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Rapid, Nondestructive Estimation of Forest Understory Biomass
Using a Handheld Laser Rangefinder

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Abstract

The forest understory is often associated with rapid rates of carbon and nutrient cycling, but cost-efficient quantification of its biomass remains challenging. We tested a new field technique for understory biomass assessment using an off-the-shelf handheld laser rangefinder. We conducted laser sampling in a pine forest with an understory dominated by invasive woody shrubs, especially *Rhamnus frangula* L. Laser sampling was conducted using a rangefinder, mounted on a monopod to provide a consistent reference height, and pointed vertically downward. Subsequently, the understory biomass was measured with destructive sampling. A series of metrics derived from the airborne LiDAR literature were evaluated alone and in combination for prediction of understory biomass using best-subsets regression. Resulting fits were good ($r^2=0.85$ and 0.84 for the best single metric and best additive metric, respectively, and $R^2=0.93$ for the best multivariate model). The results indicate that laser sampling could substantially reduce the need for costly destructive sampling within a double-sampling context.

Keywords: Light detection and ranging, vegetation structure, understory biomass, inventory, invasive species, point intercept sampling,

Introduction

The forest understory – including the herbaceous layer as well as erect woody shrubs – typically contains a small fraction of the aboveground biomass of temperate and boreal forests, but it can play a disproportionate ecological role. From a biogeochemical standpoint, understory plants can play a critical role in gross primary productivity, respiration, carbon, and nutrient fluxes (Yarie 1980; Misson et al. 2007; Moore et al. 2007; Powell et al. 2008). From a community perspective, the understory contributes biodiversity in its own right, provides crucial structure and cover resources for wildlife, and can mediate ecological interactions involving mycorrhizal fungi, invertebrates and their predators, and overstory trees (Muir et al. 2002; Gilliam 2007). The understory can serve as fuel, predisposing the community to rapid change in fire-dominated ecosystems (Arno 2000), and can also modify long-term community and ecosystem response to disturbance through competitive interactions with seedlings and saplings of potential dominant tree species (Oliver and Larson 1996; Wagner et al. 2006; McCarthy et al. 2011). As a result, the forest understory can be viewed as a key ecological indicator (Kerns and Ohmann 2004), and one that recent authors have argued deserves closer scrutiny (e.g. Dickie et al. 2011; Gonzalez et al. 2013).

Unfortunately, direct quantification of basic understory attributes such as biomass can be labor-intensive, and prediction from readily measured variables can be challenging (Suchar and Crookston 2010; Eskelson et al. 2011). Reliance on destructive sampling alone is typically too costly in extensive survey applications (Russell et al. 2014), and can be detrimental in the context of intensive experimental studies or permanent sample plots. Allometric approaches continue to be used widely, based either upon individual plant attributes (such as height, basal diameter, or crown area) or height and cover of the community as a whole (e.g. Muukkonen et al. 2006; Porté et al. 2009; Heinrichs et al. 2010). However, these often rely on the development of species-specific equations through destructive sampling (e.g. Smith and Brand 1983; Alaback 1986; Andariese and Covington 1986; Paton et al. 2002), and their reliability is open to question when the equations are used to estimate biomass outside the population

within which they were originally developed. Thus, there is a need for simple, rapid approaches that can yield objective, reliable estimates of understory biomass (Porté et al. 2009).

Light Detection and Ranging (LiDAR), usually using an instrument mounted on an airborne or spaceborne platform, is a relatively new technology but is now widely used for estimating forest overstory biomass and characteristics (see, e.g., Leeuwen and Nieuwenhuis 2010; Kershaw et al. 2016, ch. 13).

