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Carbon pools and fluxes in small temperate forest landscapes: Variability and implications for sampling design

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ABSTRACT

Assessing forest carbon storage and cycling over large areas is a growing challenge that is complicated by the inherent heterogeneity of forest systems. Field measurements must be conducted and analyzed appropriately to generate precise estimates at scales large enough for mapping or comparison with remote sensing data. In this study we examined spatial variability in three small temperate forest landscapes. Our objectives were (1) to quantify the magnitude and scale of variability in stand structure, carbon pools and carbon fluxes and (2) to assess how this variability influences both optimal sampling strategy and required sampling intensity. Stand structure was consistently less variable than carbon pools or fluxes, suggesting that measuring carbon dynamics may require more intense sampling than traditional forestry inventories. Likewise, the magnitude of variability differed substantially among response variables, implying that sampling efficiency can be enhanced by adopting a flexible sampling strategy that is optimized for each carbon pool. Our results indicate that plots dispersed across the study area are generally more effective than clustered plots for characterizing carbon dynamics.

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1. Introduction

Terrestrial ecosystems contain substantial carbon pools whose dynamics may impact and interact with atmospheric CO_2 concentrations (Schimel, 1995; Steffen et al., 1998), potentially influencing climatic conditions (IPCC, 2007). Consequently, quantifying forest carbon dynamics over areas substantially larger than measurement plots or relatively homogeneous forest stands is a central goal for ecosystem ecologists (Sellers et al., 1997). Furthermore, forest ecosystems are notoriously heterogeneous in space (Townsend et al., 1996; Wilson and Meyers, 2001), and accounting for that heterogeneity is a substantial obstacle to scaling carbon estimates from plots and stands to landscapes and regions (Botkin et al., 1993; Jarvis, 1995; Enquist et al., 2007).

Approaches to assessing spatial heterogeneity generally fall into three complimentary categories: measurement of carbon pools and/or fluxes using biometric methods at the plot-level (Botkin et al., 1993; Brown and Schroeder, 1999; Burrows et al., 2003; Zheng et al., 2003), continuous monitoring of whole ecosystem carbon balance with micrometeorological towers (Baldocchi et al., 2001; Hollinger et al., 2004; Kim et al., 2006), and analysis of remotely sensed imagery (Schimel, 1995; Turner et al., 2000; Ollinger et al., 2002; Turner et al., 2003). Biometric measurements provide direct quantification of carbon pools as well as annual or multi-year carbon accumulation and decomposition at individual locations (Curtis et al., 2002; Ohtsuka et al., 2005). By comparison, continuous flux tower data generate insight into the impact of environmental conditions on net ecosystem carbon balance (Baldocchi, 2003; Monson et al., 2005; Desai et al., 2008). Remotely sensed imagery facilitates the scaling of these insights to regional and global areas by measuring light absorption and relating it to vegetation composition and structure as well photosynthetic rates (Roughgarden et al., 1991; Running et al., 2004). Each approach has advantages and limitations, and the most robust insights into forest carbon dynamics over large areas rely on insights from multiple approaches integrated into ecological simulation models (Reich et al., 1999; Running et al., 1999; Turner et al., 2004b; Kennedy et al., 2006). These approaches compliment

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each other because they measure the same response variable over very different spatial and temporal scales, providing validation of each other (Cohen and Justice, 1999; Canadell et al., 2000; Cook et al., 2004; Ollinger and Smith, 2005; Turner et al., 2006a,b).

However, these differences in scale also present an obstacle to comparison between methods. One of the most confounding differences is the variability in spatial scale between biometric field plots and both flux tower measurements and remotely sensed imagery. Individual field plots often cover between 200 and 500 m^2 (8–12 m radius circles), although very large, labor intensive plots may sample areas as large as 900 m^2 (30 m by 30 m; Ollinger and Smith, 2005; Turner et al., 2005), and even larger plots have been installed in some studies (Leigh et al., 2004). By contrast, flux tower footprints, while more difficult to define, can extend several hundred meters from the tower, potentially covering >50,000 m^2 (Baldocchi, 1997) and can be much larger during periods of high wind and in areas with variable topography (Finnigan, 2004). Although pixels for commonly available remotely sensed imagery can be as small as ~900 m^2 (Landsat ETM), complications of image registration and blurring mean that relating specific pixels to field measurements requires sampling an area 4 times the pixel size, or roughly 3600 m^2 (Curran and Williamson, 1986). In addition, remotely sensed imagery currently used for regional and global vegetation studies has much larger minimum pixel sizes (i.e. 250 m minimum pixel size on MODIS; Hook et al., 2001). The obstacle to reconciling these data sources is that plots measure carbon dynamics over hundreds of m^2 whereas both flux towers and remote sensing measure carbon dynamics over thousands of m^2.

The challenge in bridging this gap in spatial scales involves determining how to collect and analyze field measurements to precisely estimate carbon pools and fluxes over areas that can be directly compared to flux tower footprints and remote sensing pixels (Wessman, 1992; Turner and Chapin, 2005). For assessment of large-scale forest carbon pools and fluxes, important unanswered questions include: How much does the magnitude of spatial variability differ between various carbon pools and fluxes, and how many plots are necessary to precisely characterize pools or fluxes within small landscapes? To address these questions we measured stand structure, carbon pools and carbon fluxes in nested forest plots distributed across small landscapes in three temperate forest ecosystems. Our objectives were (1) to quantify the magnitude and spatial scale of variability in stand structure, carbon pools and carbon fluxes and (2) to assess how this variability influences both optimal sampling strategy and required sampling intensity. Few studies have directly addressed spatial variability and sampling design, but with increasing interest in quantifying forest carbon dynamics at landscape and larger scales, such an examination can help ecologists move beyond using somewhat arbitrary guidelines (Kloeppel et al., 2007) to guide sampling design.

