CARBON ACCUMULATION AT THE HARVARD FOREST:

A COMPARISON OF METHODS FOR MEASURING TREE BIOMASS FOR

REGIONAL EXTRAPOLATION OF THE EDDY-FLUX TOWER FOOTPRINT

by

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ABSTRACT

       Questions about regional carbon cycling dynamics are particularly important for northeastern forests because of their significance in the North American terrestrial carbon sink. The long-term study of CO_2 exchange at Harvard Forest has been a key indicator of carbon uptake by northeastern forests, but establishment of the eddy-flux tower's relevance to the regional carbon budget requires scaling of the tower's CO_2 flux measurements to the surrounding forested region. Acquisition of extensively placed variable-radius 'BigFoot' plots provided an opportunity to investigate the spatial representativeness of the tower flux data and of the associated fixed-radius plots in the tower footprint. The utility of the BigFoot data was first investigated through the comparison of the variable- and fixed-radius measurement methods. Stand measurements from the BigFoot plots were then compared with those from the tower footprint. Comparison of the different plot types indicates that variable-radius plots were not sufficiently accurate for forest carbon accounting. Fixed-radius measurement of the extensively placed BigFoot allowed them to be compared with the tower footprint. Results of this comparison show that the forest composition of the tower footprint is representative of the region, and thus that the tower effectively samples regional trends in carbon sequestration.   Potential changes in land-use across the region highlight the need for additional measurements of extensively placed plots for validation of the tower as a representative site.

INTRODUCTION

Atmospheric carbon dioxide (CO_2) concentrations have been increasing

since the industrial revolution at a rate that is unprecedented in the last 20,000 years.

As a consequence, atmospheric CO_2 levels are higher today than they have ever

been in the past 420,000 years, and possibly even in the past 20 million years.

Between 1990 and 1999, 6.3 ($\pm$ 0.4) petagrams of CO_2 were emitted each year

(PgC/yr) by anthropogenic activities, namely fossil fuel combustion. Numbers in

parenthesis represent a $\pm$1 standard error. At the same time, atmospheric CO_2

levels increased by 3.2 ($\pm$ 0.1) PgC/yr, only about half the total amount emitted

(IPCC, 2001).

The difference in the amount of CO_2 that has been released to the

atmosphere and the amount that remains is attributed to global oceanic (Broecker et

al., 1979) and terrestrial carbon sinks (Tans et al., 1990; Ciais et al., 1995). While

the scientific community has largely reached a consensus surrounding the presence

and relatively static magnitude of an oceanic carbon sink (Tans et al., 1990;

Takahashi, 2004), our ability to understand and quantify a terrestrial carbon sink

remains contested (Wofsy, 2001; Houghton, 2002; Janzen, 2004).

A Terrestrial Carbon Sink

Accounting of the global carbon budget demonstrates that the terrestrial

biosphere must be a net carbon sink (Tans et al., 1990), but the temporal and spatial

distribution of that sink is highly variable (Battle et al., 2000). Temperate forests of

the Northern Hemisphere make up a large portion of the terrestrial carbon sink (Dixon et al., 1994). In North America alone, forests are estimated to sequester 1-2 PgC/yr (Fan et al., 1998; Pacala et al., 2001), about one-quarter of the carbon that is emitted by fossil fuel combustion each year (Wofsy, 2001).

Researchers propose a variety of causes for forests' current high rates of carbon sequestration. Some hypothesize that trees are experiencing enhanced growth due to CO_2 fertilization, N deposition, and/or climate change (Schimel et al., 2000). However, evidence overwhelmingly demonstrates that the net carbon gain of North American forests is attributable to changes in land-use, namely forest re-growth after agricultural abandonment, harvest reduction, and fire suppression (Houghton et al., 1999; Caspersen et al., 2000). Forests in the northeastern U.S., in particular, have high rates of carbon sequestration due to their growth and buildup of biomass as they recover from the agricultural development that dominated the landscape in the 19th century (Munger et al., 1994).

Despite over a decade of data that demonstrate mid-latitude forests' role in carbon sequestration, the magnitude and spatial distribution of that uptake remains controversial (Pacala et al., 2001). Inverse atmospheric models, which back-calculate carbon sources and sinks from the distribution of atmospheric CO_2 concentrations (Schimel et al., 2001), provide particularly strong evidence for the presence of global terrestrial carbon sinks in the Northern Hemisphere (Conway et al., 1994; Ciais et al., 1995; Francey et al., 1995). However, inverse models are highly variable (Bousquet et al., 2000; Schimel et al., 2001), and ground-based

inventories often point to a much smaller magnitude in the terrestrial carbon sink (Wofsy, 2001; House et al., 2003).

The discrepancy that persists between atmosphere-based CO_2 measurements and ground-based biomass inventories makes evident the inadequacy of these indirect methods for measuring carbon budgets. Alternatively, to *directly* measure ecosystem, regional, and global carbon budgets, we must monitor the actual exchange of CO_2 between the atmosphere and biosphere through long-term, continuous measurements (Baldocchi et al., 1996). Coupling biomass inventories with flux measurements allows us to estimate total ecosystem carbon storage, as well as partition carbon estimates into smaller carbon pools within the ecosystem (Barford et al., 2001).

The Eddy-covariance Technique

Flux measurements of CO_2 and other important greenhouse gases between the atmosphere and biosphere are possible with the use of a micrometeorological technique called eddy-covariance (Baldocchi et al., 1988). The eddy-covariance technique capitalizes on the movement of turbulent air above an ecosystem's canopy and on eddies, or smaller, circular currents of air, within the ecosystem that move against larger air disturbances (Fig. 1). Eddy-covariance measures the net ecosystem exchange (NEE) of CO_2 by summing the efflux of CO_2 across a horizontal plane above the canopy as the gas is emitted through respiration and the accumulation of CO_2 below the plane as it is consumed through photosynthesis (Baldocchi et al., 1988). For instance, during the day, the flux measurement is
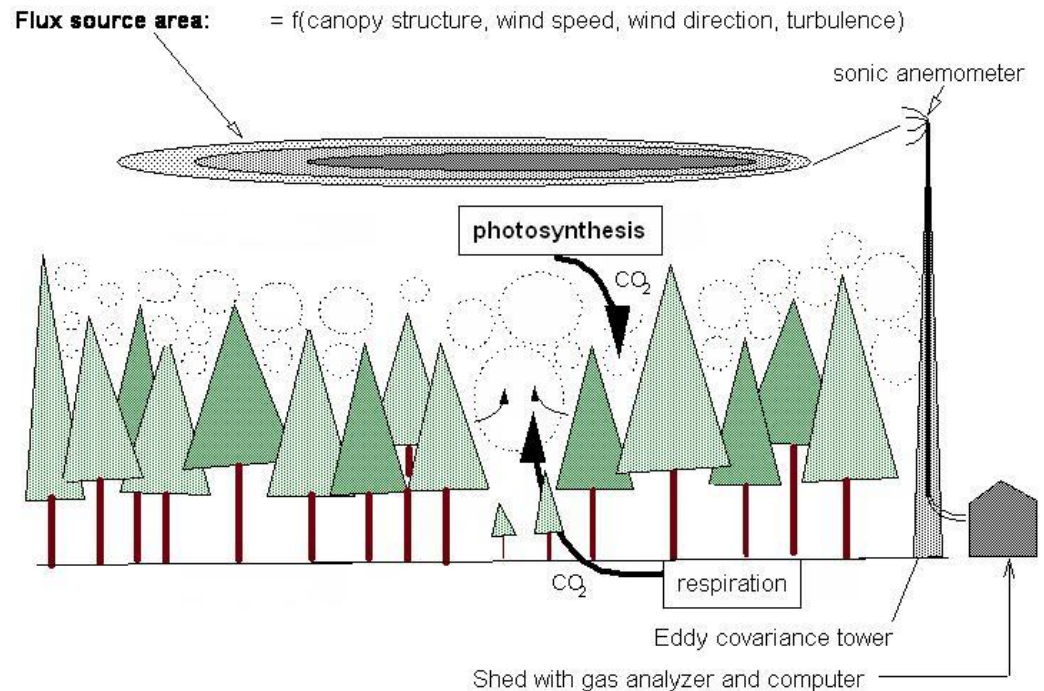
Figure 1.   Measurement of ecosystem CO_2 exchange with the eddy-covariance method. The large turbulence of air is depicted above the forest canopy, as well as the smaller eddies of air within the ecosystem. A sonic anemometer at the top of the eddy-flux tower is pointed into the prevailing wind direction and simultaneously measures wind velocity in three dimensions. Several gas inlets at incremental heights along the tower pull in CO_2, which is measured with an infrared gas analyzer in the shed at the base of the tower. The eddy CO_2 flux is calculated as the covariance of vertical wind velocity and CO_2 concentration every half an hour at the top inlet. Net ecosystem exchange is the sum of this flux plus the change in the amount of CO_2 below the anemometer, inferred from the concentrations at the lower inlets." Illustration by J. Hadley, Harvard University.

usually negative as turbulent eddies transport CO_2 into the biosphere where it is consumed in photosynthesis.

