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Estimating plant biomass in early-successional subtropical vegetation using a visual obstruction technique

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Keywords
Above-ground plant biomass; Bahamian coppice; Robel pole; Structurally diverse vegetation; Subtropical shrubland

Abbreviations
KW = Kirtland's warbler; VO = visual obstruction

Nomenclature
Correll & Correll (1996)

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Abstract

Aim: Non-destructive methods for quantifying above-ground plant biomass are important tools in many ecological studies and management endeavours, but estimation methods can be labour intensive and particularly difficult in structurally diverse vegetation types. We aimed to develop a low-cost, but reasonably accurate, estimation technique within early-successional Bahamian broadleaf shrub vegetation.

Location: Eleuthera, The Bahamas.

Methods: Our biomass estimation technique was based on a visual obstruction method originally developed for use in grassland vegetation, but modified to suit our mixed vegetation structure. Visual obstruction measures were recorded for a total of 90 0.25-m^2 quadrats from which all standing vegetation was subsequently collected, dried and weighed. Regression models were then developed to predict vegetation dry weight (biomass) from visual obstruction.

Results: The field time and equipment costs required to obtain our visual obstruction measures were low, and the accuracy of our above-ground plant biomass predictions was on par with that reported for other estimation techniques. Should increased accuracy or additional structural information be desired, our basic technique can be enhanced by adding other easily obtained measures (e.g. woody stem circumference).

Conclusions: Our low-cost technique yields reasonably accurate estimates of above-ground plant biomass and should be transferable to any shrubland vegetation type where the maximum height of vegetation is typically below 2 m.

Introduction

Non-destructive methods for quantifying above-ground plant biomass are important tools in many ecological studies and in land management. Biomass estimates may be utilized for a wide variety of purposes, including fire modelling (e.g. Sah et al. 2004), estimating carbon sequestration potential (e.g. Litton & Kauffman 2008) or estimating availability or abundance of various natural resources (e.g. Harmoney et al. 1997; Schmer et al. 2010). Over the past few decades, several methods to estimate plant biomass have been developed including: (1) estimating biomass of individual species through allometric relationships, (2) estimating collective biomass of multiple species using one or more measures highly correlated with biomass, or (3) using photo keys with accompanying biomass data to infer biomass in similar stands (reviewed in Catchpole & Wheeler 1992). Regardless of the method used or its precision, calibration (or prior development of photo keys) within the vegetation type of interest is an important initial step. To our knowledge, no methods have yet been developed or calibrated within the subtropical broadleaf shrub vegetation ('coppice') characteristic of many Bahamian and Caribbean islands.

Early-successional Bahamian coppice serves as habitat for many resident and migratory bird species including the

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US federally endangered Kirtland's warbler (*Setophaga kirtlandii*) (Mayfield 1992; Currie et al. 2005; Wunderle et al. 2010). As part of a larger study investigating potential Kirtland's warbler winter habitat management techniques, we developed and calibrated a non-destructive biomass estimation procedure in recently disturbed (3–4 yrs) coppice on the island of Eleuthera in the central Bahamas.

Accurate estimation of above-ground plant biomass through indirect means is often difficult in stands of diverse vegetation, and the precision of estimates varies with the intensity of labour required to obtain them (Catchpole & Wheeler 1992; Radloff & Mucina 2007). Older stands of Bahamian coppice are largely dominated by tall shrubs and trees, but young stands are more structurally diverse. Along with low or regenerating shrubs and trees, recently disturbed coppice stands may include large bunch grasses, dense herbaceous or woody vines and moderate to high cover of suffrutescent herbs or subshrubs. Although the various growth forms (or common species) may occur in small and distinct patches, they are very frequently inter-mixed within a relatively small area (e.g. 1 m^2 or less with small to large grasses underneath regenerating shrubs which are covered by vines; see Appendix S1).

We were investigating the use of controlled goat grazing on utility corridors (e.g. power and telephone line rights-of-way) as an economical means of managing vegetation around utility lines while maintaining coppice in a state suitable for the warblers. We considered measures of plant biomass as potentially useful for a variety of purposes, including estimating relative amounts of forage available to or consumed by goats, estimating vegetation recovery following grazing or monitoring fuels for fire management efforts on utility corridors. However, our financial and time constraints necessitated a low-cost/low-labour means of estimating total biomass (rather than species-specific) within the structurally complex habitat. Therefore, we employed a visual obstruction technique similar to that developed by Robel et al. (1970) in grassland vegetation, but modified to suit our habitat and potentially allow partitioning of plant biomass within vertically-oriented strata (or height classes).