2. Methods

2.1. Site description

We examined variability of aboveground carbon pools and fluxes in small landscapes of three temperate forest ecosystems (Fig. 1): northern hardwoods in central NH (Bartlett Experimental Forest), mixed forests of northern MN (Marcell Experimental Forest), and subalpine Rocky Mountain forests in CO and WY (3 sites).

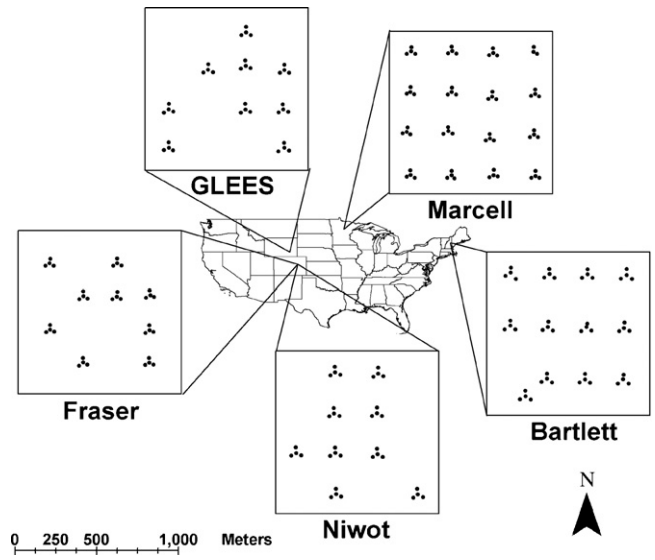

Fig. 1. Site locations and plot layouts for sampling of stand structure, carbon pools and carbon fluxes in 3 forest types. Plots are organized into 4-plot clusters (similar to FIA protocol) within small landscapes of 1 km by 1 km (scale bar refers to square zoomed views of study areas). Forest types include Northern Hardwoods (Bartlett), northern mixed forests (Marcell) and subalpine Rocky Mountains (GLEES, Niwot and Fraser).

Bartlett Experimental Forest. Bartlett consists primarily of second-growth northern hardwoods dominated by *Fagus grandifolia*, *Betula alleghaniensis*, *Acer saccharum*, and *Tsuga canadensis* with scattered stands of *Acer rubrum*, *Betula papyrifera*, *Populus tremuloides*, *Picea rubens* and *Pinus strobus*. Summer air temperature highs often top 32 °C and winter lows reach −34 °C while average annual precipitation is 127 cm, well distributed throughout the year (Table 1). Bartlett soils are moist but generally well drained spodosols. In the late 19th century, the lower third of Bartlett was logged while upper portions were less impacted. Natural disturbances at Bartlett include hurricanes (1938) and ice storms (1998) and occasional small scale wind storms (Anderson et al., 2006). Variation in stand characteristics and annual net primary production across the Bartlett landscape have been reported by Ollinger and Smith (2005).

Marcell Experimental Forest. Marcell includes both upland forests and peatlands. Uplands forests are generally dominated by *P. tremuloides* and *grandidentata*, but contain substantial components of *B. papyrifera*, *Pinus resinosa*, *P. strobus*, and *Pinus banksiana*. Lowland tree species include *Larix laricina*, *Picea mariana*, *Fraxinus nigra*, and *Thuja occidentalis*. Climate at Marcell is subhumid continental, with air temperature extremes of −46 °C and 38 °C (Table 1). Upland soils at Marcell are mainly loamy sands or fine loams sandy whereas the fen or bog soils contain substantial peat ranging from highly to moderately decomposed (Nichols and

Table 1
Climatic conditions, sample size and general stand structure for forested landscapes in NH, MN, CO and WY.

Site	Latitude, longitude	Mean annual temperature (°C)	Mean annual precipitation (mm)	Elevation (m)	Plots	Maximum age (years)
Bartlett	44°2′39″N, 71°9′56″W	6	1270	275	48	120
Marcell	47°30′N, 93°28′W	3	785	425	63	69
Fraser	39°4′N, 105°52′W	0	737	3100	36	246
Glees	41°22′N, 106°15′W	−2	1000	3180	36	247
Niwot	40°2′N, 105°33′W	4	800	3050	36	137

Verry, 2001). Forests of the Lake States region experienced widespread logging around the turn of the 20th century (Stearns, 1997), including much of the Marcell landscape, and natural disturbances at Marcell include wind storms of variable intensity and rare wildfires (Schulte and Mladenoff, 2005).