Airborne LiDAR has been used successfully to characterize shrub biomass in a variety of forest systems (e.g. Estornell et al. 2012). Terrestrial LiDAR has also been used to characterize forest structure, including the forest understory, but terrestrial laser scanners remain expensive and postprocessing can be complicated (e.g. Skowronski et al. 2011; Hardiman et al. 2013; Palace et al. 2016). We propose to “miniaturize” the airborne LiDAR approach, using a relatively inexpensive laser rangefinder pointing vertically down at the forest floor, to estimate the aboveground biomass of the herb and shrub layer. Our overall goal is not to propose advanced instrumentation or analytical techniques, but rather to evaluate whether simple techniques and equipment could be used to reduce the cost and expense associated with destructive sampling. Our specific objectives are to:

1. Describe an approach for conducting measurements in the field,
2. Describe LiDAR-related metrics that can be calculated easily from field data,
3. Evaluate and compare the predictive capacity of alternative metrics using biomass measurements from destructive sampling, and
4. Outline how the approach might be used in an operational context to estimate the aboveground biomass of forest understories.

Methods

Study Site Description

We collected field data in a forest stand in Durham, New Hampshire, USA, located at 43.133° N, 70.942° W. The current stand grew on a pasture that was abandoned in the early 20th century, and a portion was planted in the 1930s with *Pinus resinosa* Ait., though a considerable number of volunteer

Pinus strobus L. also became established at the same time. The stand has seen little if any subsequent management. The stand has an overstory dominated by *Pinus strobus* and *Pinus resinosa*, with occasional *Acer rubrum* L., *Quercus rubra* L., and *Tsuga canadensis* Carr. The understory has been heavily invaded by non-native *Rhamnus frangula* L.; invasion timing and rate of spread have been described for this stand by Frappier et al. (2003). Although *Rhamnus frangula* now dominates much of the understory, other native and invasive species are present in low density, including *Vaccinium angustifolium* Ait., *Vaccinium corymbosum* L., *Lonicera japonica* Thunb. ex Murray, *Dennstaedtia punctilobula* Michaux, *Pteridium aquilinum* (L.) Kuhn, and *Mitchella repens* L. Grasses and sedges are sparse or absent. Field work was conducted in late October and early November, 2011, after leaf-fall of the deciduous overstory but while most understory shrubs had not yet shed their foliage. Laser sampling was followed immediately by destructive sampling at each plot.

Field Methods

We established 40 measurement plots within the stand following a crude ocular stratification based on vegetation density (continuous or nearly continuous cover, moderate but not continuous cover, and sparse cover) and maximum height (less than 50 cm, between 50 and 100 cm, and taller than 100 cm). At each plot, a collapsible wooden frame with marks every 10 cm on the edges was used to delineate a 1 m² square quadrat which served as the basis for both laser measurement and destructive sampling.

Within each measurement plot we collected 100 laser measurements systematically spaced on a 10 by 10 cm grid, using the reference marks on the frame to aid positioning. We used a Leica DISTO 8 rangefinder with a 635 nm laser (Leica Geosystems AG, Switzerland), mounted on a standard camera monopod, to conduct laser measurements (Figure 1). At each measurement point the laser rangefinder returns a distance, either to the forest floor or to vegetation, that either can be manually recorder or transferred via Bluetooth to a data-collection device. The internal digital inclinometer of the rangefinder was used to ensure measurements were vertical, while the monopod was always used fully extended. The

distance measurement from the rangefinder to a tile floor, while the rangefinder was identically mounted, had previously been recorded (160 cm) and was subsequently used to translate distance measurements into heights above the monopod ground.

Immediately following laser measurement, all vegetation within the quadrat up to 1.5 m in height was clipped to the ground surface, placed within a paper bag, and returned to the laboratory for fresh weight measurement. Vegetation was then dried at 55° C for a minimum of 48 hours, before dry weight determination.