Here we present the details of our visual obstruction procedure along with results from regression analyses used to estimate above-ground plant biomass (standing vegetation dry weight per unit area). Although our method was developed in the context of a goat grazing study, it is general enough to be applied to a variety of purposes. Similarly, while our calibration model results are specific for recently disturbed coppice vegetation, the technique should be transferrable to any shrubland vegetation type where the maximum height of plants is typically 2 m or less.

Methods

Study area

Eleuthera, The Bahamas (25°15′N, 76°20′W) is a low-elevation (51 m max) subtropical island (518 km^2). The predominant vegetation (locally known as coppice) is typically dense and characterized by evergreen and semi-deciduous broadleaf trees and shrubs growing on poorly developed soils on limestone substrate (Mooney 1905; Correll 1979; Sealey 2006). The vegetation has been extensively disturbed by humans, principally for agriculture (Young 1966; Byrne 1980), resulting in a broad-scale mosaic of habitats of different ages (Helmer et al. 2010; Larkin et al. 2012).

Our fieldwork was conducted on Cape Eleuthera Resort in southwestern Eleuthera. All sampling for our biomass estimation technique was conducted within the immediate vicinity of study plots established for Kirtland's warbler (KW) winter habitat management experiments. Study plots were located within the pipeline system of a freshwater well field, where vegetation had been heavily thinned ca. 3–4 yrs prior to the onset of our study, producing early-successional coppice consistent with KW habitat. Plots were largely dominated by shrub or tree species including *Acacia choriophylla* Benth. (cinnecord), *Bourreria ovata* Miers (strong-back), and *Trema lamarckianum* (Roem. & Schult.) Blume (pain-in-the-back), but also had high cover of the vines *Jacquemontia havanensis* (Jacq.) Urb. and *Passiflora suberosa* L. (juniper-berry), along with an understorey of grasses and herbaceous perennials. The maximum height of shrub or tree species within the well field was typically around 2 m.

Visual obstruction measures and calibration sampling

We placed a 1.5-cm diameter by 2-m tall PVC pole in the centre of a 0.25-m^2 (0.5 m × 0.5 m) quadrat. The pole was divided into eight vertical height classes of 25 cm each, but was marked in 5-cm bandwidths of alternating colours, along with markings at 1-cm increments, to ease estimation (Fig. 1). Within each height class, we estimated the number of centimeters obscured by any vegetation (foliage or stems) when viewed from a horizontal distance of 0.6 m (i.e. average arm length of the crew) and a vertical eye-level of 1 m. For example, if only 50% of the pole between 50 and 75 cm above ground level were visible, the visual obstruction for that height class was recorded as 12.5 cm.

Four sets of visual obstruction (VO) estimates were made for each quadrat – one from the centre of each quadrat edge. During early testing of the method we found high similarity among observer estimates if the viewing position

Fig. 1. Apparatus and procedure used for visual obstruction estimation, demonstrated in a low-biomass quadrat, with the inset showing details of the PVC pole. Each coloured band on the pole is 5-cm wide. Grey bands designate the upper limit of each 25-cm vertical height class.

was nearly identical, but slight variations in position could lead to large differences among estimates, especially for mid-range obstruction values. To capture this variability, three observers generated independent VO estimates in each of the eight height classes at each observation position. The grand mean of all VO estimates was then generated for each height class in a quadrat (i.e. averaged across positions and observers). Those means were then summed to yield a total average VO value for the quadrat.

To calibrate the relationship between visual obstruction and plant biomass, we obtained VO estimates and harvested all standing vegetation from a total of 90 quadrats over two consecutive winters. During December 2010–January 2011, we placed three quadrats in the areas surrounding each of 20 habitat management plots (or 'sites'), yielding 60 quadrats in total. From December 2011–January 2012 we placed an additional three quadrats within ten larger sites, each encompassing two of the original 20 sites, yielding 30 quadrats in total. In both winters, the three quadrat locations at each sampling site were selected to represent low, moderate and high levels of biomass determined subjectively relative to the range of standing biomass present across the site (one quadrat per category at each site, yielding 30 quadrats in total per category). This ensured that a wide range of variation was captured in the full, multi-site sample. Additionally, attempts were made to include all growth forms present on a site in a manner reflecting the typical local-scale structure and heterogeneity of vegetation within the site. For example: grasses and herbaceous perennials were usually most abundant in low-biomass locations, often as the only growth forms or sometimes with small shrubs and low amounts of vine cover, but they could also occur in higher biomass quadrats. Woody vines were typically most abundant in moderate-biomass locations with medium-sized shrubs. Large shrubs typically dominated high-biomass locations, although a varying density of vines might still be present amid the canopy and herbs might still be present in the ground layer (Appendix S1).