Rocky Mountain Forests. We examined three small landscapes in the subalpine Rocky Mountains: The Fraser Experimental Forest, located near Fraser Colorado, the Glacier Lakes Ecosystem Experiment Site, located near Centennial Wyoming, and the Niwot Ridge Ameriflux study site (slightly west and downslope from the Niwot Ridge Long Term Ecological Research Site) located near Nederland, Colorado. Tree species consist primarily of *Abies lasiocarpa* and *Picea engelmannii* at higher elevations and *Pinus contorta* at lower elevations, with minor components of *Pinus flexilis* and *P. tremuloides* at Niwot. Climate is characterized by cold and relatively long winters (Table 1). Disturbance history includes scattered logging at Glacier Lakes over 100 years ago, widespread clearcuts at Niwot between 1900 and 1910 and selective clearcuts at Fraser in the 1950s. Wildfires and insect outbreaks are important natural disturbances in these systems and Fraser is the only site with evidence of large recent fires; Fraser experienced a widespread stand-replacing fire in approximately 1685.

2.2. Data collection

At each site, we identified a 1 km by 1 km focal study area. Within this area, we established between 36 and 64 research plots at predetermined locations on a grid overlaid upon each study area to avoid biased sampling (Hollinger, 2008). Established to closely mimic the widely used USDA forest inventory and analysis protocol (Bechtold and Patterson, 2005), plots were oriented in clusters of four, with a center plot and three satellite plots located 35 m away at 0°, 120°, and 240°. For the purposes of this study, a plot refers to a single circular area whereas a cluster is a group of 4 plots (Fig. 1).

Stand structure. We selected four variables to characterize forest stand structure: tree basal area ($m^2\ ha^{-1}$), tree density (trees ha^{-1}), mean tree height (m), and tree leaf area ($m^2\ m^{-2}$). We recorded species, location and diameter at breast height (0.37 m) for all live and dead trees within 8–10 m (depending on site) of plot centers. Saplings, seedlings and shrubs were measured in a 3 m radius micro-plot centered 5 m east of plot center. Stem density and basal area was calculated for all stems greater than 2.5 cm and height was measured for the largest 3–5 trees per plot. Leaf area was estimated from allometric equations at the Rocky Mountain sites, litterfall collections at Bartlett, and an LAI-2000 Plant Canopy Analyzer (LI-COR Biosciences, Lincoln, NE) at Marcell.

Carbon pools. We measured four carbon pools: aboveground carbon in live mass, aboveground carbon in dead woody biomass (standing and down), carbon in the forest floor and mineral soil carbon (0–20 cm). Carbon in aboveground live mass included carbon in live trees and understory vegetation. Aboveground biomass in foliage, branches and stems of trees and shrubs was estimated from allometric equations at Bartlett (Ribe, 1973; Whittaker et al., 1974; Hocker and Earley, 1983), Marcell (Perala and Alban, 1993) and the Rocky Mountain sites (Appendix A). Biomass was calculated for live and dead trees, saplings and seedlings and converted to carbon by dividing by 2 (Schlesinger, 1997). Biomass of understory herbaceous vegetation was collected at peak biomass (late summer) from three 0.25–0.5 m^2 quadrats centered 7 m from plot center at 60°, 160° and 300°. Biomass was dried, weighed and analyzed for carbon content. Aboveground dead carbon was calculated as the sum of carbon in standing dead tree stems (allometric equations above; assuming standing dead trees are all class I decay state) and down woody debris, which was measured along 4, 15 m transects at each plot. Down woody debris transects were oriented from east to west and were centered at points 9 and 3 m north and south of plot centers. Diameter and decay class (Arthur and Fahey, 1990; Busse, 1994) were recorded for all logs with diameter greater than 7.5 cm. Log diameters were transformed into cross-sectional areas by assuming that class I–III logs are circular whereas class IV and V logs are oval shaped with ratios between short and long axis of 1:4 and 1:5, respectively (Tinker and Knight, unpublished data) and plot-level volume was corrected for angular distribution of logs (Van Wagner, 1968; Brown, 1971). Total down wood biomass per transect was estimated by multiplying volume by species-specific wood specific gravity for live and dead wood (Duvall and Grigal, 1999; Jenkins et al., 2003; Kueppers et al., 2004). Forest floor biomass was quantified by harvesting all organic material (other than standing biomass) above mineral soil within three 30 cm by 30 cm quadrats located 7 m from plot center at 60°, 160° and 300°. Large tree roots (>3 mm) were not included in these samples, but fine roots were not removed if present. Forest floor samples were dried at 65 °C, weighed and the entire sample was ground, mixed and sub-sampled for analysis of total carbon and nitrogen content on a CHN analyzer. To calculate forest floor carbon, we multiplied the rock-free biomass by the measured carbon concentration for each sample quadrat. Total area-based carbon stored in the forest floor was estimated by averaging the carbon content of the three samples in each plot. Mineral soil carbon was estimated from six 2.5 cm diameter mineral soil cores collected to a depth of at least 20 cm on each plot and measured for bulk density ($n = 6$). Forest floor and mineral soil carbon were only measured center plots at Bartlett.

Carbon fluxes. We calculated two carbon fluxes: live mass increment of trees and litterfall. Annual live mass increment from 1994 and 2003 was estimated from direct measurements of tree diameter on all trees at Bartlett and from increment cores taken from 5 to 10 trees in each plot at Marcell and the Rocky Mountain sites (selected to represent all size classes and species). To estimate increments of un-cored trees, we used linear regression to relate basal area increment to DBH in cored trees and applied the results to un-cored trees. Equations were developed for each year, and were specific to each species within each plot where $n \geq 5$, or within each site if plot $n < 5$. Basal area increment was converted into DBH for previous years, which were used with allometric equations (see carbon pools above) to estimate standing biomass at each year. Live mass increment (B_{INC}) was calculated as the differences in biomass between subsequent years, and was calculated for each individual tree and summed to the plot. Litterfall collection varied slightly between sites, with 3–5 traps per plot covering 0.1–0.15 m^2 per trap. Litter was collected twice a year at the Rocky Mountain sites and 3–4 times per year at Marcell and Bartlett. Litter was dried and weighed, and analyzed for carbon content.