Data Processing

The potential complexity of patterns of laser height measurements allows the calculation of large numbers of metrics from such data, including but not limited to quantiles or percentiles, measures of dispersion, and other statistics computed from the heights of returns above ground level. In studies that use airborne LiDAR to map biomass and other characteristics of forests, it is common to calculate 20-50 such metrics and then use stepwise regression to identify a “best” model for prediction (e.g. Naesset 2002, 2004; Hall et al. 2005). However, Li et al. (2008) suggest that most metrics are highly correlated, and a simpler suite of metrics can capture the vast majority of the predictive information. Thus, we focus here on a limited number of metrics that are simple to calculate, or that have a physical or biological interpretation. Moreover, we pay particular attention to metrics that are simple additive functions of the individual probe height values, as such metrics can be deployed in an area-independent fashion (Magnussen et al. 2013). In the understory measurement context, area-independence implies that the spatial configuration of laser probes used for calibration (e.g. a regular grid over a small area from which vegetation can be clipped and dried) need not be the same as that used for broader measurement (e.g. a long transect or larger grid of probes that can capture vegetation structure over a broader area).

Let z_i denote the height above ground for the return from an individual probe. Let $v_i=1$ if an individual probe contacted vegetation, and let $v_i=0$ if it represents a ground return. We assigned $v_i=0$ for

all probes with $z_i < 0.05$ m, as these were almost invariably returns from leaf litter or other ground debris rather than vegetation. Finally, let $m=100$ be the number of probes per plot. We calculated the following additive metrics:

$$p_{ground} = \frac{1}{m} \sum (1 - v_i)$$

$$c_1 = \frac{1}{m} \sum z_i$$

$$c_2 = \frac{1}{m} \sum z_i^2$$

$$c_3 = \frac{1}{m} \sum z_i^3$$

The metric p_{ground} is simply the proportion of probes that did not strike vegetation, while for any k , c_k is the k^{th} moment of z about the origin. We also calculated the following non-additive metrics:

$$vh = \frac{\sum v_i \times z_i}{\sum v_i}$$

$$med_z = \text{median}(z)$$

$$vm ed_z = \text{median}(z : v = 1)$$

$$PAI = -\ln(p_{ground})$$

$$mh = \frac{\sum w_i \times v_i \times z_i}{\sum w_i \times v_i}$$

$$mp = mh \times PAI$$

Thus, med_z is the median value of z for a plot, and $vm ed_z$ is the median for those probes that struck vegetation. The average height of laser returns from vegetation is vh , and PAI is the MacArthur-Horn estimate of horizontally-projected plant area index (the sum of the horizontal projections of vegetative surfaces per unit area, m^2/m^2). The weight w_i is the weight derived from the MacArthur-Horn (1969) transformation of the probe heights, which corrects for the occlusion of the ground and lower vegetation

by higher vegetation elements. Thus, mh represents an estimate of the average height of vegetation elements on the plot (rather than the average height of laser returns from vegetation, vh). Finally, mp has a natural interpretation as the average height of vegetation, multiplied by its horizontally projected area.

We used best-subsets regression to identify the best predictive relationships between oven-dry weight of vegetation, and the 10 laser metrics, using package leaps (Lumley 2009) in R (R Core Team 2012). Best-subsets regression allows identification of the best predictive regression with each number of predictors (e.g. 1 variable, 2 variables, 3 variables, etc.), so that model complexity penalties can then be applied to determine the best model among these best performers. Models were fit using all 10 metrics as candidates, without interactions, and refit using only the linear subset of metrics. We used Schwarz's Bayesian Information Criterion (BIC) to compare models. Following Claeskens and Hjort (2008), we also calculated the corrected Akaike Information Criterion (AIC_c) to corroborate the model selection by BIC and to assess the sensitivity of model selection to the criterion used.