The accuracy of the eddy-covariance technique depends on a set of assumptions. Eddy-covariance assumes that no lateral transfer of air occurs below the height at which wind velocity measurements take place. This holds true when atmospheric conditions are moderate to vigorous, such as on sunny and/or windy days. The assumption is violated, however, in very still conditions, such as during calm nights when air ceases to move vertically across the forest canopy, resulting in a systematic underestimation of the accumulated CO_2 within the forest. Additionally, high winds can lead to an increased CO_2 efflux out of the soil that is not necessarily representative of increased soil CO_2 production (Goulden et al., 1996b).

Frequent interruptions of data collection due to maintenance, equipment failure, data transfer, and unsuitable atmospheric conditions also increase the uncertainty of long-term measurements. Researchers reduce sampling uncertainties by estimating the flux of missing or skewed data as a function of the physical environment during those times. For example, researchers can correct underestimated nocturnal respiration rates with respiration rates predicted according to soil temperature (Goulden et al., 1996b).

Micrometeorological techniques are favored over direct-measurement chamber techniques to measure ecosystem gaseous fluxes because they are in-situ and are able to capture the height of the entire ecosystem without disturbing the

environment (Baldocchi et al., 1988). The small size of measurement chambers, on the other hand, only allows researchers to use them for the measurement of fluxes from understory vegetation and soils, and not without physically disturbing the environment. Furthermore, eddy-covariance makes precise measurements ($\pm 5\%$) over the long-term (Goulden et al., 1996b), providing a continuity that would be nearly impossible to replicate with manual methods.

A Network of Flux Towers

The Harvard Forest houses one such eddy-covariance tower, where researchers have measured fluxes of CO_2 and other important greenhouse gases since 1989 (Wofsy et al., 1993; Goulden et al, 1996a; Barford et al., 2001). Between 1993 and 2000, eddy-flux data from the Harvard Forest showed an average net CO_2 uptake of 2.0 ($\pm$ 0.4) MgC/ha. Simultaneous biometric measurements in the footprint of the tower demonstrated an average storage rate of 1.6 ($\pm$ 0.4) MgC/ha, 60% of which was contained in the live biomass of the forest and the rest of which was stored in dead wood and soil (Barford et al., 2001). Numbers in parenthesis here and throughout the rest of the paper represent a 95% confidence interval.

The Harvard Forest site is one of many that form a network of eddy-flux towers. FLUXNET (DAAC, 2005) is a global network of hundreds of independently managed sites (that are also members of regional flux networks, such as AmeriFlux) that measure biosphere-atmosphere gas exchange with eddy-covariance towers. By sharing information among a diversity of ecosystems

and coordinating methodological protocols, flux networks strive to answer questions about terrestrial ecosystems' current role in global climate change and piece together a more detailed and accurate picture of global patterns of CO_2 exchange. With long-term, large-scale flux measurements from today, researchers will be better able to predict ecosystems' responses to future changes in their physical environment (AmeriFlux Strategic Plan, 2001) due to climate change, and consequently how they may affect their environment through systems of feedback.

Scaling Carbon Measurements

A primary goal of the AmeriFlux network is to quantify and understand spatial and temporal variations in carbon storage among America's terrestrial ecosystems (AmeriFlux Network, 2001). Many of the processes that drive CO_2 exchange are dependent on seasonal climatic events and biotic stresses, both of which are not normally captured by the temporal scale of field experiments or modeling activities (Wofsy and Hollinger, 1997). Maintenance of flux measurements over months, seasons, and years, allows researchers to capture intra- and inter-annual variation in the response of long-lived carbon reservoirs to regular and extreme climatic and biotic events (Wofsy and Hollinger, 1997).

The eddy-covariance technique is also valuable because researchers can extrapolate the measured flux to a known area of land (Baldocchi et al., 1988). Spatial scaling of eddy-covariance measurements is possible via the flux "footprint" (Schuepp et al., 1990), or the surface area upwind from the tower that contributes to the measured vertical flux. The size of the footprint varies with wind

speed and direction (Schmid, 2002) (Fig. 2), and with tower height, and usually

takes the shape of a slightly skewed ellipse (W.J. Munger, personal

communication).   The weight of the land in the flux measurements is zero at the

tower base and increases to a maximum at 150 m away from the tower during the

day and at an even farther distance during the night (S. Wofsy, personal

communication).

Geophysical and vegetative variability surrounding the tower diminishes

the accuracy of eddy-covariance measurements (Baldocchi et al., 1988). Although

this potential error is reduced by tower placement on a relatively flat and uniformly

vegetated piece of land (Baldocchi et al., 1996), naturally vegetated surfaces are

never homogeneous. Researchers apply trends perceived by eddy-covariance

measurements to areas beyond the footprint of the tower by linking them with

general ecosystem characteristics that occur in the footprint. However, the inherent

heterogeneity of the ecosystems, as well as the spatial limitation of the flux

footprint, elicit persistent questions about the spatial representativeness of

eddy-flux measurements.

The BigFoot Project

Predictions of large-scale, long-term responses of a variety of ecosystems to

changing environmental conditions are improved through the coupling of intensive

micrometeorological and biometric measurements with more extensive

measurement methods and modeling efforts. Remote sensing has increased the
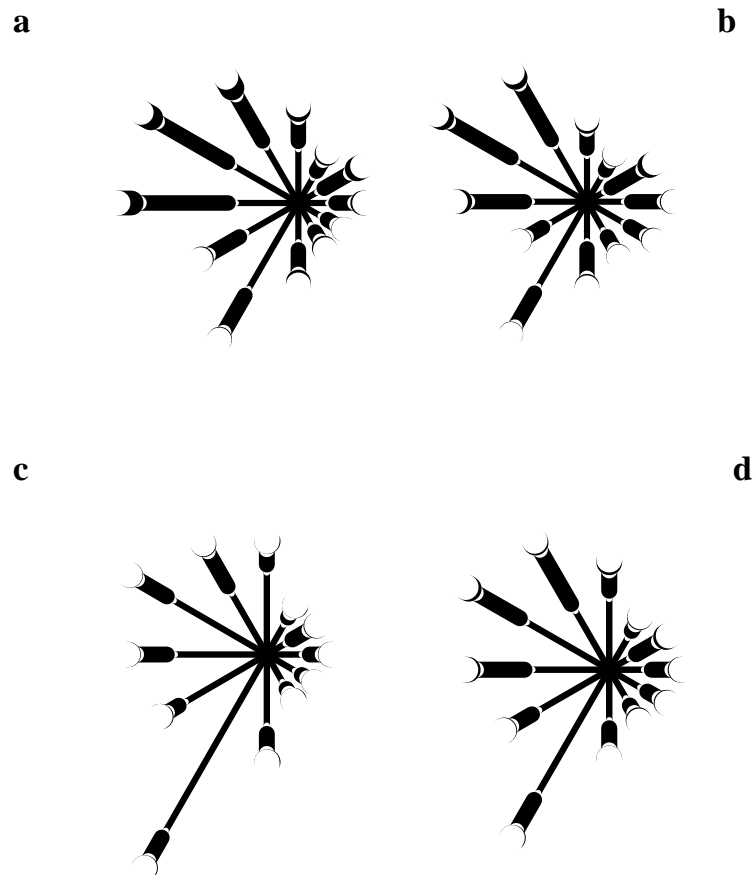
Figure 2. Wind roses from the Harvard Forest eddy-flux tower data for (a) December-February, (b) March-May, (c) July-August, and (d) September-November, 1990-2004. Arm width is a function of wind speed (binned by increments of 2.5 m/s) and arm length a function of wind frequency at each speed. Arms point in the direction of the measured wind, and the entire rose is oriented to true north. Illustration by W.J. Munger, Harvard University.

spatial applicability of ecological investigations, including carbon accounting models, by obtaining more extensive measurements than single-site studies can provide.

From 2000 to 2002, the Harvard Forest tower site was part of one such remote sensing project called BigFoot (Cohen and Justice, 1999; www.fsl.orst.edu/larse/bigfoot), which collected ground-based measurements in concert with satellite overpasses at several sites in North and South America where eddy-flux towers existed. The BigFoot group used in-situ biometric and meteorological measurements to validate MODLand (MODIS Land Discipline Group) products of land cover, leaf area index (LAI), the fraction of absorbed photosynthetically active radiation (f_{APAR}), and net primary productivity (NPP). The group took measurements in a 25 km^2 area centered on the tower. They validated measurements made within the tower footprint with tower data, and measurements made in the surrounding 25 km^2 study area with ground-based NPP measurements (Campbell et al., 1999).