2.3. Analysis

To assess variable normality, we calculated skew and excess kurtosis and conducted the Shapiro–Wilk and Kolmogorov–Smirnov normality tests using the Frequency procedure in SAS Stat Version 8 (SAS, 2001). Variable/site combinations that failed both normality tests were either square root or natural log transformed (Appendix B) and resulting distributions were tested to ensure normality. All subsequent analyses were conducted on the transformed variables and results were back-transformed for presentation and calculation of confidence intervals.

Objective 1 – quantify the magnitude and scale of variability in stand structure, carbon pools and carbon fluxes. To quantify the intrinsic spatial variability in different carbon pools and fluxes, we calculated the mean, coefficient of variation (CV), and 95% confidence interval (CI) for all 10 response variables treating plots

(single circular plots) as the experimental unit. Because some response variables were transformed to achieve normality, we present the confidence interval in terms of back-transformed lower confidence limits (LCL) and upper confidence limits (UCL). To examine the relative magnitude of within cluster or between cluster variability, we conducted a 1-way analysis of variance in which independent variables were cluster and plots nested within clusters for all 10 variables at each site. Results from this analysis provide insight into the benefits of using individual plots or clusters of plots as the experimental unit by quantifying the magnitude of variation from one cluster to another (between cluster variability) and separate it from variation from one plot to another (within cluster variability.) A large proportion of variance occurring between clusters indicates that a carbon pool or flux is highly variable at relatively large scales (<250 m), whereas a large proportion of variance occurring within clusters suggests that a carbon pool or flux is highly variable at relatively small scales (<50 m). Since this statistical approach partitions the total observed variability in a response variable into within or between cluster variation, the proportion of variability in these two sources must sum to 1, so we report only the proportion of variability occurring between cluster means.

Objective 2 – assess how variability informs sampling strategy and intensity. To determine the optimal number of plots per cluster, we used a two-stage sampling analysis technique. Presented by Cochran (1977), this method estimates variance of an overall sample as a function of the number of clusters and plots per cluster and the mean squared error results from the ANOVA described in objective 1. If y_{ij} is the observed response variable value (e.g. aboveground live carbon) for jth plot in the ith cluster, $\bar{y}_i$ is the mean value for a cluster, $\bar{\bar{y}}$ is the overall mean value, n is the number of clusters in the study area, with a theoretical maximum of N, and m is the number of plots per cluster, with the theoretical maximum of M, then an unbiased estimate of the variance $v(\bar{\bar{y}})$ is:

$$v(\bar{\bar{y}}) = \frac{1 - n/N}{n} s_1^2 + \frac{n/N(1 - m/M)}{mn} s_2^2 \quad (1)$$

where

$$s_1^2 = \frac{\sum^{n} (\bar{y}_i - \bar{\bar{y}})^2}{n-1} \quad \text{and} \quad s_2^2 = \frac{\sum_i \sum_j (\bar{y}_{ij} - \bar{y}_i)^2}{n(m-1)}$$

We calculated the expected variance $v(\bar{\bar{y}})$ for each response variable across a hypothetical range from 1 to 100 clusters and 1–10 plots per cluster. For each combination of clusters and plots per cluster, we used these estimates of expected variance to calculate the expected standard error of the estimate. To identify the most efficient sampling scheme, we characterized the specific combination of clusters and plots that minimizes effort (defined as total number of plots) while achieving a standard error that is <10% of the sample mean, a level of precision that has been used in previous studies (Hubbard et al., 2005). The specific precision threshold used will influence only the magnitude of the sampling intensity identified, not the relative sampling requirements between different carbon pools or fluxes or forest types. These results provide insight into both sampling strategy and sample size required to minimize relative error (i.e. standard error relative to the mean response.) However, in many cases, the goal of a sampling program is to achieve a particular standard of absolute error (i.e. minimizing the variability of the estimate in terms of MgC). To quantify how sample size influences absolute error, we determined the width of the 95% CI for carbon pools and fluxes as a function of the number of plots installed, ranging from 2 to 100 (Ott, 1994).

All analyses were conducted for each site independently. Results for the three Rocky Mountain sites were averaged and only mean values are presented because we found only minor differences in variability or sampling requirements among sites.

3. Results

3.1. Objective 1 – quantify the magnitude and scale of variability in stand structure, carbon pools and carbon fluxes

Across all sites, we found that the CV of stand structural properties was generally lower than either carbon pools or fluxes. Stand structure CV ranged from 8% to 81% (mean 40%) for all stand structure variables at all sites whereas carbon pool CV ranged from 23% to 81% (mean 45%) and carbon flux CVs ranged from 18% to 61% (mean 49%) (Table 2). Of the stand structure properties, tree height was consistently among the least variable (CV averaged 25%), whereas basal area and stem density were generally the most variable (average CVs near 50%).

Table 2
Estimates of stand structure, carbon pools and carbon fluxes in four small temperate forest landscapes. Results include mean, coefficient of variation, and upper and lower limits of a 95% confidence interval around the mean (LCL and UCL, respectively). Values are back-transformed where necessary.