After VO estimates for a quadrat were completed by the three observers, all standing vegetation (live or dead, but excluding ground surface litter) was clipped and bagged separately for each height class, by beginning at the top of each vegetation column and working downward to ground level. Vegetation in bags was then dried at ca. 60 °C to a constant weight (48 hr minimum drying time). Vegetation dry weight in g 0.25 m^{-2} (hereafter 'biomass') was then recorded separately for each height class within a quadrat and summed over height classes for the quadrat in total.

Statistical analyses

Linear regression analyses were used to generate models predicting total plant biomass from the total average VO value for a 0.25-m^2 quadrat. Prior to analysis, both observed weight and VO distributions were normalized via started-log transformation of values to produce a better linear relation and homoscedastic residuals (Baskerville 1972; Fig. 2). Although some authors have advocated using non-linear models for allometric relationships such as these (Tausch 1989; Packard & Boardman 2008), in preliminary analyses we found a linear model with transformed variables, on average, yielded biomass predictions for individual quadrats much closer to the observed values than a non-linear model (Appendix S2).

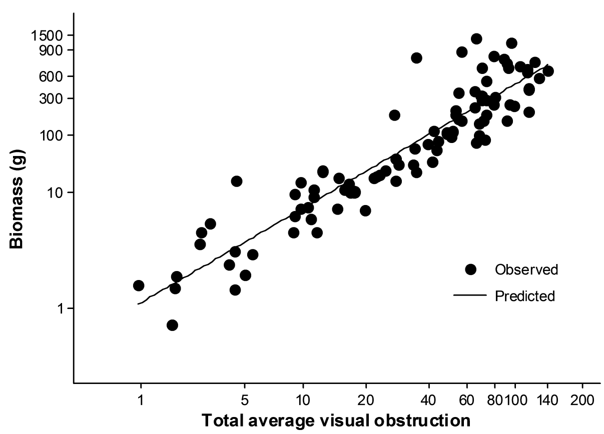

Fig. 2. Observed and predicted values of above-ground biomass within 0.25-m^2 quadrats as a function of total average visual obstruction. Scaling of both the *x*- and -axes reflects the log transformation used in linear regression analysis. Predicted values were generated from the regression model utilizing all 90 quadrats sampled.

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We used a series of regression analyses to check the robustness of biomass predictions, i.e. to ensure the prediction equation developed from the full set of data was not dependent on the inclusion of a particular combination of data points, and that the models developed from our sample would perform well on other similar samples. Specifically, fit and predictions from a model estimated using data from all 90 quadrats were compared to six 'validation' models. In the validation models, 60 quadrats were used to estimate regression coefficients that were then used to generate biomass predictions for all 90 quadrats (i.e. the 60 used to estimate coefficients and the 30 reserved for validation). For the first validation model, we estimated coefficients using the 60 quadrats from winter 2010–2011 to evaluate the quality of model predictions for the 30 quadrats from an entirely different year. For the remaining five validation models, coefficients were estimated using 60 randomly selected quadrats – 20 from each subjective biomass category (low, moderate, high) – and used to predict biomass for the 30 unselected quadrats.

For all regression models, we back-transformed biomass predictions from the log scale into the original arithmetic weight scale (grams) for comparison to their corresponding observed values. We then evaluated prediction error, relative to observed biomass, for individual quadrats. In practice, researchers are likely to utilize the mean of predictions for several quadrats sampled within a vegetation stand. However, examining whether and how prediction error for individual quadrats varied across the range of observed biomass and VO values allowed us to identify conditions under which the model did not perform well.

We calculated 'relative prediction error' for individual quadrats as a percentage of the observed quadrat biomass value: (observed – predicted)/observed × 100. Negative relative errors indicated overestimation and positive errors were underestimates. We also calculated 'absolute error' as the absolute value of relative error (i.e. ignoring over- vs underestimation). Use of a correction factor in back-transformation yielding the mean rather than the median of the log-normally distributed response variable has been advocated for logarithmic regression, particularly for the purpose of estimating the total biomass of a larger area based on smaller unit samples (Baskerville 1972; Miller 1984). We found the correction factor substantially exaggerated percentage errors associated with overestimation of biomass in individual quadrats, but had less influence on underestimation and resulted in larger average errors. Consequently, for better clarity in evaluating the precision of individual quadrat predictions across the distributions of VO values and observed biomass, we used only a simple back-transformation. However, for the purpose of scaling up from the sample quadrats to the stand level it would still be advisable to employ a correction factor (see Appendix S3).