In 2000, the BigFoot project established 100 ecological measurement plots at the Harvard Forest. In 44 of those plots, the BigFoot group took repeated measurements of aboveground live tree biomass over a three year period to estimate annual NPP. The tower research group is interested in continuing to monitor the BigFoot plots that fall outside of the tower footprint to enhance the spatial context of tower measurements. Although the tower group could not directly correlate measurements made outside of the tower footprint with the tower

data itself, they could use periodic measurements of the more extensively placed BigFoot plots to inform questions about the spatial representativeness of the tower footprint.

Initial comparisons of the two groups' estimations of carbon content in the aboveground live biomass, however, revealed a discrepancy. In 2002, the tower footprint plots yielded an average of 111 (± 12) MgC/ha, while the BigFoot plots yielded an average of 73 (± 8) MgC/ha (p < 0.01). It was initially thought that the difference in carbon content estimates reflected true differences in forest composition as sampled by the two spatially distinct series of plots. However, carbon estimates from just those BigFoot plots that fell within the same area as the tower footprint plots remained significantly different from the tower plot estimates at 78 (±14) MgC/ha (p < 0.01).

A Methods Comparison

The discrepancy could result from the different methods employed by each group to measure the aboveground woody increment: Whereas the tower plots have a fixed-radius, the BigFoot project used a prism method to establish variable-radius plots. Proofs of the two methods' unbiased and statistical equivalence are well-established in the literature (Grosenbaugh and Stover, 1957; Oderwald, 1981). However, departures from their equivalence for estimating mean basal area and volume in various field situations are also frequent (Avery, 1955; Husch, 1955; Deitschman, 1956; Kirby, 1965) (Table 1).

Table 1. Summary of comparisons of fixed (f-r) and variable-radius (v-r) plot sampling in the literature. A similar table is available in Sukwong (1970).

Author, year	Stand condition	Experimental design	Major findings	Concluding remarks
Avery, 1955	Secondary-growth, saw-timber pine in southeastern Arkansas	Compared volume estimates of v-r cruises and a 100% tally. Miscellaneous hardwoods were discounted.	Errors in v-r estimates ranged from –2 - 20%. Six of the eight cruises were within 10% of the correct volume	V-r method worked well when volume estimates were desired and was useful for making quick estimates on short notice.
Husch, 1955	Mixed hardwoods in southeastern New Hampshire	Compared basal area estimates of v-r sampling using three different critical angles with 100% tallies on four 10-acre tracts.	Errors in v-r basal area estimates ranged from –63.9 to –26.7%, –28.5 to –13.5%, and –13.4 to +8.7%, respective to increasing critical angle size. Errors in v-r volume estimates were even larger. Estimates for the full 40 acres yielded by the largest critical angle alone had errors of –4.6% for basal area and –7.6% for volume.	Indicating the presence of a systematic error. Recommended using a larger critical angle because its correspondingly smaller plot size reduces the possibility of missing trees.

Author, year	Stand condition	Experimental design	Major findings	Concluding remarks
Deitschman, 1956	Uneven aged upland hardwoods in southern Illinois	Compared basal area and volume estimates of v-r sampling with 100% tallies in six stands of various sizes.	V-r sampling consistently over-estimated basal area of small poles (5-7 in. DBH) by an average of 50%, and under-estimated basal area of larger trees ($\geq$ 8 in. DBH) by an average of 20%.	Noted difficulty in determining whether certain trees should be counted. Advised prior training and testing of the v-r method before using it extensively.
Grosenbaugh and Stover, 1957	Southeast Texas	Sampled 655 points i with ¼-acre f-r plots and v-r plots.	Differences in basal area and volume estimates between v-r and f-r sampling were insignificant at the 5% level	Attributed previous studies' invalidation of v-r sampling to improper instrument calibration, inconsistent application of volume to basal area ratios, brush bias, edge-effect bias, biased treatment of doubtful trees, biased placement of sampling points, and misinterpretation of normal sampling variation. Emphasized superiority of v-r plot sampling

Author, year	Stand condition	Experimental design	Major findings	Concluding remarks
Afansiev, 1958	Even-aged, secondary growth longleaf pine stand in southern Mississippi	Sampled 296.4 acres with 1/5-acre f-r plots at a 10% intensity, and v-r plots at the same locations. Compared basal area and volume estimates with strip cruises, which were used to obtain a total estimate.	V-r plots were highly accurate for estimating basal area when Afansiev considered all 296.4 acres one unit. When he considered individual compartments, errors in v-r sampling for estimating basal area range from –22.7% to + 103.8%. Errors became even larger when stands were subdivided by size of trees. Errors in volume followed the same general trends as those of basal area.	• Stated that Hush (1955), Avery (1955), and Deitschman (1956) sampled tracts that were too small in size with intensities that were too low to yield accurate results by any method • Found the v-r to be just as favorable as the f-r method, and even more desirable in consideration of the shorter time cost.
Avery and Newton, 1965	Bottomland hardwood and loblolly-shortleaf pine tracts in the Georgia Piedmont	Placed v-r plots and five sizes (1/5, 1/10, 1/20, 1/40, and 1/80-acres) of f-r plots at 50 plot locations.	The largest f-r plots provided the greatest sampling precision.	V-r plots were the most efficient for sampling the hardwood stand.

Author, year	Stand condition	Experimental design	Major findings	Concluding remarks
Kirby, 1965	Varying-aged spruce-aspen stand in Saskatchewan	Estimated basal area for 272 1/5th acre f-r plots and v-r plots.	V-r estimates were significantly lower than f-r estimates when Kirby considered all trees > 0.5 in. DBH. V-r and f-r estimates were not significantly different when he considered trees > 3.5 in. DBH.	Attributed underestimation of small trees to a bias in the selection of plot locations at more open areas. Accuracy could have been increased by implementing method more carefully and by eliminating human judgment. Admitted economic justification of v-r sampling.
Sukwong et al., 1971	Modeled stands with varying spatial distributions, diameter distributions, and stand densities	Sampled modeled stands with fixed- and variable-radius plot methods for comparison.	More variation resulted from fixed-radius plot sampling, indicating that variable-radius plot sampling is more statistically efficient for basal area estimation.	Found that spatial pattern and diameter distribution strongly effect sampling precision.

The majority of empirical comparisons of the two methods focus on their economic value in situations of forestry (Husch, 1955; Afansiev, 1958; Kirby, 1965). Application of the variable-radius sampling method to long-term carbon-stock inventories, which require periodic resurveys to account for stand mortality and recruitment, are absent from the literature. The tower research group remains interested in continuing to measure the extensively placed BigFoot plots to provide a spatial context for the tower footprint plots. Before the tower group can do this, however, they must reevaluate the BigFoot plots and resolve the discrepancy in carbon content estimates between the tower and BigFoot plot measurements.

Fixed-Radius Plot Sampling

When taking an inventory of a forest stand, groups of trees are measured in plots to obtain an estimate of the measurement of interest, such as basal area or tree density, for the entire stand or parcel of land. One of the simplest designs for forest inventory sampling is the division of the parcel of interest into a series of non-overlapping, equal-area units, or plots, which generally are in the shape of rectangles or hexagons. Foresters take measurements in as many plots as possible, or as many as is deemed necessary to obtain an adequate representation of the entire parcel without measuring a single unit more than once, and then enumerate the sample over the entire parcel of land. The more plots that are sampled, the more representative measurements are of the entire parcel (Stage and Rennie, 1994).

Circular plots represent a theoretical divergence from the above sampling method, which requires division of the *entire* parcel of land, because a series of non-overlapping circles cannot completely cover the parcel. The use of circular plots thus prevents every point on the parcel from having an equal chance of being included in the inventory (Stage and Rennie, 1994).

Circular plots are the most commonly used plots today because they are easily implemented. Surveyors count all of the trees that fall within the plot border. One checks trees in question by drawing a tape from the center of the plot out to the tree. Trees that fall on the plot border are considered in if at least half of their diameter is within the plot boundary (B.C. Forest Service, 2004). Surveyors can either randomly distribute circular plots across the parcel of land or place them in a pattern that corresponds with their needs, such as a grid or clustering pattern.

Variable-Radius Plot Sampling

The variable-radius method for measuring basal area of a forest stand was first introduced to the U.S. by Grosenbaugh in 1952. Originally coined the Bitterlich method after its inventor (1948), the method was promoted as especially speedy because it did not require the measurement of plot radii, nor tree DBHs (diameter at breast height). The woodsman would use an angle gauge, which he could make on his own, to tally the total number of trees "in" (Grosenbaugh, 1952). He would divide that count by the number of points sampled and multiply it by a given factor, proportional to the gauge of his instrument, to yield an estimate for the average basal area in square feet per acre. The variable-radius method is also

referred to as the "angle-count method" (Husch et al., 1972), "plotless cruising" (Avery 1955), or "point sampling" (Grosenbaugh 1952).

