davison and Hinkley 1997). The coefficient of variation (CV) of the RMSE expresses the stability of the models. Plots and Pearson's linear correlations of observed and predicted AGB values further illustrate the accuracy of predictions.

All analysis and plotting were performed in the R environment (R Development Core Team 2011), and relied on the boot (Canty and Ripley 2010), ggplot2 (Wickham 2009), lmtest (Zeileis and Hothorn 2002) and packfor (Dray et al. 2009) packages.

Results

Among the ten species of shrubs observed, five are sparse or have no homogeneous distribution between the different stands (Table 1): *Cotoneaster integerrimus* Medik. and *Thymus serpyllum* L. (1 sample unit each), *Arctostaphyllos uva-ursi* L. (3 sampling units), *Empetrum nigrum* L. (7) and *Lonicera nigra* (10). Their dry AGB is generally low (<200 kg ha^{-1}) except for *L. nigra* (766 ± 181 kg ha^{-1};

Table 1 Mean dry aboveground biomass (AGB), height and cover measurements of shrub species

Species	Sample numbers[a]	AGB (kg ha^{-1})[b]	Height (cm)[b]	Cover (%)[b]
Juniperus sibirica	23	2,225 ± 510	31 ± 2	15 ± 4
Arctostaphyllos uva-ursi	3	998 ± 554	17 ± 2	2 ± 2
Cotoneaster integerrimus	1	45 ± 0	Not measured	~0
Empetrum nigrum	7	198 ± 70	15 ± 2	9 ± 7
Lonicera nigra	10	766 ± 181	57 ± 4	13 ± 6
Rhododendron ferrugineum	40	4,048 ± 593	45 ± 2	22 ± 3
Thymus serpyllum	1	60 ± 0	Not measured	~0
Vaccinium myrtillus	58	1,220 ± 135	27 ± 1	27 ± 3
Vaccinium uliginosum	21	1,830 ± 228	25 ± 1	37 ± 4
Vaccinium vitis-idaea	32	244 ± 57	10 ± 1	3 ± 1

[a] Number of samples represents the number of sampling units in which the species were present

[b] Data are presented as mean ± standard error (SE)

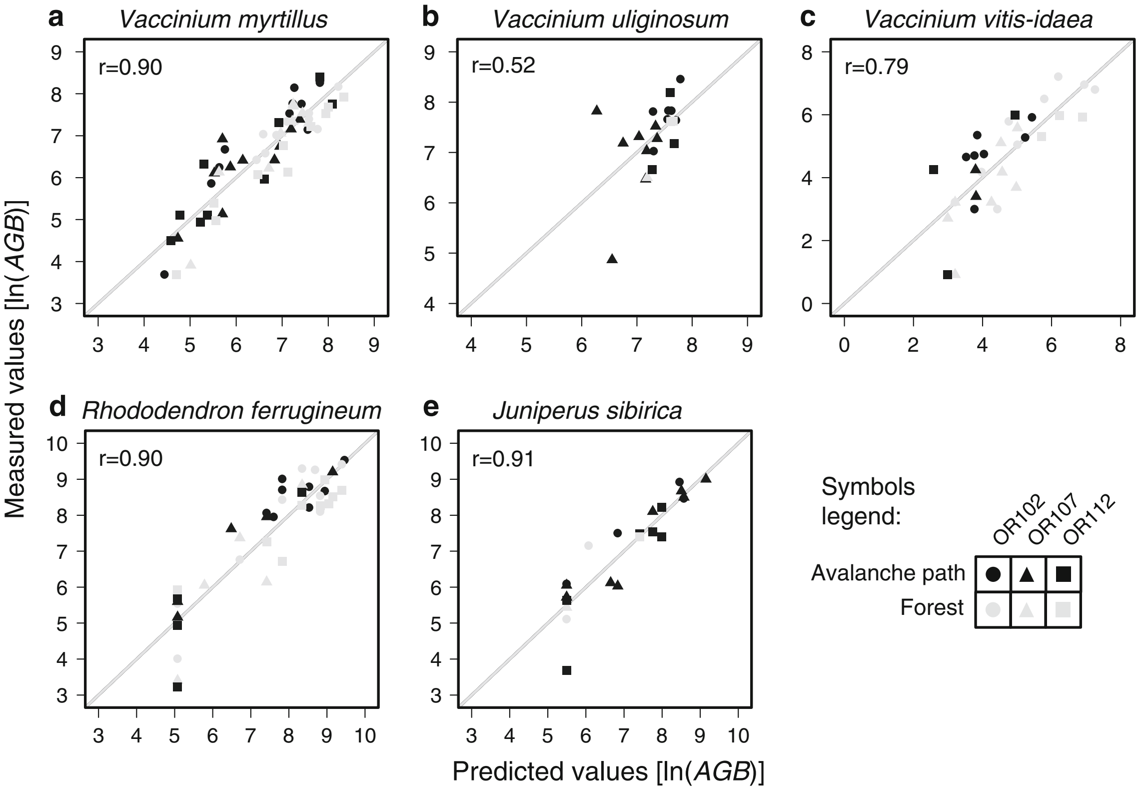

Fig. 1 Correlation between the observed values of dry aboveground biomass and the model predicted values (AGB, kg ha^{-1}). *Grey line* 1:1 ratio