Category	Variable	Units	Bartlett				Marcell				Rocky Mountains			
			Mean	CV	LCL	UCL	Mean	CV	LCL	UCL	Mean	CV	LCL	UCL
Stand structure	Leaf area	$m^2\ m^{-2}$	3.4	24%	3.2	3.6	2.4	42%	1.9	2.9	5.6	51%	4.436	6.7
	Height	m	19.0	8%	18.57	19.4	11.1	44%	8.8	13.65	12.5	10%	11.8	13.18
	Basal area	$m^2\ ha^{-1}$	32	27%	30	35	22	81%	17	26.01	50	48%	42	58
	Stem density	stems ha^{-1}	616	13%	572.7	660	579	57%	429.	2 750.4	1152	47%	943.2	1376
Carbon pools	Live AGBio	MgC ha^{-1}	96	27%	88	103	44	53%	33	56	89	41%	70	110
	Dead AGBio		18	33%	15	22	8	80%	5	12	17	53%	12	24
	Forest floor		19	23%	18	20	5	65%	5	6	72	47%	62	83
	Soil carbon		16	34%	14	17	34	22%	32	36	61	31%	55	67
Carbon fluxes	Tree B_{INC}	MgC ha^{-1} $year^{-1}$	2.3	61%	1.9	2.7	1.3	58%	1.0	1.7	1.4	52%	1.2	1.7
	Litterfall		1.1	18%	1.1	1.2	0.9	61%	0.8	1.0	1.0	43%	0.8	1.1

	Variable	Bartlett		Marcell		Rocky Mountains	
		CV	CI width	CV	CI width	CV	CI width
Category means	Structure	18%	–	56%	–	39%	–
	Pools	30%	6.8	55%	8.7	43%	21.5
	Fluxes	39%	0.46	60%	0.51	48%	0.38

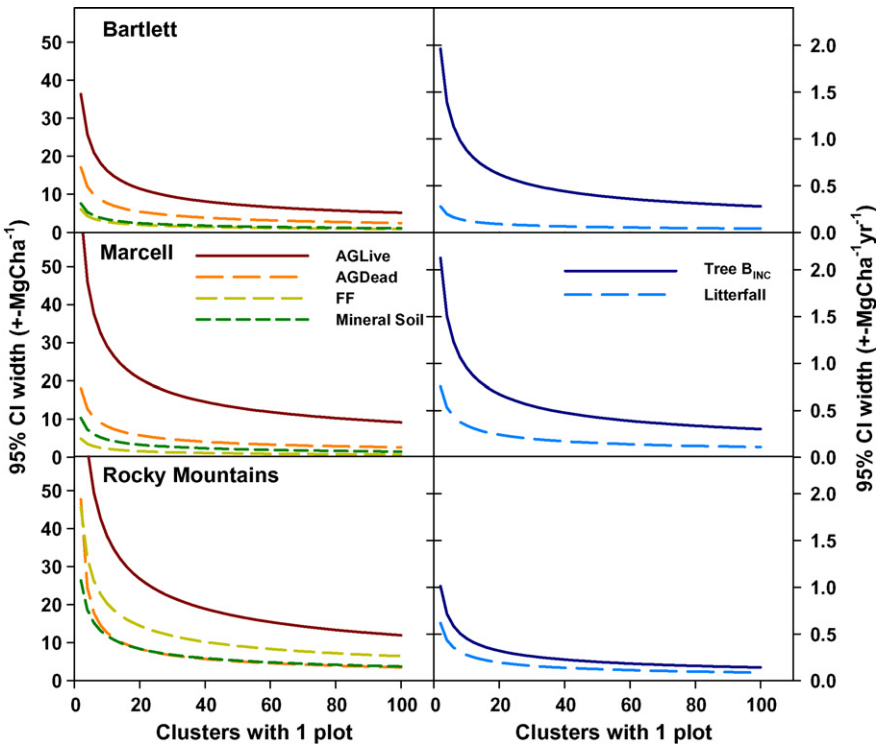

Fig. 2. Width of the 95% confidence interval around the mean as a function of sample size for carbon pools (left panel) and carbon fluxes (right panel) at Bartlett (top), Marcell (middle) and the Rocky Mountain sites (bottom). This illustrates how the absolute estimation uncertainty is consistently higher for live mass and tree B_{INC} compared to soil carbon or litterfall. Also note the high uncertainty in forest floor estimates at the Rocky Mountain sites compared to Bartlett and Marcell. *Abbreviations*: AGLive: aboveground live mass; AGDead: aboveground dead woody biomass; FF: forest floor; Tree B_{INC}: tree biomass increment.

For carbon pools and fluxes, we examined both relative variability (CV: variability relative to the mean) and absolute variability (CI width: variability in units of carbon). In all forest types, carbon in aboveground dead woody biomass displayed more relative variability than either carbon in aboveground live mass or forest floor carbon (Table 2). Mineral soil carbon was the least variable at both Marcell and the Rocky Mountain sites, but not at Bartlett. In terms of absolute variability, the carbon pool results were somewhat different. Because of the large amount of carbon stored in live mass, carbon in aboveground live mass consistently displayed the largest confidence interval width, followed by carbon in aboveground dead woody biomass, forest floor carbon, and mineral soil carbon. Absolute variability at the Rocky Mountain sites diverged from these trends because the size of the forest floor carbon pool was substantially higher than either Bartlett or Marcell, resulting in much larger confidence intervals than carbon in either aboveground dead woody biomass or mineral soil. Of the two carbon fluxes that we examined, tree biomass increment displayed higher relative variability than litterfall at both Bartlett and the Rocky Mountain sites, but very similar relative variability at Marcell (Table 2). Because the magnitude of litterfall is substantially lower than tree biomass increment, litterfall consistently displayed lower absolute variability (Fig. 2).