The variable-radius plot is called such because it is actually comprised of several, concentric, circular plots, each of which is centered on a tree. In variable-radius plot sampling, the surveyor stands holding an angle-gauge, Spiegel relaskope, or wedge prism over the sampling point (Bell and Dilworth, 1993) (Fig 3). She rotates around the sampling point, visualizing each tree within her line of sight through the instrument, which projects a horizontal angle onto each sighted tree (Husch et al., 1972) (Fig. 4). The surveyor calls the tree "in," "out," or "borderline," according to the projected image of the tree at DBH (Fig. 5).

If surrounding trees or underbrush obscure the surveyor's line of sight to a particular tree, she may step to the side, so long as the distance between the tree and the sample point is maintained (Bell and Dilworth 1993). Borderline trees are determined "in" or "out" by measuring the distance from each tree's center to the sampling point. If that distance is less than or equal to the tree's plot radius, the tree is called "in" (Bell and Dilworth, 1993; B.C. Forest Service, 2004).

Each tree's plot radius, and thus its plot area, is directly proportional to its basal area (Oderwald, 1981). A tree's plot size is also related to a constant, called the "prism radius factor" (PRF), which is a reciprocal of the "basal area factor" (BAF), or the "critical angle" of the instrument used (B.C. Forest Service, 2004). For example, if one uses a prism with a relatively large critical angle or BAF, the projection of each tree will be more offset, the PRF will be proportionally smaller,
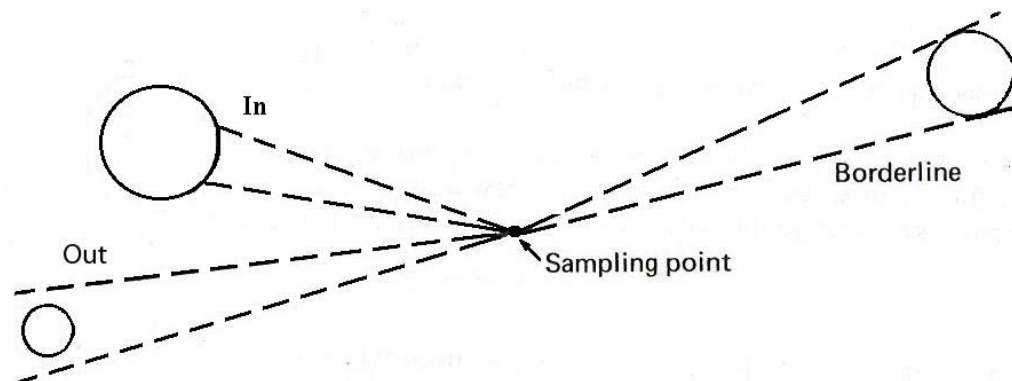
Figure 3. In variable-radius sampling, the surveyor holds the angle-gauge at the sampling point and visualizes each tree through the gauge. The tree's status as "in," "out," or "borderline" depends on the size of the angle projected onto each tree, relative to the tree's size and distance from the sampling point. The larger the tree and the closer it is to the sampling point, the more likely the sampling point is to fall within the tree's plot, deeming the tree "in". Adapted from Husch et al., 1972.
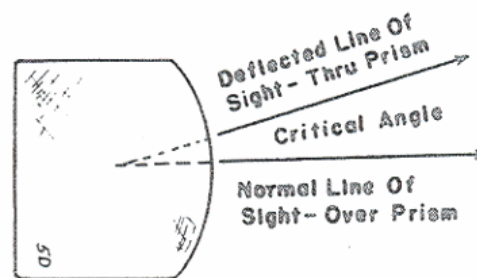
Figure 4. Wedge prism showing the projected critical angle, which is formed by the bending of light through the prism, and the normal line of sight, which is viewed over or under the prism. Reproduced from Bell and Dilworth, 1993.
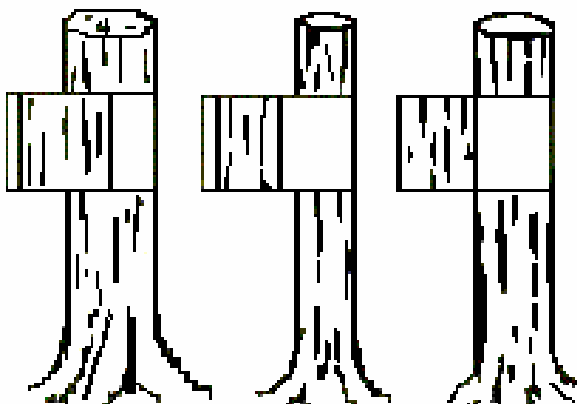
Figure 5. View of trees through a wedge prism. The first tree would be called "in," the second tree "out," and the third tree "borderline". Adapted from Bell and Dilworth, 1993.

and fewer trees will be counted in overall (see Fig. 6 for a sample calculation).
Therefore, the critical angle of the prism can be modified according to the
biological question at hand or the ease of implementation that is desired (Stage and
Rennie, 1994). If one wanted to decrease the error of her estimate by increasing her
sample size, she could use a prism with a smaller BAF to survey her plots. BAFs
are chosen according to the structure of the stand such that the larger the average
DBH of the stand and/or the more dense the stand, the larger the BAF one would
use (Bell and Dilworth, 1993).

Methodological Framework

Fixed- and variable-radius plots share a common framework (Stage and
Rennie, 1994). With each method, foresters take the same kinds of measurements,
depending on the question at hand, such as measuring DBH to estimate basal area.
Both methods employ circular plots distributed across a parcel of land. Both are
based on a measurement of distance between the sampling point and the tree.
However, in fixed-radius plots, the plot center corresponds with the sampling point,
and a tree is counted in if it falls within the sampling point's plot. In variable-radius
plots, on the other hand, the plot center corresponds with the tree's center. That tree
is counted in if the sampling point falls within the tree's plot area (Stage and Rennie,
1994) (Figure 6).

Figure 6. Sample calculation of the tree density (trees/ha) and basal area (m^2/ha) represented by a 50 cm DBH tree using (a) variable- and (b) fixed-radius plot methods. In the variable-radius plot, two of the four trees fall within the plot, although a calculation is shown only for the striped tree. In the fixed-radius plot, four out of five trees fall within the plot. Figures are not to scale. This sample calculation does not demonstrate that variable- and fixed-radius methods are not equivalent for measuring tree frequency and basal area. In the variable-radius plot, the likelihood that a tree will be measured method is proportional to its size, whereas with the fixed-radius plot the sampling likelihood is the same for trees of all sizes. Therefore, the smaller frequency and basal area of the single tree in the variable-radius plot will be compensated for in the plot's cumulative tree frequency and basal area estimate through the sampling of more large trees than a fixed-radius plot in the same place would capture, thereby yielding an overall equivalent plot measurement.

a   **Variable-Radius Plot Sampling**   **b**   **Fixed-radius Plot Sampling**

Sampling point

Sampled tree

17.5 m

Plot

DBH = 0.5 m

Plot

Sampled tree

Sampling point

DBH = 0.5 m

15 m

PRF = prism radius factor
BAF = basal area factor
BA = basal area

$\text{PRF} = \dfrac{1}{2\sqrt{BAF}} = \dfrac{1}{2\sqrt{2}} = 0.35$

Plot radius = DBH $*$ PRF = 50 cm $*$ 0.35 = 17.5 m

Plot area = $\pi\, r^2 = \pi\, 17.5\ m^2 = 962\ m^2$

Plots per hectare = $\dfrac{1ha}{962m^2} = \dfrac{10{,}000m^2}{962m^2} \cong 10$

BA = $\pi\, r^2 = \pi\, (0.25m)^2 = 0.20\ m^2$

BA per hectare = $\dfrac{0.2m^2}{plot} * \dfrac{10\,plots}{ha} = 2.0\ m^2/ha$

- This tree represents 10 trees
  and 2 m^2 of basal area per hectare.

Plot area = $\pi\, (15m)^2 = 707\ m^2$

Plots per hectare = $\dfrac{1ha}{707m^2} = \dfrac{10{,}000m^2}{707m^2} = 14$

BA = $\pi\, (0.25m)^2 = 0.20\ m^2$

BA per hectare = $\dfrac{0.2m^2}{plot} * \dfrac{14\,plots}{ha} = 2.8\ m^2/ha$

- This tree represents 14 trees
  and 2.8 m^2 of basal area per hectare.

Advantages and Assumptions

The greater the variation that occurs between measurements, the less statistically accurate the method is. For our situation of designing a plot for the measurement of trees, variance occurs in two areas: (1) between individual trees in reference to their attribute of interest, such as basal area, relative to the plot area, and (2) between each sampling point in terms of the basal area measured relative to the land area represented (Stage and Rennie, 1994). Fixed-radius plots are more accurate for measurement of tree frequency because the probability that a tree will be selected is proportional to its frequency of occurrence. Variable-radius plots are more accurate for basal area measurements because the probability that a tree will be selected, is proportional to its basal area (Grosenbaugh, 1957).