Observer bias

To examine whether total average VO values or biomass predictions for a quadrat were substantially influenced by the number or identity of observers, four separate sets of total VO values for each quadrat were generated based on (1) the VO estimates from all three observers, as described earlier, and (2) each combination of only two observers. We also generated biomass predictions for each quadrat using the total average VO values from each two-observer combination and coefficients from the full 90-quadrat regression model. Similarity of the total average VO values and the relative prediction errors among observer sets were examined using: (1) bivariate correlations and (2) repeated measures ANOVA followed by pair-wise contrasts comparing the mean of each two-observer set to the mean of the three-observer set, utilizing a Bonferroni correction to maintain an overall alpha of 0.05 (per comparison $\alpha = 0.017$). In the latter case, a significant omnibus test for the ANOVA indicated a likelihood that at least one observer, compared to the others, generally estimated significantly higher or lower obstruction values across all quadrats, otherwise observer differences would be expected to average out across quadrats. The follow-up comparisons aided identification of the observer and nature of his/her bias. Separate comparisons were made for data collected in 2010–11 and 2011–12 since identity of some observers differed between seasons.

Individual height class models

After generating predictive models for total quadrat biomass, we generated similar regression models for each of the eight height classes separately. For these height class-specific models we generally considered data from all 90 quadrats for parameter estimation. However, this led to a preponderance of zero values for both the VO and corresponding observed biomass in upper height classes where vegetation was sometimes entirely absent. So, to normalize distributions while minimizing introduction of bias we excluded instances where the VO and corresponding observed biomass values were zero, both for a given height class and all those above it within a quadrat. Consequently, sample size varied among models for each height class and was lowest for the uppermost height classes. For non-excluded cases where the observed biomass was zero (i.e. associated VO value was non-zero, or upper height classes had non-zero biomass or VOs), the zero value was substituted with 0.05 g (half of the lowest measured weight for any height class) to avoid division by zero in the calculation of prediction error as a percentage of the observed biomass.

Results

Total average visual obstruction values for quadrats ranged from 0.96 to 140.1 cm in 2010 (median = 34.1 cm) and 4 to 122.1 cm in 2011 (median = 52.4 cm). Total dry weight of vegetation (biomass) in each quadrat ranged from 7.2–1877.2 g (median = 202.4 g) in 2010 and 24.9–1477.3 g (median = 397.3 g) in 2011.

Among all regression models (full and validation) for predicting total quadrat biomass, log VO accounted for more than 80% of the variance in observed log biomass ($P < 0.001$; Table 1, Fig. 2a). Regression coefficients, high correlations between observed and predicted values, and the distribution of prediction errors all showed strong consistency between the model using the full 90 quadrat data set and all validation models, indicating robustness of prediction (Table 1).

Based on coefficients from the full 90 quadrat regression model, predicted biomass for individual quadrats had a median absolute prediction error of 29%, but a negative mean relative error indicated more over- than underestimations overall (Table 1). Relative errors did not show obvious bias across the distribution of visual obstruction values, but some bias was noted at the extremes of the observed weight distribution (Fig. 3a,b). Overestimations were more common and most severe (>50% absolute error) at the lower end of the observed biomass distribution (Fig. 3b). In general, these overestimates were associated with either (1) quadrats with both very low VO and low biomass (e.g. small-sized symbols at the lower left of Fig. 3a,b), or (2) quadrats with moderate to high VO but relatively low biomass (e.g. medium to large symbols at the lower left of Fig. 3b). The first case illustrates the difficulty of accurate prediction of values close to zero (or, more generally, at the extremes of the variable distribution). The second case was probably characterized by quadrats with large bunch grasses, dense herbaceous vine thickets or high amounts of leafy shrub canopy without larger woody branches. The most severe underestimations were also primarily located at the extremes of the observed weight distribution, but with a larger number at the upper end, where errors >50% were associated with quadrats with low to moderate VO estimates, but relatively high biomass (e.g. medium-sized symbols toward the upper right of Fig. 3b or largest symbols in the upper centre of Fig. 3a). This was often due to the presence of slender, but heavy, woody trunks that did not contribute as much to obscurance of the pole as to vegetation weight within the quadrat.

Observer bias

Bivariate correlations among the four sets of total VO values derived from different combinations of two or all three observers were very high (Spearman's *rho* ≥ 0.98), as were correlations of relative biomass prediction error (Pearson's $r \geq 0.93$), indicating a high correspondence among values from different observer combinations. However, significant repeated measures ANOVAs comparing differences in mean log-scale total VO values among the four observer-based sets suggested systematic observer differences were present (2010–11: $F_{3,57} = 10.42$, $P < 0.001$; 2011–12 $F_{3,27} = 22.19$, $P < 0.001$). Follow-up contrasts indicated significant differences in mean total VO between the three-observer estimate and some two-observer estimates generally arose due to one observer typically estimating lower obstruction values (2010–11: two significant pair-wise contrasts, $P \leq 0.006$) or higher obstruction values (2011–12, two significant pair-wise contrasts, $P < 0.001$) compared to the other two observers. Nonetheless, the magnitudes of the differences were small. The maximum differences in median total average VO between the three-observer estimate and a two-observer estimate were 2.5 and 4.6 cm in winter 2010–11 and winter 2011–12, respectively, or ca. 7% and 9% of the median values for each sample.