The laser measurements are quick and cheap to carry out while the destructive sampling is expensive and time-consuming leading to a classic setting for application of double sampling. In a double sampling context, the laser measurements are the auxiliary variable, which is obtained for all plots while the destructive sampling only is obtained for a subset. To evaluate the potential utility laser measurements as part of a sampling campaign for estimation of understory biomass, we used the resulting regression fits to calculate the standard error of a double sampling with regression estimator under different combinations of sample sizes, and compared those with the results that would be obtained using simple random sampling with destructive sampling only. For simple random sampling, the standard error is

$$s_{\bar{y}} = \sqrt{\frac{\sigma_y^2}{n}}$$

where σ_y^2 is the population variance of the variable of interest (in this case, dry weight per m^2) and n is the number of destructively harvested plots. In double sampling with regression, the n plots with destructive harvesting are a random subset of n' total units, on which laser measurement is conducted. If p laser metrics $x_1, x_2, \dots, x_p$ are used to develop a linear predictive regression for y , then the double sampling estimator of the population mean of y is

$$\hat{y}_{reg} = \bar{y} + \sum_{j=1}^p \hat{\beta}_j (\bar{x}'_j - \bar{x}_j)$$

where the $\hat{\beta}_j$ are regression coefficients, $\bar{x}'_j$ is the sample mean for the j^{th} metric from the full n' plots, and $\bar{x}_j$ is the corresponding sample mean from the subset of n plots that provide direct measurements of y . The standard error of $\hat{y}_{reg}$ is approximately

$$s_{\hat{y}_{reg}} = \sqrt{\frac{\sigma_y^2}{n'} + \left(\frac{n' - n}{n'}\right) \frac{\sigma_y^2 (1 - R^2)}{n}}$$

where R^2 is the coefficient of determination (see, e.g., Cochran 1977, Särndal et al. 1992, Ringvall et al. 2003; r^2 is substituted for R^2 when $p=1$).

Results

Dry weight of the understory on square meter plots averaged 89 g/m^2 , with a standard deviation of 102 g/m^2 . Individual plot values ranged from 1.5 g/m^2 to 541 g/m^2 , with a median of 55 g/m^2 .

Results of the best-subsets regression for up to 4 variables, allowing both non-additive and additive variables, are shown in Table 1. The variables c_1 , c_3 , and PAI were not selected in any of the best models of this complexity. The best model employing only a single predictor uses mp , which has a natural interpretation as the average height of vegetation, weighted by its horizontally projected area

(Figure 2a). Model selection using BIC would indicate a three-variable model, including c_2 , med_z , and $vmed_z$. The less-conservative AIC_c criterion would indicate a four-variable model. However, the gain in actual performance (as measured by R^2) is minimal and would lead to trivial improvements in the standard error of any estimates in practice.

Restricting the regression analysis to include only additive metrics, the best-subset regression identified a model using c_1 as the best single-variable model (Table 1; Figure 2b). Both BIC and AIC_c increased when moving to a two-variable model, indicating that the choice of a one-variable model is robust to the choice of model selection criterion. As judged by R^2 , BIC, and AIC_c , the performance of the c_1 model is very close to that of the model using the non-additive mp metric: between these two models, $\Delta BIC = \Delta AIC_c = 1.38$, indicating that c_1 retains substantial support in comparison with mp .

Within a double sampling context, linear models with fit similar to either of the single-variable models ($r^2 = 0.84$) or the best multivariate model ($R^2 = 0.92$) would allow the laser method to substantially reduce the requirement for destructive sampling. Figure 3 shows the standard error as a function of number of laser plots n' , for different values of n (the number of plots used to develop regression equations). For example, suppose it were desirable to obtain estimates of understory biomass with a standard error of approximately 20% of the mean, or 17.8 g/m². Obtaining estimates of that quality using destructive sampling alone would require harvesting 33 plots, each one meter square. One could fit a multivariate model based on 20 destructively harvested plots, with laser measurement conducted on those plus an additional 15 plots for a total of $n' = 35$. Alternatively, one could fit a single-variable model based on 10 destructively harvested plots, with laser measurement conducted on those plus an additional 48 plots for a total of $n' = 58$. Because laser sampling is much faster in the field than clipping and bagging, and requires no follow-on lab work to dry or weigh the samples, the cost savings would be significant.