This makes variable-radius sampling a more statistically efficient method for measuring stand basal area because the method's sampling area is proportional to the trees' basal area and thus reflects the stand's composition in terms of tree size. For this reason, most foresters also consider variable-radius plots superior because they sample larger, more economically valuable trees with more intensity (Grosenbaugh and Stover, 1957; Stage and Rennie, 1994). While the variable-radius method will in theory automatically adjust to changes in the mean DBH and density of stands by correspondingly yielding basal area estimates that reflect that change, fixed-radius plot are vulnerable to becoming maladapted to changing stand compositions by remaining unchanged no matter the conditions (Stage and Rennie, 1994).

When comparing the two methods, many authors also focus on their efficiency in the field, which is a function of both their accuracy and cost of implementation (Avery and Newton, 1965; Bell and Dilworth, 1993; Stage and Rennie, 1994). For their purposes, foresters would like to know the cost of reaching the same sampling error with each method, or the sampling error that is reached when each method is limited by a predetermined, fixed cost (Bell and Dilworth, 1993). Foresters generally prefer the variable-radius plot sampling method over fixed-radius plot sampling because they can implement it faster without too large a reduction in accuracy. It is thus much less costly (Grosenbaugh, 1957; Afanasiev, 1958; Bell and Dilworth, 1993).

Still, variable-radius plot sampling also involves several potential errors that are not present in fixed-radius sampling. To obtain precise measurements, variable-radius plot sampling requires that the following assumptions are true: (1) the terrain is level, (2) all trees are truly vertical, (3) all sample trees are visible from the points that select them, and (4) all tree cross-sections are truly circular (Grosenbaugh, 1958). In variable-radius sampling, large trees can be long distances from the sample point and still be in, increasing their chances of being missed, a mistake that would result in a significant underestimation of stand basal area. Additionally, the determination of whether very small trees are in or out of variable-radius plots is subject to more bias than for other sizes of trees because their plot radii are so small (Stage and Rennie, 1994).

The great degree of error that can be involved in measuring the largest and

smallest trees with the variable-radius plot method requires surveyors to conduct more careful fieldwork (Deitschman, 1956; Kirby 1965, Stage and Rennie, 1994) than the method was originally intended for (Grosenbaugh, 1952). To reduce potential sampling error when estimating basal area with variable-radius plots, Stage and Rennie (1994) even suggested measuring trees of the largest and smallest size-classes with fixed-radius plots.

Application to Long-term Carbon Accounting

Many contend that the variable-radius method, if implemented properly, is statistically advantageous for measuring basal area. Still, none of the previous studies that analyzed the utility of variable-radius plot sampling applied the method to a system of repeated measures, nor to long-term studies of forest carbon cycling. Most forest carbon inventories make use of only fixed-radius plots (FIA, 1996). The potential faultiness involved in using the variable-radius method to call the smallest trees "in" or "out" portends its imprecision for purposes of tree recruitment, a vital component for tracking annual changes in stand composition. While the speediness and economic efficiency of variable-radius plot sampling may serve traditional forestry purposes well, its potential for missing trees, especially the largest ones, can cause extrapolation of biomass estimates from basal area estimates to become severely skewed.

Project Goals

By conducting the variable-radius and fixed-radius methods at each BigFoot plot, I was able to do a plot-by-plot comparison of the two methods in an attempt to distinguish whether differences in initial comparisons represented a methodological or spatial disparity.   After resolving the initial confusing result, I examined the spatial context of tower plots by comparing them with more extensively-placed plots. Finally, I sought to explore the potential of pairing ground-based measurements with remote sensing data.

MATERIALS AND METHODS

Site Description

The Harvard Forest is located in the town of Petersham in central Massachusetts (43.53° N, 72.18° W; elevation 340 m) (Fig. 7). At the Harvard Forest, the Environmental Measurement Site (EMS) is located near the eastern boundary of the Prospect Hill tract (Fig. 8a) and is surrounded by nearly continuous forest for several km in the dominant wind directions (southwest and northwest) (Fig. 2). The EMS tower is 31 m tall and 30 cm in diameter (Fig. 8b). A shed that houses analytical instruments and data acquisition equipment is located 15 m east of the tower. The EMS is only accessible by a dirt road, which is closed to the public. When the EMS was constructed in 1989, all assembly was done by hand and branches and vegetation surrounding the tower were left intact to minimize physical disturbances (Munger et al., 2004).

Land-use History

Prior to European settlement, the majority of Prospect Hill was forested (Motzkin et al., 2004), as was most of temperate eastern North America (Curtis et al., 2002). Between 1790 and 1830, the land was cleared for agricultural uses (Foster, 1992). By the mid 1800s, only 16% of Prospect Hill remained wooded while 7% of the land was in cultivation and 15% was pastureland. Most settlers abandoned the land of agricultural uses by the early twentieth century, and it was planted in conifer plantations or allowed to naturally re-vegetate. Since its
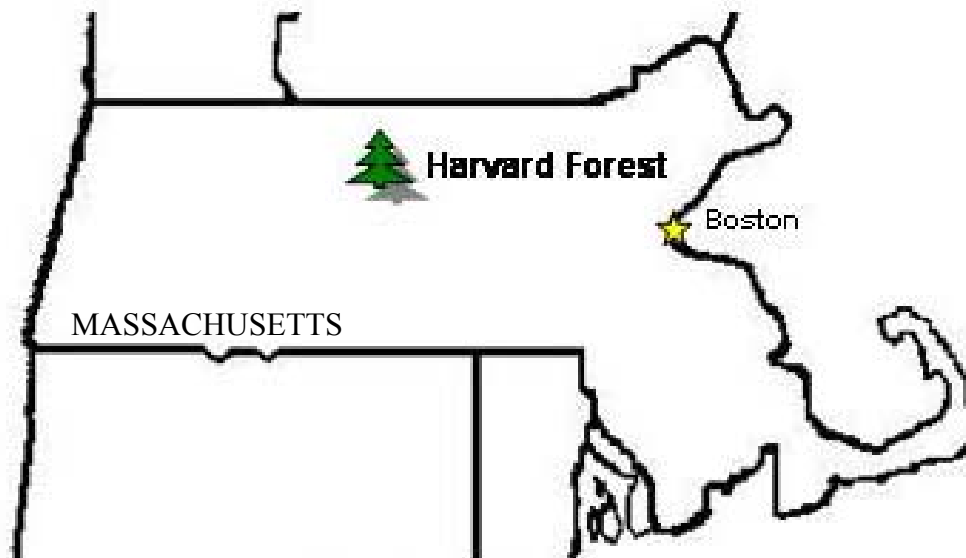
Figure 7. Location of the Harvard Forest in Petersham, Massachusetts, U.S. (43.53° N, 72.18° W; elevation 340 m).
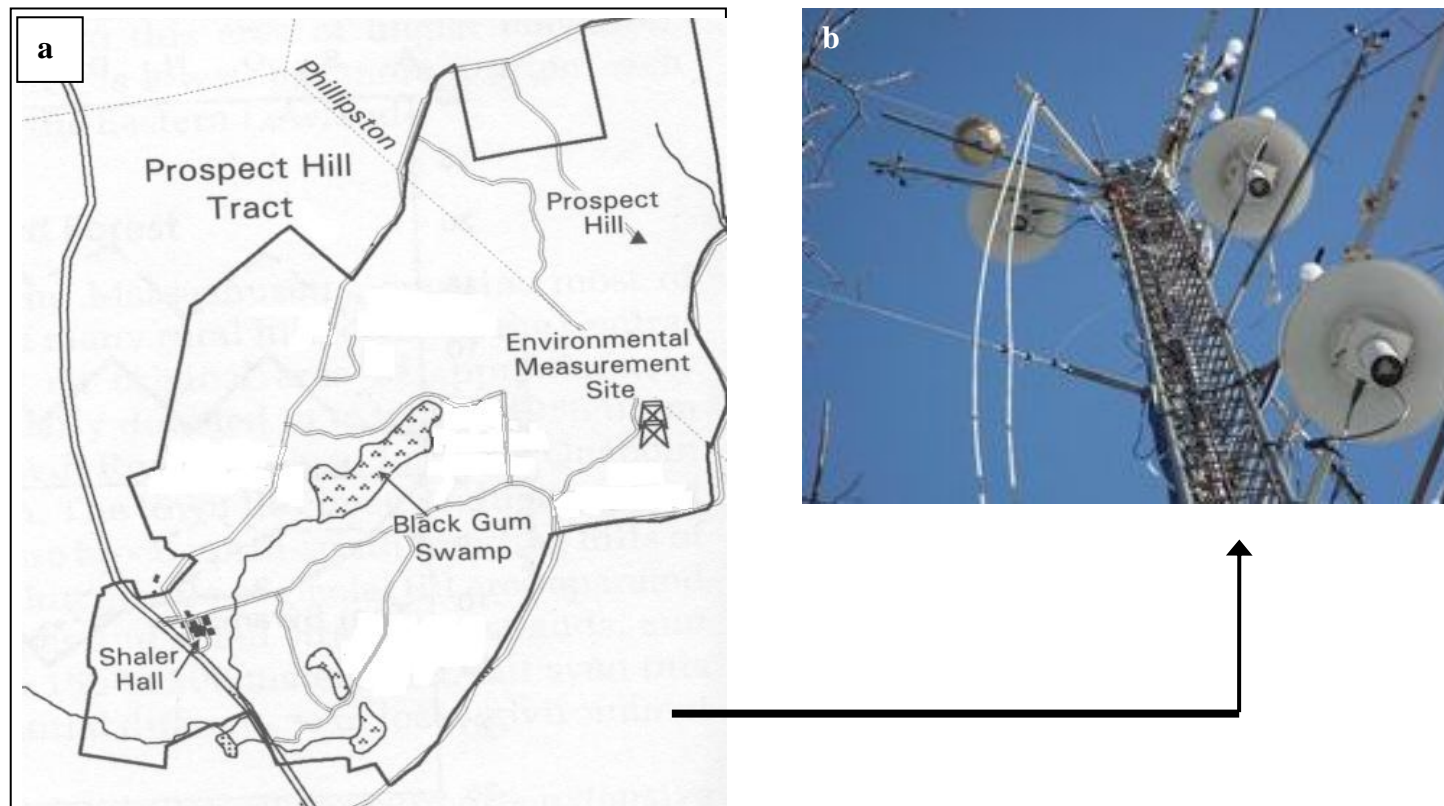
Figure 8. (a) Map of the Prospect Hill research tract at the Harvard Forest, indicating the location of the (b) environmental measurement site (EMS) tower. Shaler Hall represents the Harvard Forest headquarters. Map adapted from Foster, 2004 and photograph reproduced from the Harvard Forest website, http://harvardforest.fas.harvard.edu.