We detected a similar pattern of results for differences in relative error among two- and three-observer subsets (repeated measures ANOVAs with significant [$P < 0.001$] omnibus F-tests and at least one significant [$P \leq 0.007$] pair-wise contrast in each sample year). As with the total VO estimates, magnitudes of differences in relative error were small. In 2010–11 the most disparate two-observer subset had a mean relative error of −9.3% compared to a three-observer mean of −13.5%; in 2011–12 the most disparate subset had a mean relative error of −11.9% compared to −5.9% for the three-observer set.

Individual height class models

Where vegetation was present (i.e. excluding those cases where a given height class within a quadrat and all those above it had zero values for both VO and biomass), median VO values (averaged across observers) mostly decreased from the ground up, ranging from 10.0 cm in the lowest to 4.6 cm in the uppermost height class (Fig. 4). Median observed biomass ranged from 86.4 g in the lowest to 3.2 g in the uppermost height class. Prediction of biomass from visual obstruction within the eight vertical height classes was less accurate than the total quadrat prediction. Compared to the total quadrat model, log VO values accounted for 16–35% less variance in observed log biomass within height classes, and prediction errors were

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Table 1. Results from linear regression models predicting log of total dry vegetation weight in a 0.25-m^2 quadrat from log of the sum of average visual obstruction estimates. Several validation models (2010 & V1–V5), utilizing only 2/3 of the data to estimate coefficients, were compared to a model utilizing all the data to estimate coefficients. For all models, the corrected coefficient of determination (R^2_{adj}) is derived only from the set of data used to estimate regression coefficients (B_0 and B_{lnVO}).

	Data							
	All	2010	V1	V2	V3	V4	V5	V_{ave} [d]
N (for model estimation)	90	60	60	60	60	60	60	–
R^2_{adj}	0.852	0.860	0.870	0.815	0.861	0.833	0.870	–
B_0	1.769	1.867	1.708	1.868	1.832	1.548	1.76	–
B_{lnVO}	1.063	1.028	1.084	1.045	1.051	1.111	1.056	–
R [a]	0.924	0.929	0.934	0.904	0.929	0.913	0.934	–
$R_{unselected}$ [a]	–	0.903	0.904	0.949	0.916	0.957	0.902	–
SEE [b]	0.486	0.492	0.460	0.502	0.457	0.524	0.471	–
$SEE_{unselected}$ [b]	–	0.499	0.554	0.477	0.559	0.441	0.536	–
Median% Absolute error [c]	29.2	32.1 (26.6)	28.7 (33.6)	30.7 (37.9)	29.4 (35.0)	33.6 (21.0)	29.8 (22.8)	30.7 (29.5)
Mean% Relative error [c]	−10.9	−11.6 (−2.7)	−9.4 (−16.9)	−11.6 (−22.2)	−9.1 (−21.8)	−12.1 (10.4)	−10.7 (−0.2)	−10.6 (−12.4)
Min% Relative error	−130.4	−146.0 (−106.0)	−120.9 (−120.8)	−143.6 (−150.8)	−108.7 (−143.0)	−103.3 (−73.4)	−126.5 (−88.0)	−124.3 (−113.7)
Max% Relative error	80.0	74.2 (80.6)	79.8 (72.9)	79.4 (72.3)	79.6 (72.5)	81.0 (75.9)	72.7 (80.7)	77.8 (75.8)

[a] Pearson correlations between observed and predicted log weight values are shown for both the set of data used to estimate coefficients (R) and the 30 cases not used for estimation in validation models ($R_{unselected}$).

[b] SEE is the standard error of the estimate (population SD of the residuals, or square root of the mean squared log-scale error) for model estimation and validation data sets.

[c] Percentage (%) error is the difference between the observed weight in grams and back-transformed predictions from regression models, expressed as a percentage of the observed weight; 'absolute' error ignores over- vs underestimation, while negative values for 'relative' error indicate an overestimation of weight. Prediction errors are shown separately for the model estimation and, in parentheses, validation data sets.

[d] Average prediction errors across the six validation models are shown under V_{ave}.