mean ± SE) and *A. uva-ursi* (998 ± 554 kg ha^{-1}). This pattern means that these species are not frequent and have patchy distributions. Other species occur in at least 30% of sample units (i.e. >20/60 sampling units), and their biomass is generally high (>1,000 kg ha^{-1}), except for *Vaccinium vitis-idaea* which has an AGB of 244 ± 57 kg ha^{-1} (Table 1). The most abundant species is *R. ferrugineum* (4,048 ± 593 kg ha^{-1}), and the most frequent is *V. myrtillus* (58/60 units). The total AGB estimated for this subalpine ecosystem is 11,634 kg ha^{-1} (~1.2 kg m^{-2}) based on the sum of all species' mass.

Only five of the ten observed species present enough data for the development of allometric equations (Fig. 1). Table 2 displays the whole range of mean height (MH) and cover measurements (*C*) along with the allometric equations obtained after forward selection of explanatory variables for these five species. For *J. sibirica* and *R. ferrugineum* the equation is based only on term *C*; although the correlation between MH and *C* for *J. sibirica* is not significant ($r = 0.11$, $p > 0.05$, Table 2), *J. sibirica* AGB seems to depend mostly on its cover, the model being such that:

Table 2 Allometric equations for dry aboveground biomass (AGB, kg ha^{-1}) for the five most abundant shrubs species

Species	Equation	MH (cm)	*C* (%)	MH–*C r*	*p*	Adjusted R^2	*F* statistic	*p*	RMSE	CV (RMSE)
Juniperus sibirica	$\ln AGB = 0.835 \ln C + 5.492$	16–55	1–80	0.11	>0.05	0.82	101.30	<0.001	0.63	0.09
Rhododendron ferrugineum	$\ln AGB = 1.016 \ln C + 5.076$	20–65	1–75	0.47	<0.01	0.80	167.00	<0.001	0.77	0.10
Vaccinium myrtillus	$\ln AGB = 0.723 \ln C + 0.688 \ln MH + 2.415$	13–52	1–95	0.59	<0.01	0.80	118.90	<0.001	0.53	0.08
Vaccinium uliginosum	$\ln AGB = 0.183 \ln C \times \ln MH + 5.307$	16–35	1–70	−0.33	>0.05	0.23	7.14	<0.05	0.84	0.11
Vaccinium vitis-idaea	$\ln AGB = 0.361 \ln C \times \ln MH + 0.958 \ln MH + 1.665$	3–19	1–20	0.40	<0.05	0.59	23.71	<0.001	1.07	0.23

MH mean height range, *C* cover range, *MH–C r* Pearson's correlation coefficient permutation test between mean height and cover and associated *p* value (*p*), *Adjusted* R^2 adjusted coefficient of determination, *F statistic* Fisher's exact test value and associated *p* value, *RMSE* root mean squared error, *CV(RMSE)* coefficient of variation from the leave-one-out cross-validation

$$\ln \mathrm{AGB} = a \ln C + b \tag{1}$$

With only the vegetation cover, the equations describe more than 80% (adjusted R^2) of the measured AGB ($p < 0.001$). The models are solid, with a coefficient of variation of the root mean squared error, CV(RMSE), of 0.09 and 0.10 for *J. sibirica* and *R. ferrugineum*, respectively, which indicate a good stability of the model (Table 2). For *V. myrtillus*, both MH and *C* are kept by forward selection although these two variables are linked ($r = 0.59$, $p < 0.01$, Table 2), and the allometric equations have the following form:

$$\ln \mathrm{AGB} = a \ln C + b \ln \mathrm{MH} + c \tag{2}$$

The adjusted R^2 is high (0.80) and the CV(RMSE) indicates a good stability (0.08, Table 2). For *V. uliginosum*, although the CV(RMSE) is low (0.11), the adjusted R^2 is low and explains only 23% of the measured AGB distribution. The allometric equation is based only on the interaction term. *C* and MH where not significantly correlated for this species ($r = -0.33$, $p > 0.05$, Table 2):

$$\ln \mathrm{AGB} = a \ln C \times \ln \mathrm{MH} + b \tag{3}$$

For *V. vitis-idaea*, despite a more complex equation incorporating both MH and the interaction term, although *C* and MH are correlated ($r = 0.40$, $p < 0.05$, Table 2), the adjusted R^2 is not very high (0.59) but highly significant (Table 2):

$$\ln \mathrm{AGB} = a \ln C \times \ln \mathrm{MH} + b \ln \mathrm{MH} + c \tag{4}$$