establishment in 1907, silvicultural activities have occurred at the Harvard Forest such as the planting of conifers, harvesting of old-field white pine stands, and selective cutting of hardwood and mixed stands. Disturbances of the Prospect Hill tract over the last century include the chestnut blight, which began in 1913, the outbreak of other pests and pathogens, the 1938 hurricane, a few wildfires, and persistent snow, ice, and wind storms (Motzkin et al., 2004).

Today, 95% of the Prospect Hill tract is wooded (Wofsy et al., 1993) with a 50-70 year old, mixed-deciduous forest. Most of the forest is dominated by red oak (*Quercus rubra*), red maple (*Acer rubrum)*, and Eastern hemlock (*Tsuga canadensis*), and the canopy is approximately 24 m in height. Yellow birch (*Betula alleghaniensis*), black birch (*Betula lenta*), white pine (*Pinus strobes*), and beech (*Fagus grandifolia*) also occur on Prospect Hill in less frequent numbers. The forest on the Prospect Hill tract is heterogeneous, reflecting topographical variation and a complex land-use history. Whereas hemlock stands occur almost solely where the land was never cleared, red maple and red oak grow on what was once pasture, woodlot, or lightly tilled land. Pines are often remnants of plantations or plowed land (Motzkin et al., 2004).

Tower Plots

In 1993, the tower research group randomly placed 40 ~314 m^2 (10 m radius) circular plots on 100 m segments of eight 500 m transects that extended northwest and southwest (the dominant wind directions (Fig. 2)) from the eddy-covariance tower on Prospect Hill (Fig. 9). In 2001, three plots in the
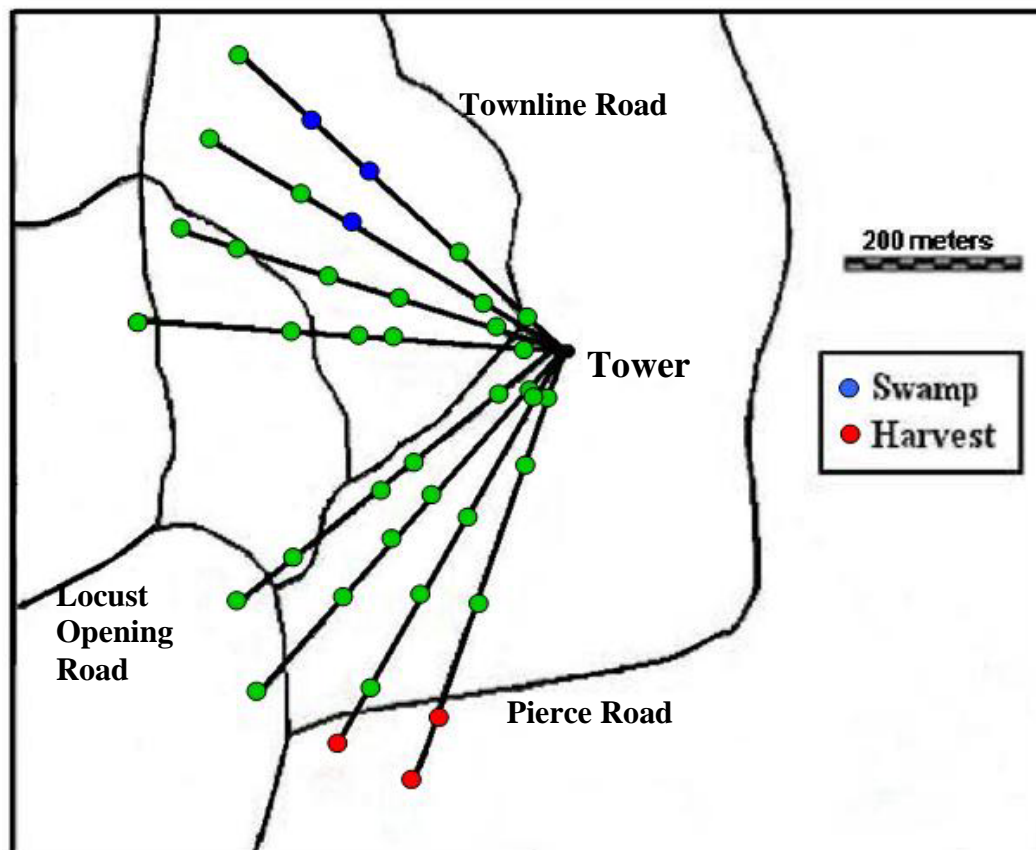
Figure 9. Layout of the tower plots in the footprint of the eddy-flux tower on Prospect Hill at the Harvard Forest. The blue and red plots are no longer measured due to changes in forest condition at these locations.

northwest became flooded and the tower group removed them from the measurement regime. In 1999, three plots in the southwest were removed from the footprint inventory in preparation for a logging operation.

The tower research group first measured the DBHs of all trees ≥ 10 cm DBH in the tower plots in 1993 and again in 1998. The research group has calculated tree DBHs from 1999 to the present using steel dendrometer bands, which they placed on the trees in 1998 (Barford et al., 2001). The tower research group has accounted for mortality and recruitment and measured the incremental increase in the aboveground woody biomass annually since 1998. In the fall of 2004, students inventoried the understory (trees of 1.5-10 cm DBH) in each tower plot (O. Soong and J. Vallimont, personal communication). We assimilated trees ≥ 5 cm DBH from this survey into the 2004 tower plot measurements.