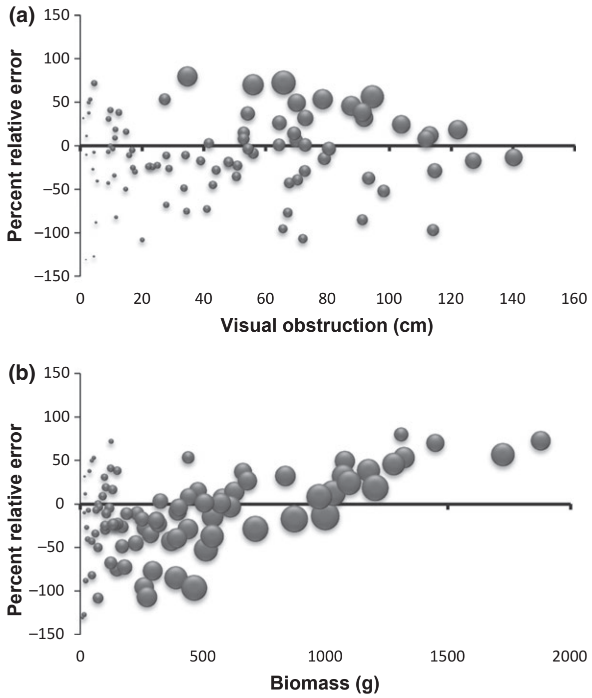

Fig. 3. Relative error (*y*-axis) in above-ground biomass predictions (vegetation dry weight) for individual 0.25-m^2 quadrats vs (a) total average visual obstruction and (b) observed biomass. The zero value on the *y*-axis separates overestimates (negative errors) from underestimates (positive errors). Dashed lines emphasize errors exceeding ±50%. To illustrate the interactive influence of biomass and visual obstruction on relative error, symbol size increases with observed biomass in (a) and with visual obstruction in (b).

much larger (Table 2). Absolute error averaged 50.8% across all height classes, and was highest in the three uppermost height classes with the lowest average biomass (Table 2). The most extreme absolute errors (>100%) were, in some cases, more than an order of magnitude larger than those seen in the total quadrat model, but were almost exclusively overestimations of low observed weights (Figs 4 and 5). Errors in excess of 1000% were all associated with observed biomass under 1 g.

As in the total quadrat model, the most extreme overestimates of biomass within height classes were associated with either (1) both very low VO and low biomass, or (2) relatively high VO compared to the relative amount of biomass. The latter co-occurrence was particularly evident in the upper height classes (e.g. classes 7 and 8 in Fig. 5), and likely a consequence of canopy within lower height classes obscuring the observer's view of top portions of the pole, even though little to no vegetation was present at those heights. A parallel phenomenon occurred when viewing lower height classes, but those height classes were less likely devoid of vegetation so relative errors would likely be minimized.

Discussion

Though originally developed and widely used for biomass estimation in grassland vegetation, we found the Robel et al. (1970) visual obstruction method could be successfully modified for use in more structurally complex vegetation. Although extra time was required initially for calibration sampling and regression analyses, the time required for three observers to generate visual obstruction estimates in the field was low, averaging about 8 min per 0.25-m^2 quadrat. This is roughly equivalent to the time required for the mini-disk method used by Radloff & Mucina (2007) in structurally diverse South African renosterveld. We initially considered using the mini-disk method, but the materials needed to construct their sampling apparatus (e.g. custom-sized plexiglass, aluminium framing) were not readily or inexpensively obtainable on Eleuthera. More importantly, we suspected use of the apparatus would become cumbersome in our taller vegetation (up to ca. 2 m in height vs <1.5 m in the renosterveld).

Our modified visual obstruction method yielded total quadrat regression results on par with the mini-disk method, other modified visual obstruction methods and with many other allometric models for estimating biomass. For example, utilizing different variations of the Robel method in grassland and heathland vegetation, respectively, Benkobi et al. (2000) and Davies et al. (2008) generated regression models with coefficients of determination (R^2) ranging from 0.64–0.88. In their 1992 review, Catchpole & Wheeler cite R^2 values of 0.61–0.99 for a variety of other double-sampling techniques with moderate to high prediction accuracy.

The average prediction accuracy and range of relative errors for our total quadrat model were also on par with those reported by others (e.g. Benkobi et al. 2000; Mascaro et al. 2011), and the predictions should at least be sufficient for comparing relative differences in biomass across space or time. Performance of prediction models within vertical height classes was far less ideal, but predictions from these models might still be useful as a coarse relative index of biomass within individual height classes in studies where the relative amount of vegetation within vertical strata is of interest. However, because the average prediction error varies among height classes, use of this method as an index of comparison between different height classes would be less appropriate than use to compare similar height classes between sites or time periods.