We found that the proportion of total variance that occurred between cluster means ranged between roughly 50% to over 90% with most variables falling between 60% and 80% (Table 3.) At Bartlett, the response variables that we examined had an average of 64% of the variability between clusters, compared to 77% and 71% at Marcell and the Rocky Mountains, respectively.

3.2. Objective 2 – assess how variability influences sampling strategy and intensity

Our assessment of the relationship between precision and sampling strategy consistently indicated that having only one plot per cluster is the most efficient way to achieve a specific level of precision in the small landscapes that we examined (Table 4). Increasing the number of plots per cluster had only minor impact on the total estimate of standard error and that installing additional 1-plot clusters was much more effective at characterizing stand structure, carbon pools and carbon fluxes (Fig. 3).

Because we found that independent plots are most efficient approach to minimizing uncertainty at these small landscapes, we conducted our examination of sampling intensity by using plots that are independent of cluster, and quantified the number of plots necessary to control relative or absolute variability. In terms of

Table 3
Proportion of landscape variability occurring between clusters as opposed to within clusters.

	Bartlett	Marcell	Rocky Mountains
Leaf area	71%	86%	81%
Height	49%	78%	66%
Basal area	67%	69%	71%
Stem density	67%	79%	73%
Live AGBio	63%	68%	74%
Dead AGBio	53%	68%	70%
Forest floor		74%	57%
Soil carbon		81%	73%
Tree B_{INC}	72%	78%	75%
Litterfall	68%	92%	67%

Table 4
Most efficient combination of clusters and plots necessary to achieve a standard error that is <10% of the sample mean.

	Bartlett		Marcell		Rocky Mountain	
	Clusters	Plots	Clusters	Plots	Clusters	Plots
Leaf area	4	1	7	1	9	1
Tree height	1	1	7	1	2	1
Basal area	4	1	11	1	7	1
Stem density	2	1	9	1	8	1
Aboveground live carbon	4	1	7	1	6	1
Aboveground dead carbon	4	1	11	1	8	1
Forest floor	3	1	9	1	6	1
Mineral soil	4	1	4	1	5	1
Tree B_{INC}	9	1	9	1	8	1
Litterfall	3	1	11	1	6	1

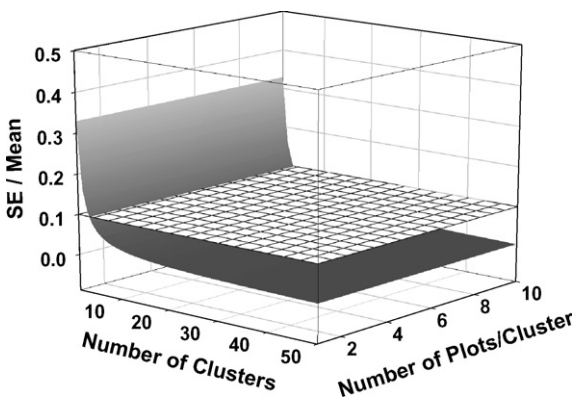

Fig. 3. Sample plot of standard error as a proportion of the mean (a measure of relative estimation uncertainty) for aboveground live mass at Bartlett as a function of both the number of clusters and the number of plots per cluster. This figure illustrates how increasing plots per cluster has relatively minor impact on uncertainty (a consistent result for all variables and sites). The plane for SE = 10% of the mean is shown because it was used as a threshold to define an acceptable level of relative variability for quantifying the most efficient sampling strategy (Table 4).

relative variability, we found that the minimum number of clusters with 1 plot that are necessary to achieve a standard error <10% of the sample mean within our 1 km^2 sampling area averaged 5.9 for stand structural variables and carbon pools and 7.7 for carbon fluxes (Table 4). For carbon pools, mineral soil carbon required the fewest plots and carbon in aboveground dead woody biomass required the most by a wide margin. Sampling requirements for relative variability for all variables were consistently lower at Bartlett compared to Marcell or the Rocky Mountain sites.

In terms of absolute variability, we found that carbon in aboveground live mass consistently required more plots than the other carbon pools (Fig. 2). Precise quantification of forest floor and mineral soil carbon required substantially more sampling at the Rocky Mountain sites than either Bartlett or Marcell. We found that tree biomass increment required substantially more plots than litterfall to achieve a given level of absolute certainty.

4. Discussion

Most research on forest structure or carbon dynamics examines how these variables relate to other conditions, notably forest age (Chapin et al., 2002; Pregitzer and Euskirchen, 2004), disturbance history (Pastor and Post, 1986; Goodale et al., 2002), land management (Dixon et al., 1994; Houghton et al., 1999), soil conditions (Oren et al., 2001), or climate (Goulden et al., 1998; Barford et al., 2001). These results are essential for understanding the controls over forest carbon pools and fluxes and identifying relationships that aid efforts to quantify pools or fluxes over large areas (Botkin et al., 1993; Schimel et al., 1997; Waring and Running, 1998; Kennedy et al., 2006). However, efforts to characterize forest carbon pools or fluxes at intermediate scales – too large to be directly measured yet too small to encompass a wide range of conditions where predictive relationships apply – must rely on field measurements alone (Hinckley et al., 1998). In these cases, understanding the inherent variability in a pool or flux is essential for designing an effective and efficient sampling strategy (Dutilleul, 1998). Although many studies have assessed variability in total biomass or productivity within contrasting forest types or ages (Turner et al., 2004a; Law et al., 2006), relatively few studies quantify the magnitude of variability at multiple scales within a landscape in individual pools or fluxes (although see Botkin et al., 1993; Burrows et al., 2003), and very few focus explicitly on variability for the purpose of informing sampling design (Kloeppel et al., 2007).