BigFoot Plots

In 2000, the BigFoot group established 100 plots at the Harvard Forest and surrounding area. Eighty of those plots fell within 1 km^2 of the eddy-flux tower and were referred to as "intensive". The BigFoot group arranged the intensive plots in a grid pattern that extended 925 m from east to west and 550 m from north to south (Fig. 10). The group placed the other 20 plots in the surrounding area and referred to them as "extensive" (Fig. 11). They randomly distributed the extensive plots throughout the 25 km^2 sampling area such that each plot was at least 600 m away from any other plot (Campbell et al., 1999). Land-ownership issues prevented the extensive plots from being placed on any parcels other than those owned by the
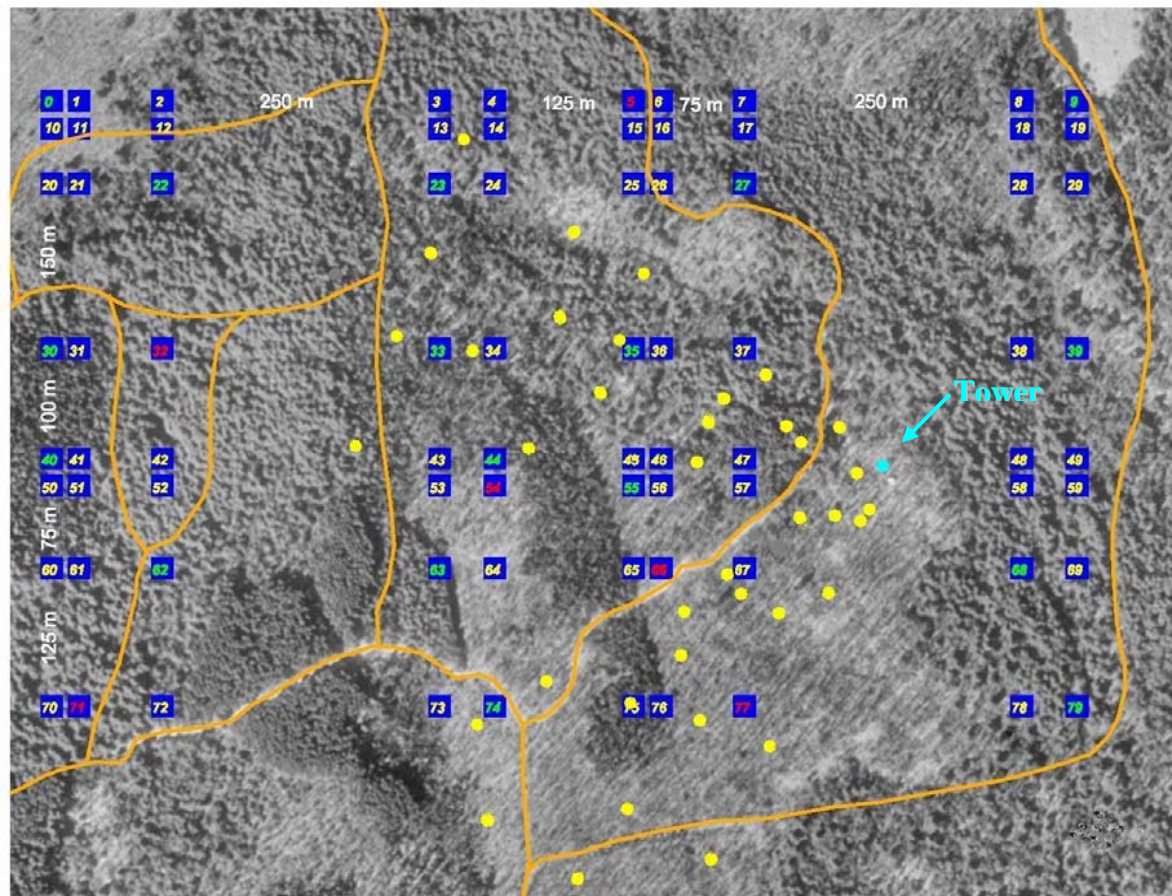
Figure 10. Arial photograph of the intensive BigFoot sampling area, indicating the location of the 80 intensive Bigfoot plots (colored squares) and the 40 tower plots (yellow dots). Red numbers indicate first-order plots, green numbers second-order plots, and yellow numbers third-order plots (adapted from A. Kirschbaum, personal communication).
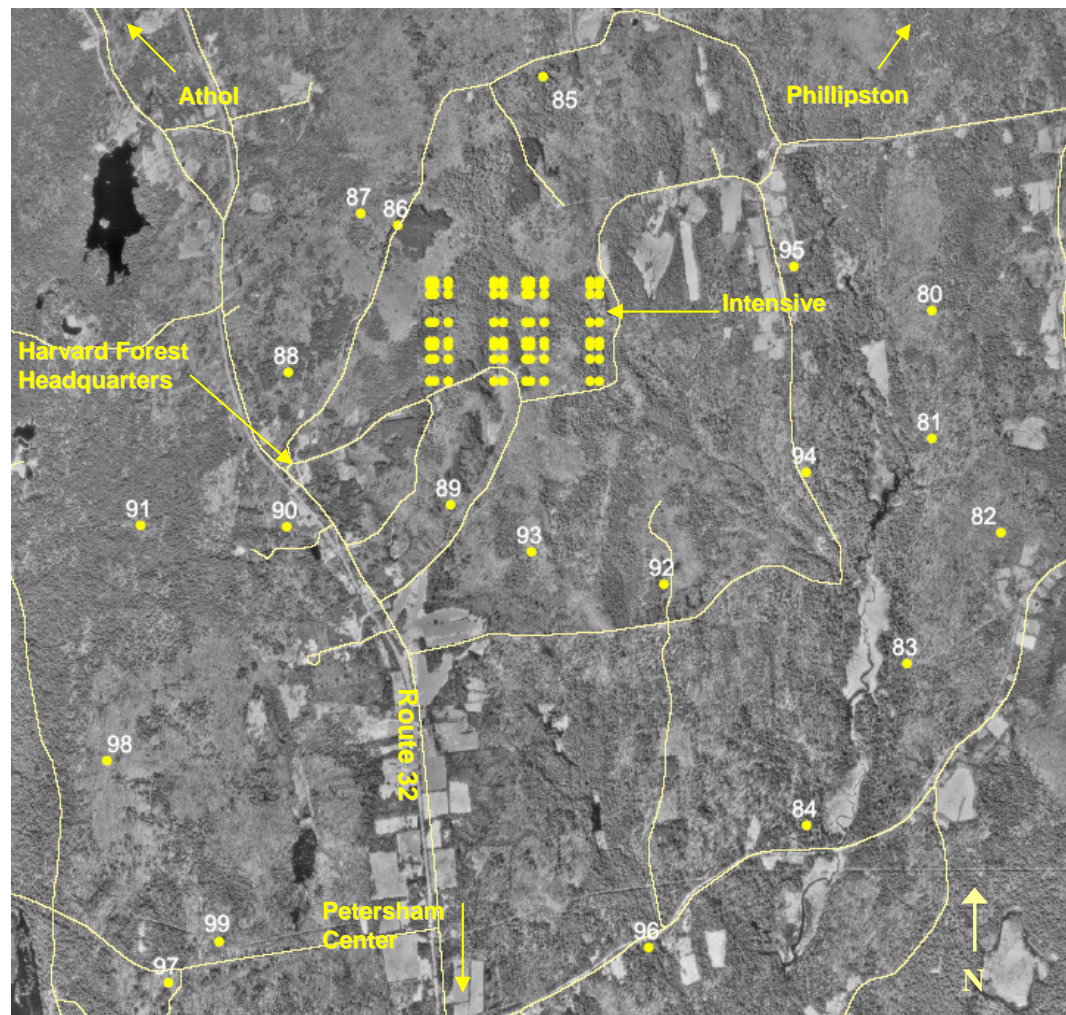
Figure 11. Arial photograph of BigFoot sampling area, indicating the location of the extensive BigFoot plots, which are numbered 80-99, as well as the intensive plots. Various sizes of roads and foot-trails are also highlighted (adapted from A. Kirschbaum, personal communication).

Harvard Forest, the state, or one particular acquaintance (Fig. 12) (A. Kirschbaum, personal communication).

The BigFoot group classified six of their plots as first-order, 38 as second-order, which included all extensive plots, and 56 as third-order (Fig. 10). Each of these classifications refers to a different measurement regime. In the third-order plots, the BigFoot group took measurements of vegetation cover, species composition, plant biomass, leaf area index (LAI), and the fraction of absorbed photosynthetically active radiation (f_{APAR}). In the second-order plots, they made the same measurements as in the third-order plots in addition to measuring aboveground NPP. In the first-order plots, the BigFoot group measured the same attributes they did in the second-order plots as well as belowground NPP (Campbell et al., 1999).

I revisited the 44 first- and second-order BigFoot plots between the months of June and August, 2004 where the BigFoot group measured NPP during the original survey. I re-sampled each BigFoot plot location with both fixed- and variable-radius plots. I placed fixed, ~707 m^2 (15 m radius) plots at each BigFoot plot site and recorded the DBH and species of all trees $\geq$ 5 cm DBH in each plot. Those trees that fell on the plot border were counted in if at least half of their diameter was within the plot. I measured a total of 3,161 trees in the fixed-radius, BigFoot plots.

Figure 12. Harvard Forest (dark shading) and state-owned (medium shading) parcels of land on which the BigFoot project placed extensive plots. Notice that the majority of extensive plots in Figure 11 fall within these areas. The third, privately-owned parcel of land on which the project also placed plots is not highlighted. Map prepared by Brian Hall, Harvard Forest.

For the variable-radius method, I replicated the methods employed by the BigFoot project (Campbell et al., 1999; A. Kirschbaum, personal communication) as closely as possible. I established five variable-radius sublots at each of the 44 BigFoot plot sites (Fig. 13). The plot center was considered the first subplot and the other four subplots were placed 9 m away from the center in each cardinal direction (taking into account a declination of 14.5° W). I conducted a prism sweep at each subplot using a prism factor of 1, 2, 2.5, or 3 cm (Appendix A). I recorded the DBH and species of each tree that fell "in" each subplot according to the prism sweep. I measured a total of 3,088 trees in the variable-radius, BigFoot plots.