The biases and larger relative errors noted among the predictions of individual quadrat biomass in cases with dense herbaceous cover or heavy wood with low foliage should be less important when averaging across quadrats sampled within vegetation stands (see Appendix S3), unless a stand is dominated by such anomalous structure

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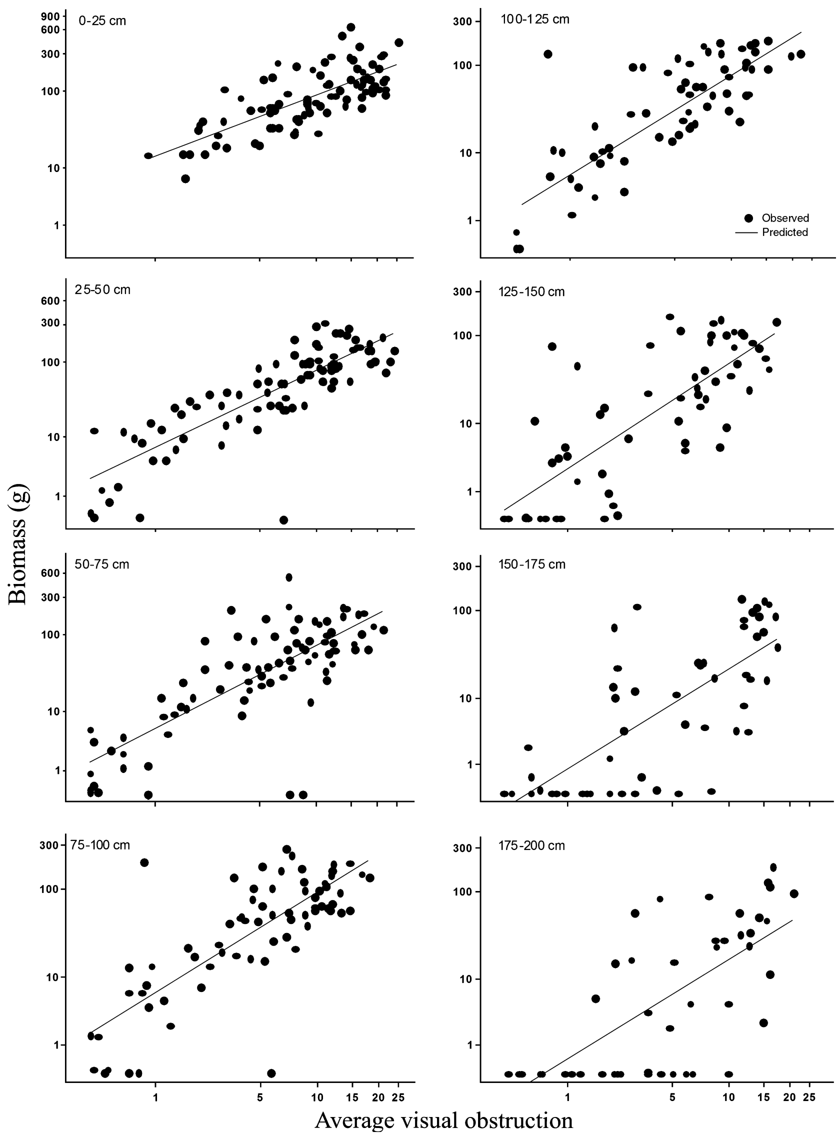

Fig. 4. Observed and predicted values of above-ground biomass in eight vertical height classes spanning 25-cm increments from ground level within 0.25-m^2 quadrats. Scaling of both the *x*- and *y*-axes reflects the log transformation used in linear regression analysis. Note the changing range of the *y*-axis due to generally decreasing biomass with increasing distance from ground level.

(Mascaro et al. 2011). If a number of anomalous stands are to be sampled, separate calibration and estimation equations may be warranted. There might also be some concern about estimation accuracy when applying the method before and after some disturbance that substantially alters plant composition. For example, in our application, goats, as selective consumers, could potentially alter vegetation composition so that the calibration vegetation community poorly reflects the post-grazing community to which the calibration equation is subsequently applied. In cases where the post-disturbance community is profoundly altered, especially long-term, separate calibration equations may again be warranted, since the focus may effectively be on two different vegetation types. In our study system, however, we expect any grazing-induced compositional changes will not have a substantial influence on post-grazing biomass estimation accuracy. First, the locally heterogeneous nature of our coppice vegetation ensured that a wide range of species and compositional mixtures were captured by our set of calibration quadrats. In some cases, one or two species dominated a quadrat, in others quadrats included a mixture of several species. Thus, the calibration procedure and subsequent estimation equation included reference points for post-browsing quadrats that

Table 2. Results from linear regression models predicting log vegetation dry weight from log visual obstruction estimates within eight vertically-oriented height classes in a 0.25-m^2 quadrat.