Discussion

The results of our field trial illustrate that the laser-derived metrics show a strong correlation to understory biomass and indicate that laser sampling is effective in this understory vegetation type. Employed in a double sampling setting, the proposed approach could be deployed to significantly reduce the field and laboratory expense associated with understory biomass estimation in comparison with destructive sampling used alone. Given the need for rapid approaches that can yield objective, reliable estimates of understory biomass (Porté et al. 2009), the proposed approach may be one of the needed solutions. Laser sampling as deployed here has additional advantages over some methods that are occasionally used to develop whole-community allometric equations. For example, the proportion of ground returns constitutes a point intercept sample that is complementary to a percent cover estimate. Both the percent cover, and height statistics from the returns, are objective and should be more repeatable than ocular estimates of either percent cover or dominant height, especially in situations where height is locally variable.

The sample size equations used in this paper (Cochran 1977, Särndal et al. 1992, Ringvall et al. 2003) are based on classical sampling theory, and assume a rather rigid approach to double sampling with regression. Thus, they are somewhat conservative with respect to the cost savings that might be obtained using the laser sampling technique. Specifically, the assumption is that sampling in the first phase – the laser samples used only to estimate the mean of any x variables (covariates) – is conducted in exactly the same fashion as is done to fit the regression that calibrates the relationship between y (i.e. biomass) and the covariates. However, if a metric such as c_1 is used that is a strictly additive function of properties of the laser height returns, then the metric is area-independent (Magnussen et al. 2013). Thus, the first-phase samples need not be deployed in exactly the same configuration. For example, it is intuitive that collecting laser returns systematically along a series of parallel transects will cover the heterogeneity in understory conditions within a given area much more efficiently than distributing a similar number of probes in batches of 100, clustered within small 1 m² areas. Thus, the idea of calibrating a very simple regression on c_1 with destructive sampling on a small number of compact plots, then conducting a wider-ranging laser sample to estimate average height of returns over a broader area, has great appeal. Even if

c_1 does not present the highest possible fit among candidate metrics, so long as it is fairly competitive, the practical simplicity and speed of implementation may make such a strategy attractive.

The approach presented here is new, and has only been tested in this study. Thus, its performance may vary from ecosystem to ecosystem, and other methods are likely to be attractive in some circumstances. A somewhat similar approach, using a much more expensive scanner mounted to a tractor, has been used to estimate forage in an agricultural context (Radtke et al. 2010). The equipment used here is relatively portable and inexpensive, and can have collateral uses in the context of forest vegetation sampling (e.g. distance measurement, tree height measurement), so we believe it to be worthwhile testing the approach in other contexts. As with conventional allometric approaches, we would urge caution in applying regression equations developed in one population or system to another. We also speculate that it may be necessary to use more complex models, or incorporate additional covariates, in forested understories that contain a complex and varying mixture of different structural life forms (e.g. woody shrubs, ferns, sedges, and low forbs). Nonetheless we view these initial results as promising, and believe that the techniques proposed here could be a valuable addition to the applied vegetation ecology toolkit.

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References

- Alaback, P.B. 1986. Biomass regression equations for understory plants in Coastal Alaska: effects of species and sampling design on estimates. *Northwest Sci.* **60**(2): 90–103.
- Andariese, S.W., and Covington, W.W. 1986. Biomass estimation for four common grass species in Northern Arizona Ponderosa pine. *J. Rangeland Manage.* **39**: 472–473. doi 10.2307/3899456.
- Arno, S.F., 2000. Fire regimes in western forest ecosystems. In: Brown, J.K., Smith, J.K. (Eds.), *Wildland fire in ecosystems: effects of fire on flora*. USDA Forest Service, Rocky Mountain Research Station. General Technical Report RMRS GTR-42, Vol. 2.
- Claeskens, G., and Hjort, N.L. 2008. *Model Selection and Model Averaging*. Cambridge University Press, Cambridge, UK. doi: 10.1017/CBO9780511790485.
- Cochran, W.G., 1977. *Sampling techniques*. 3rd ed. John Wiley & Sons, New York.
- Dickie, I.A., Yeates, G.W., St. John, M.G., Stevenson, B.A., Scott, J.T., Rillig, M.C., Peltzer, D.A., Orwin, K.H., Kirschbaum, M.U.F., Hunt, J.E., Burrows, L.E., Barbour, M.M., and Aislabie, J. 2011. Ecosystem service and biodiversity trade-offs in two woody successions. *J. Appl. Ecol.* **48**(4): 926–934. doi: 10.1111/j.1365-2664.2011.01980.x
- Eskelson, B.N., Madsen, L., Hagar, J.C. and Temesgen, H. 2011. Estimating riparian understory vegetation cover with beta regression and copula models. *For. Sci.* **57**(3): 212-221.