Stratification of the study area prior to plot layout provides a valuable and commonly used framework for increasing sampling efficiency (e.g. Botkin et al., 1993). Unlike many landscape-scale ecological studies, our study sites and plot locations were not stratified by forest type or age (i.e. our clusters were not selected to fall entirely within a given "patch"). Although potentially time consuming, our approach avoids bias toward very similar plots within individual clusters and allows us to relate the magnitude of variability within or between plot clusters to spatial scale and optimal sampling strategy (Bradford et al., 2008b). Furthermore, this unbiased strategy allows us to examine several response variables, some of which may not be strongly related to patch types designated by stratification (Bradford et al., 2009). However, because stratification has been so commonly used in previous studies and is likely to be widely applied in future landscape-scale assessments, our results about the consequences of un-stratified sampling may have limited applicability. Our conclusions may also be limited by the relatively small size of the landscapes that we examined. Although the 1 km by 1 km focal areas that we examined were quite large by comparison with typical field plots, they are certainly not large enough to capture the range of variability in forest age, stand structure or carbon pools that exist in the forest types that we examined. This is especially true at the relatively homogeneous Bartlett study area, as evidenced by the relatively low variability in height, basal area and stem density (Table 2). Furthermore, our field methods for some variables (e.g. coarse woody debris and leaf area) differed slightly across the three forest types we examined, potentially complicating cross-site comparisons.

Despite these limitations, our results illustrate several potentially important lessons for future sampling efforts over areas larger than individual forest stands. In all three forest types, stand structure was generally less variable than carbon pools and carbon fluxes, suggesting that traditional forestry sampling procedures, which were designed to assess structural characteristics relevant to timber harvesting (Avery and Burkhart, 1994; Husch et al., 2003), may not provide adequate characterization of carbon pools or fluxes.

Another clear result was the finding that over half of the variability occurs between clusters, which suggests that adding plots within clusters will not add as much information as adding new independent plots. This result indicates that the most efficient plot layout for quantifying forest carbon pools and fluxes in small landscapes consists of individual plots dispersed across the study area, rather than plots grouped into clusters. This may imply that the effort required to sample very large

plots (i.e. 30 m × 30 m Turner et al., 2005) would be less effective than sampling a greater number of smaller plots (Dutilleul, 1998). One important caveat to this result is that our calculations did not consider how the per-plot "cost" may be substantially lower when plots are clustered together (due to saving on travel time and expenses; Cochran, 1977). Indeed, this travel cost consideration becomes increasingly important as the area being examined increases, and helps explain the 4-plot clusters adopted by the USFS Forest Inventory and Analysis program (Bechtold and Patterson, 2005). Since our sites typically encompassed more than single forest type, the conclusion that individual plots are more efficient than clusters suggests that our response variables (structure, carbon pools and carbon fluxes) are reasonably consistent across the forest types.

Some of the carbon pools and fluxes were non-normally distributed within the study area, and in some cases the non-normality appeared to be scale-independent across reasonable sampling scales, because cluster-level estimates for some variables also failed normality tests (results not shown). The non-normal distributions in some carbon pools and fluxes indicate that scaling plot-level measurements to larger areas by simply multiplying up to a larger area, a common approach (Husch et al., 2003; Wu and Harbin, 2006), may introduce bias. Although the need for non-normality tests and appropriate data transformations are well recognized when conducting statistical analysis (Box et al., 1978; Gotelli and Ellison, 2004), our results underscore the necessity of these procedures when applying plot-level measurements to large areas. The existence of non-normality in these response variables suggests that carbon pools or fluxes should be sampled well enough to precisely characterize the distribution, ensuring that plots represent any "hot spots" where values are substantially different from the rest of the landscape. When necessary the data should be transformed to normality or scaled up using an appropriate non-normal distribution. A notable example is carbon stored in aboveground dead woody material, which displayed heavily skewed distributions at four of the five landscapes.

We found that relative and absolute variability can differ dramatically, indicating that investigators attempting to characterize a carbon pool or flux at landscape scales should be aware of the choice between basing sample size on relative or absolute precision (Kloeppel et al., 2007). For example, aboveground live carbon does not have especially large standard error relative to the mean, but because of the large size of this pool, aboveground live carbon requires by far the most plots to achieve a given confidence interval. Estimating sample size from standard error will fail to account for this high absolute variability, resulting in large uncertainty in landscape-scale estimates.