	Height class (cm from ground)							
	0–25	25–50	50–75	75–100	100–125	125–150	150–175	175–200
N	90	89	84	71	63	61	53	48
R^2_{adj}	0.54	0.69	0.61	0.61	0.63	0.60	0.54	0.50
B_o	2.04	1.20	0.92	1.01	1.01	0.21	−0.39	−0.64
B_{lnVO}	1.03	1.31	1.42	1.47	1.40	1.54	1.47	1.46
R [a]	0.74	0.83	0.79	0.78	0.80	0.78	0.74	0.71
SEE [b]	0.59	0.76	1.01	0.96	0.83	1.10	1.23	1.31
Median% Absolute error [c]	41.0	48.5	49.4	46.0	49.6	53.8	64.7	53.2
Mean% Relative error	−9.6	3.6	7.6	1.2	−1.6	−6.1	5.8	7.3
Min% Relative error	−216.0	−5375.6	−3494.8	−2514.8	−396.6	−6781.0	−32521.5	−7624.6
Max% Relative error	80.4	79.8	91.3	97.4	96.8	97.8	100.6	94.9

[a] Pearson correlation between observed and predicted log weight values.

[b] Standard error of the estimate (population SD of the residuals).

[c] Percentage error is the difference between the observed weight in grams and back-transformed predictions from regression models, expressed as a percentage of the observed weight; 'absolute' error ignores over- vs underestimation, while negative values for 'relative' error indicate an overestimation of weight.

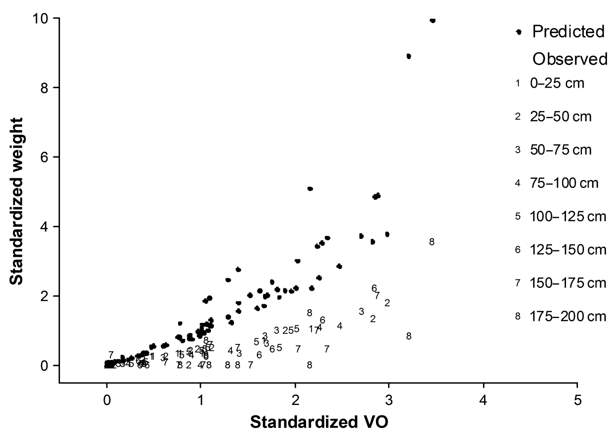

Fig. 5. Predicted and observed standardized weights (observed/median within height class) vs standardized visual obstruction (VO) for height class data with absolute prediction errors exceeding 100%. Numerical symbols represent 25-cm height classes with values increasing upward from ground level.

might be dominated by one or two unpalatable species. Furthermore, it is unlikely that all post-browsing quadrats in our heterogeneous vegetation would be dominated in the same fashion, so that estimation error for the site would be minimized by averaging over quadrats. Second, the term 'coppice' refers to the resprouting tendency of most of the plants within the community. So, while there could be pronounced compositional changes and increased estimation error immediately following a single goat grazing treatment, the effect is likely to be reduced over time as browsed species recover from underground rootstocks or remaining branches.

More generally, greater accuracy might be achievable by adding other easily obtained measures to our basic model. For example, we also measured the basal circumference of the largest woody stem within calibration quadrats sampled in 2011. Comparison of a regression model including only visual obstruction from those 30 quadrats with a second model including both visual obstruction and stem circumference showed a modest improvement in R^2 (0.08 increase) and average prediction error (median absolute prediction error decreased ca. 1%; see Appendix S4 for more detail). The magnitude of the most extreme relative errors was also reduced in the second model (−97.3 to 79.7% vs −72.2 to 65.3%), indicating the biases noted in our basic model could be minimized through including additional variables relevant to plant structure. Including such variables might also improve suitability of model predictions for certain applications, such as use in fire behaviour models requiring fuel size class information.

While we did find evidence for systematic individual observer bias in visual obstruction estimates, the influence of this bias on the overall quality of predictions was not substantial. Predictions are likely to be more reliable when based on estimates from three observers, rather than two. Yet, it is also possible that additional training could minimize individual observer bias and produce reliable predictions with a minimal number of observers.

Conclusions

We believe Robel's visual obstruction method is a flexible procedure that can be adapted for use in estimating collective (vs species-specific) plant biomass within a variety of

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vegetation types, including relatively tall (ca. 2 m) and structurally diverse associations. It has the distinct advantages of relatively low sampling time, once the initial calibration has been completed, and of requiring very little specialized equipment. The latter advantage may prove particularly important in field settings where availability of construction materials is limited or their cost high. Whether the prediction accuracy is sufficient will depend on the intended application, but increased accuracy will almost certainly involve increased cost.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Photographs of early-successional coppice on Eleuthera and examples of calibration sampling quadrats.

Appendix S2. Results from exploratory analyses comparing prediction of biomass from visual obstruction (VO) measures based on three different regression techniques.

Appendix S3. Prediction errors for sites based on quadrat averages.

Appendix S4. Results from exploratory regression analyses comparing prediction of biomass from (a) only total visual obstruction for a 0.25-m^2 quadrat, vs (b) total visual obstruction plus basal circumference (mm) of the largest woody stem within the quadrat.

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