The main problem with the last equation is the CV(RMSE) of 0.23, a rather high value showing the instability of the model. A larger data set should allow for stabilization of the model for *V. vitis-idaea*.

Discussion

Allometric equations were obtained for the main five subalpine shrubs representing most of the woody AGB of the European mountain ecosystems. The specific AGB is within the same range as values measured in other areas of the Alps for *R. ferrugineum* (Pornon and Doche 1996; Genries et al. 2009), *V. vitis-idaea* and *V. myrtillus* (Gerdol et al. 2004; Genries et al. 2009). The total estimated AGB for this subalpine ecosystem (~ 1.2 kg m^{-2}) is of similar magnitude to the AGB assessed for dwarf shrub communities on both acidic and calcareous soils from the eastern Alps (Tappeiner et al. 2008), but clearly above the range of AGB inferred for the European boreal-type ecosystems (Wardle et al. 1997), suggesting that these subalpine ecosystems are probably more productive than those of the northern European boreal forest composed of *Picea abies* and *Pinus sylvestris* with an understorey dominated by *V. myrtillus* or *Empetrum nigrum*.

The adjusted coefficients of determination (R^2) are high, except for *V. uliginosum* (Table 2). Consequently, the allometric equations provide reliable predictions for four species: *R. ferrugineum*, *V. myrtillus*, *V. vitis-idaea* and *J. sibirica*. These four species are the most abundant subalpine species in the Alps. Only one abundant species is absent from our data set, which is *R. hirsutum* L., an abundant species co-existing with *R. ferrugineum* only in the central and the eastern Alps. The physiognomy of *R. hirsutum* and *R. ferrugineum* is very close, but differs in terms of chemical-related soil preferences (Larcher and Wagner 2004) and drought-related physiological plasticity (Mayr et al. 2010). But, we assume that our equation could also be used to estimate the biomass of *R. hirsutum*, because of the great similitude between the two rhododendron species. Although significant ($p < 0.05$), the adjusted R^2 for *V. uliginosum* is rather low. The equation for *V. uliginosum* must be used with caution and remains to be confirmed by new measurements, especially for values below 400 kg ha^{-1} ($\ln\text{AGB} = 6$), which is certainly the main limitation of the distribution to adjust the model.

The large CV(RMSE) for the *V. vitis-idaea* model (0.23, Table 2) could result from an underestimation of C for this species. Indeed, *V. vitis-idaea* is usually shorter than all other shrubs considered here (Table 1) and this could hinder visual estimation of cover. Moreover, *V. vitis-idaea* generally grows in the understorey of the other dwarf shrubs and its physiognomy (herb-like) differs when the plant is directly exposed to sun light compared with plants growing within the forest.

The observed infrequent dwarf shrubs (*Arctostaphyllos uva-ursi*, *Cotoneaster integerrimus*, *Empetrum nigrum*, *Lonicera nigra*, *L. caerulea*, *Sorbus chamaemespilus*, *Thymus serpyllum*) were too rare to assess allometric equations. A specific protocol should be adapted for these species that display patchy distributions in the forest, taking into account a different sampling effort and strategy compared with taxa such as *Rhododendron*, *Vaccinium* or *Juniperus*. However, a non-destructive method might not needed for these infrequent species in subalpine forests, because they might not be relevant from a biomass-based functional perspective. When these species are recognized, it should be possible to cut and weigh them if the issue is to obtain a representative assessment of shrub biomass of all species at the stand scale.

Conclusion

We developed allometric equations that allow the estimation of the AGB without total plant destruction. These equations were established for five species that are the most abundant dwarf shrubs of subalpine ecosystems, *R. ferrugineum*, *V. myrtillus*, *V. uliginosum*, *V. vitis-idaea* and *J. sibirica*. Although these equations are solid, those for *V. uliginosum* and *V. vitis-idaea* need to be consolidated with additional data. Ideally, all these equations should be tested with larger data sets encompassing ecological contexts not presently taken into account, including gradients in soil productivity, elevation and slope. Such equations will be useful for studies that need to estimate the AGB to test the effect of ecological stresses or disturbances.

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