- 297 Estornell, J., Ruiz, L.A., Velázquez-Martí, B. and Fernández-Sarría, A. 2011. Estimation of shrub
298 biomass by airborne LiDAR data in small forest stands. *For. Ecol. Manage.* 262(9): 1697-1703.
299 doi: 10.1016/j.foreco.2011.07.026
300
- 301 Frappier, B., Lee, T.D., Olson, K.F., and Eckert, R.T. 2003. Small-scale invasion pattern, spread rate,
302 and lag-phase behavior of *Rhamnus frangula* L. *For. Ecol. Manage.* 186(1-3): 1-6. doi:
303 dx.doi.org/10.1016/S0378-1127(03)00274-3
304
- 305 Gilliam, F.S. 2007. The ecological significance of the herbaceous layer in temperate forest ecosystems.
306 *Bioscience* 57(10): 845–858. doi: 10.1641/B571007.
307
- 308 Gonzalez, M., Augusto, L., Gallet-Budynek, A., Xue, J., Yauschew-Raguenes, N., Guyon, D., Trichet, P.,
309 Delerue, F., Niollet, S., Andreasson, F., Achat, D.L., and Bakker, M.R. 2013. Contribution of
310 understory species to total ecosystem aboveground and belowground biomass in temperate *Pinus*
311 *pinaster* Ait. forests. *For. Ecol. Manage.* 289: 38-47. doi: 10.1016/j.foreco.2012.10.026
312
- 313 Hall, S.A., Burke, I.C., Box, D.O., Kaufmann, M.R., and Stoker, J.M. 2005. Estimating stand structure
314 using discrete-return lidar: an example from low density, fire prone ponderosa pine forests. *For.*
315 *Ecol. Manage.* 208: 189-209. doi: 10.1016/j.foreco.2004.12.001
316
- 317 Hardiman, B.S., Bohrer, G., Gough, C.M. and Curtis, P.S. 2013. Canopy structural changes following
318 widespread mortality of canopy dominant trees. *Forests* 4: 537-552
319
- 320 Heinrichs, S., Bernhardt-Roemermann, M., and Schmidt, W. 2010. The estimation of aboveground
321 biomass and nutrient pools of understorey plants in closed Norway spruce forests and on
322 clearcuts. *Eur. J. For. Res.* 129(4): 613–624. doi: 10.1007/s10342-010-0362-7

Kerns, B.K. and Ohmann, J.L. 2004. Evaluation and prediction of shrub cover in coastal Oregon forests (USA). *Ecol. Indicators* 4(2): 83–98. doi: 10.1016/j.ecolind.2003.12.002

Kershaw, J.A. Jr., Ducey, M.J., Beers, T.W., and Husch, B. 2016. *Forest Mensuration*, 5th edition. Wiley, New York. doi: 10.1002/9781118902028

Li, Y., Andersen, H. E., and McGaughey, R. 2008. A comparison of statistical methods for estimating forest biomass from light detection and ranging data. *West. J. Appl. For.* 23(4): 223-231.

Lumley, T. (2009) leaps: regression subset selection. R package version 2.9. <http://CRAN.R-project.org/package=leaps>.