Perhaps most importantly, this study illustrates that variability, either relative or absolute, can be markedly different for different carbon pools or fluxes. For carbon pools, our results indicate that carbon in aboveground live mass, despite having a lower standard error relative to the mean, has dramatically higher sampling requirements than carbon in aboveground dead woody biomass, which in turn has higher sampling requirements than either forest floor or mineral soil. Likewise, our carbon flux results indicate that litterfall requires fewer samples than tree biomass increment. Although some variability patterns appear to be specific to certain forest types, notably the large size of the forest floor pool at the Rocky Mountain sites (Bradford et al., 2008a) and the subsequently high absolute variability (Table 2), our findings can strengthen future attempts to quantify landscape-scale carbon storage. In cases where the variability of response variables is reasonably well known, future efforts may consider measuring some variables on all plots and other variables on fewer plots. One important challenge inherent in this variable sampling intensity approach is that the variability must be known, and the variability, in absolute or relative terms, could change from one sampling period to the next in response to rapid episodic events like disturbances and/or slower processes like age-related forest succession. In addition, a variable sampling intensity approach may generate unbalanced datasets that create obstacles to statistical analysis. Despite these limitations, these results may provide valuable insight for improving the effectiveness of bottom–up biometric assessments of forest carbon dynamics. These results can be combined with site-specific estimates of time and cost involved in various measurements to better understand the overall cost of alternative carbon assessment strategies.

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Appendix A

References for allometric equations used to estimate leaf area index and carbon stocks from DBH and height measurements for the four dominant species in subalpine Rocky Mountain forests.

Component	Lodgepole pine	Engelmann spruce	Subalpine fir	Aspen
Wood density	Jenkins et al., 2003			
Leaf area	Kaufmann et al., 1982			
Foliage biomass	Pearson et al., 1984 with Gholz et al., 1979 for saplings/seedlings	Gholz et al., 1979		Wang et al., 1995
Branch biomass				
Stem biomass	Myers, 1967	Myers, 1972		
Bark biomass	Gholz et al., 1979			
Root biomass	Comeau and Kimmins, 1989	Ker and Van Raalte, 1981		Ruark and Bockheim, 1988 with Bond-Lamberty et al., 2002 for saplings/seedlings

Appendix B Descriptors of the statistical distribution of stand structure, carbon pools and carbon fluxes in small landscapes of three temperate forest ecosystems. Descriptors include skew, kurtosis, the Shapiro–Wilk test statistic W, and the Kolmogorov–Smirnov test statistic D. Variable and site combinations that failed both normality tests were transformed to achieve normality and are shown in bold.

Response variable	Bartlett				Marcell				Fraser				GLEES				Niwot			
	Skew	Kurt	$p < W$ S-W	$p > D$ K-S	Skew	Kurt	$p < W$ S-W	$p > D$ K-S	Skew	Kurt	$p < W$ S-W	$p > D$ K-S	Skew	Kurt	$p < W$ S-W	$p > D$ K-S	Skew	Kurt	$p < W$ S-W	$p > D$ K-S
Leaf area	0.24	−0.64	0.59	>0.15	−0.86	−0.06	**<0.01**	**<0.01**[a]	1.07	0.52	**<0.01**	**0.028**[a]	0.00	−1.23	0.024	>0.15	0.27	−1.01	0.112	0.034
Tree height	−0.76	1.81	0.08	>0.15	−0.61	−0.17	**<0.01**	**0.02**[a]	0.13	−0.68	0.655	>0.15	−1.15	0.77	**<0.01**	**<0.01**[b]	−1.00	1.98	**0.011**	**<0.01**[b]
Basal area	0.54	0.35	0.30	>0.15	1.02	1.76	<0.01	0.06	0.48	0.32	0.14	0.098	−0.04	−1.27	0.022	>0.15	−0.67	−0.22	0.089	>0.15
Stem density	0.82	2.60	**0.01**	**<0.01**[a]	0.79	0.45	**<0.01**	**0.02**[a]	0.44	−0.69	0.12	>0.15	1.39	1.28	**<0.01**	**<0.01**[a]	0.44	−0.20	0.474	>0.15
AG live	0.19	−0.58	0.68	>0.15	1.46	3.48	**<0.01**	**0.01**[a]	0.97	1.00	**<0.01**	**0.041**[a]	0.18	−1.33	0.009	0.077	−0.89	−0.10	**<0.01**	**<0.01**[b]
AG dead	0.42	−0.97	**0.02**	**0.04**[a]	1.60	1.98	**<0.01**	**<0.01**[a]	0.89	0.31	0.015	>0.15	1.90	3.95	**<0.01**	**<0.01**[b]	1.69	2.40	**<0.01**	**<0.01**[b]
Forest floor	−0.34	−1.42	0.25	>0.15	0.13	−0.32	0.05	>0.15	0.45	0.11	0.077	0.016	1.02	1.25	0.032	>0.15	−0.55	0.74	0.385	>0.15
Mineral soil	0.20	−0.96	0.89	>0.15	−0.41	−0.40	0.33	>0.15	0.38	−0.25	0.143	0.082	0.11	−0.84	0.558	>0.15	2.03	6.93	<0.01	>0.15
Tree biomass increment	0.16	−0.65	0.30	>0.15	1.79	5.33	**<0.01**	**<0.01**[a]	0.50	−0.58	0.119	>0.15	0.04	−0.79	0.096	>0.15	0.87	1.15	0.086	>0.15
Litterfall	0.45	−0.29	0.41	>0.15	−0.30	−0.96	0.01	>0.15	0.58	−0.61	0.042	0.128	1.41	3.12	<0.01	0.06	0.56	−0.30	0.051	0.011

[a] Square-root transformed.
[b] Natural log transformed.

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