MacArthur, R.H. and Horn, H.S. 1969. Foliage profiles by vertical measurements. *Ecol.* 50(5): 802-804. doi: 10.2307/1933693

Magnussen, S., Næsset, E., and Gobakken, T. 2013. Prediction of tree-size distributions and inventory variables from cumulants of canopy height distributions. *Forestry* 86(5): 583-595. doi: 10.1093/forestry/cpt022.

McCarthy, N., Bentsen, N.S., Willoughby, I., and Balandier, P. 2011. The state of forest vegetation management in Europe in the 21st century. *Eur. J. For. Res.* 130(1): 7–16. doi: 10.1007/s10342-010-0429-5

Misson, L., Baldocchi, D.D., Black, T.A., Blanken, P.D., Brunet, Y., Curiel Yuste, J., Dorsey, J.R., Falk, M., Granier, A., Irvine, M.R., Jarosz, N., Lamaud, E., Launiainen, S., Law, B.E., Longdoz, B.,

Loustau, D., McKay, M., Paw, U.K.T., Vesala, T., Vickers, D., Wilson, K.B., and Goldstein, A.H., 2007. Partitioning forest carbon fluxes with overstory and understory eddy-covariance measurements: a synthesis based on FLUXNET data. *Agric. For. Meteorol.* 144(1-2): 14–31. doi: 10.1016/j.agrformet.2007.01.006

Moore, P.T., van Miegroet, H., and Nicholas, N.S. 2007. Relative role of understory and overstory in carbon and nitrogen cycling in a southern Appalachian spruce-fir forest. *Can. J. For. Res.* 37: 2689–2700.

Muir, P.S., Mattingly, R.L., Tappeiner II, J.C., Bailey, J.D., Elliott, W.E., Hagar, J.C., Miller, J.C., Peterson, E.B., and Starkey, E.E., 2002. Managing for biodiversity in young Douglas-fir forests of western Oregon. U.S. Geological Survey, Biological Resources Division, Biological Science Report USGS/BRD/BSR–2002-0006.

Muukkonen, P., Makipaa, R., Laiho, R., Minkinen, K., Vasander, H., Finér, L., 2006. Relationship between biomass and percentage cover in understory vegetation of boreal coniferous forests. *Silv. Fenn.* 40, 231–245.

Naesset, E. 2002. Predicting forest stand characteristics with airborne laser using a practical two-stage procedure and field data. *Remote Sens. Environ.* 80(1): 88-99. doi: 10.1016/S0034-4257(01)00290-5

Naesset, E. 2004. Practical large-scale forest stand inventory using a small-footprint airborne scanning laser. *Scand. J. For. Res.* 19(2): 164-179. doi: 10.1080/02827580310019257

Oliver, C.D. and Larson, B.C.. 1996. *Forest Stand Dynamics*, update ed. New York: Wiley. 520 pp.

- 375
376
377 Palace, M., F.B. Sullivan, M.J. Ducey, and C. Herrick. 2016. Estimating tropical forest structure using a
378 terrestrial lidar. PLoS One 11(4): e0154115. doi:10.1371/journal.pone.0154115.
379
380 Paton D., Nunez, J., Bao, D., and Munoz, A. 2002. Forage biomass of 22 shrub species from Monfrague
381 Natural Park (SW Spain) assessed by log-log regression models. J. Arid Environ. 52(2): 223–231.
382 doi: 10.1006/jare.2001.0993.
383
384 Powell, T.L., Gholz, H.L., Clark, K.L., Starr, G., Cropper Jr., W.P., and Martin, T.A. 2008. Carbon
385 exchange of a mature, naturally regenerated pine forest in north Florida. Global Change Biology
386 14(11): 2523–2538. doi: 10.1111/j.1365-2486.2008.01675.x
387
388 R Core Team. 2012. R: A language and environment for statistical computing. R Foundation for
389 Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>.
390
391 Radtke, P.J., Boland, H.T. and Scaglia, P. 2010. An evaluation of overhead laser scanning to estimate
392 herbage removals in pasture quadrates to estimate herbage removals in pasture quadrats. Ag. For.
393 Meteorol. 150(12): 1523-1528. doi: 10.1016/j.agrformet.2010.07.010.
394
395 Ringvall, A., Ståhl, G., Teichmann, V., Gove, J.H., and Ducey, M.J. 2001. Two-phase approaches to
396 point and transect relascope sampling of downed logs. Can. J. For. Res. 31(6): 971-977. doi:
397 10.1139/x01-027
398

- Russell, M.B., D'Amato, A.W., Schulz, B.K., Woodall, C.W., Domke, G.M. and Bradford, J.B. 2014. Quantifying understorey vegetation in the US Lake States: a proposed framework to inform regional forest carbon stocks. *Forestry* 87(5): 629-638. doi: 10.1093/forestry/cpu023
- Särndal, C.-E., Swensson, B., and Wretman, J. 1992. *Model Assisted Survey Sampling*. Springer-Verlag, New York.
- Skowronski, N.S., Clark, K.L., Duveneck, M. and Hom, J. 2011. Three-dimensional canopy fuel loading predicted using upward and downward sensing LiDAR systems. *Rem. Sens. Environ.* 115(2): 703-714. doi: 10.1016/j.rse.2010.10.012.
- Smith W.B. and Brand, G.J. 1983. Allometric biomass equations for 98 species of herbs, shrubs, and small trees. Research Note NC-299, USDA, Forest Service, North Central Experiment Station, 8 p.
- Suchar, V.A., and Crookston, N.L. 2010. Understory cover and biomass indices predictions for forest ecosystems of the Northwestern United States. *Ecol. Indicators* 10(3): 602–609. doi: 10.1016/j.ecolind.2009.10.004
- van Leeuwen, M. and Nieuwenhuis, M. 2010. Retrieval of forest structural parameters using LiDAR remote sensing. *Eur. J. For. Res.* 129(4): 749–770. doi: 10.1007/s10342-010-0381-4
- Wagner, R.G., Little, K.M., Richardson, B., and McNabb, K. 2006. The role of vegetation management for enhancing productivity of the world's forests. *Forestry* 79: 57–79.

424 Yarie, J. 1980. The role of understory vegetation in the nutrient cycle of forested ecosystems in the
425 mountain hemlock biogeoclimatic zone. *Ecol.* 61(6): 1498–1514.
426
427

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Table 1. Coefficients ($\pm$ standard errors) and fit statistics for the best regression models for up to four predictor variables, with both additive and non-additive metrics allowed to enter the model; and for the best single-variable model, when only additive metrics are allowed.

Variables	Intercept	c_1	c_2	med_z	$vmed_z$	vh	mh	mp	R^2	BIC	AIC_c
All Metrics Allowed											
1	11.18 $\pm$ 8.40							5.80 $\pm$ 0.40	0.845	-67.20	414.45
2	2.54 $\pm$ 6.72		0.091 $\pm$ 0.009	8.45 $\pm$ 1.34					0.909	-85.00	395.44
3	-6.20 $\pm$ 7.00		0.072 $\pm$ 0.011	9.05 $\pm$ 1.26	0.95 $\pm$ 0.35				0.925	-88.71	390.66
4	-25.97 $\pm$ 11.26			9.14 $\pm$ 1.35	1.15 $\pm$ 0.52	-44.80 $\pm$ 9.37	45.67 $\pm$ 8.96		0.930	-87.98	390.48
Additive Metrics Only											
1	-25.98 $\pm$ 10.45	10.76 $\pm$ 0.76							0.840	-65.82	415.83

Figure 1. Illustration of laser sampling.

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440 **Figure 2.** Best simple regression models among all metrics (mp) and allowing only additive metrics (c_1).

441 For descriptive statistics, see Table 1.

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Figure 3. Standard error of the double sampling with regression estimator, as a function of number of samples used for regression calibration (n) and total sample size (n').