Carbon-content Calculation

To scale mid-summer DBH measurements to the end of the growing season, I applied species-specific growth rates to each tree. I calculated mean growth rates for each species using annual growth increments from the 2000-2002 BigFoot data. I assumed that each tree was last measured on August 1. To calculate each tree's size at the end of the growing season on October 31, I added one-third of the species-specific average annual growth rates to each tree in the variable- and fixed-radius BigFoot plots based on growth patterns observed in frequently measured tower plots.

I used species-specific biomass equations (Tritton and Hornbeck, 1982; Smith and Brand, 1983; Ter-Mikaelian and Korzukhin, 1997) to calculate each tree's dry weight. I assumed that half of each tree's biomass is comprised of carbon (Roy and Saugier, 2001). For the fixed-radius plots, I summed the carbon
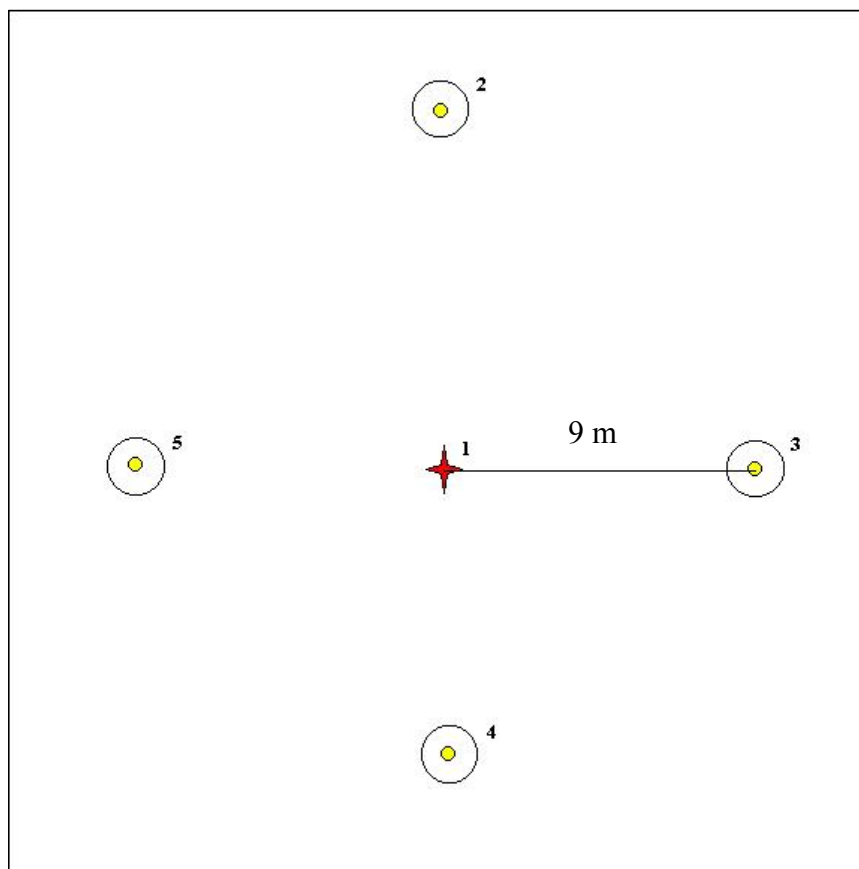
Figure 13. Plot design for variable-radius BigFoot plots. Subplot 1 is located at the center of the plot and the other four subplots are located 9 m away in each cardinal direction. Adapted from A. Kirschbaum, personal communication.

contained in each tree per plot and divided the sums over plot area to yield

plot-by-plot estimates of MgC/ha. For the variable-radius plots, I multiplied each

tree's carbon weight in megagrams by its frequency in trees per hectare. (See Fig. 6

for an example of the variable-radius tree frequency calculation.) I summed the

carbon per hectare numbers for individual trees in each plot to yield plot-by-plot

estimates of MgC/ha.

Accounting for Recruitment and Mortality

Protocol for the variable-radius method recommends that a borderline tree's

distance from the sampling point be measured to assess its status as "in" or "out"

(Bell and Dilworth, 1993; B.C. Forest Service, 2004). However, when sampling

from 2000-2002, the BigFoot group called every other borderline tree "in" without

measuring each tree's distance (A. Kirschbaum, personal communication).

Although I attempted to replicate the BigFoot project's methods for variable-radius

sampling as closely as possible, initial comparisons between 2002 and 2004

measurements pointed to a difference in how we dealt with borderline trees. Initial

comparisons of the 2002 and 2004 variable-radius surveys of the BigFoot plots

showed over a 30% recruitment rate, which is an unlikely representation of natural

processes, in comparison to the annual recruitment rate of approximately 1% that is

observed in the tower footprint plots (E. Hammond Pyle, personal communication).

Also some of the added trees were relatively large and close to the sampling point,

so much so that they could not have grown into the plot since the BigFoot survey.

To compensate for possible errors in the judgment of both myself and past surveyors about borderline trees, I returned to all the trees that were counted "in" in 2004, but not in 2002, and measured their distance to the sampling point so as to determine with certainty their status within the variable-radius plots (Fig. 14). Those added trees that, upon closer inspection, fell out of the plots were removed from the 2004 variable-radius dataset. To investigate the possibility that the BigFoot group missed a portion of the 2004 additions that should have been counted "in" during the original survey, I back-calculated the trees that I correctly added in 2004 to 2000 through 2002 with the species-specific growth rates described in the previous section.

Methods Comparison

Estimates of tree frequency, basal area per hectare, and carbon-content per hectare from fixed- and variable-radius BigFoot plots, both in 2002 and 2004, are all normally distributed, allowing me to use parametric statistics to compare them. I was able to evaluate the data from the original survey in light of last year's data by forward calculating the DBH measurements taken in 2002 to 2004 using the species-specific growth rates. I then compared plot measurements yielded by each method in 2004, and those yielded by the variable-radius method in 2002, projected to 2004, with a one-way analysis of variance (ANOVA) in S-PLUS 6.0 (Insightful, 2001).
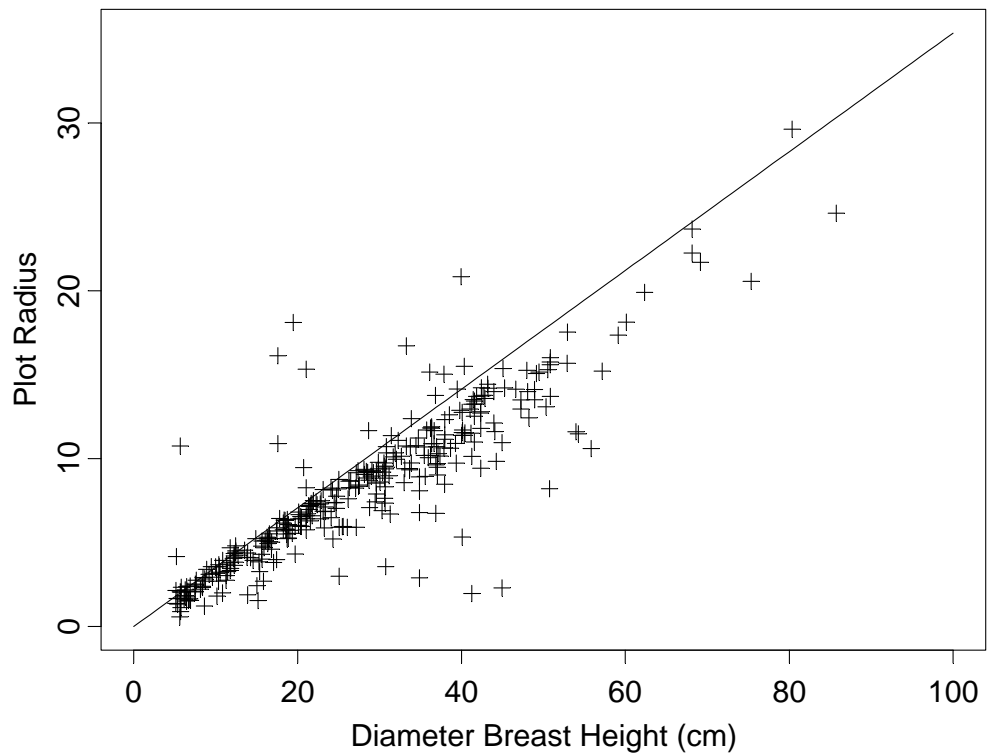
Figure 14. Added trees in plots where we used a prism radius factor of 2 cm (Appendix A). The line represents the maximum distance from the plot center a tree of a given DBH may be (i.e. the tree's plot radius) to be called "in". Each point represents an individual tree and is plotted according to that tree's actual DBH and distance from the plot center. Those points that fall on or under the line were correctly added. Those points that fall above the line do not fall within the plot and were removed from the 2004 variable-radius dataset.

Spatial Comparison

For the spatial analysis, I divided the Bigfoot plots and tower plots into three spatial categories: extensive, intensive, and tower. The first category was comprised of the 20 extensive BigFoot plots (Fig. 11). The tower plot category included the 34 tower plots and 12 intensive BigFoot plots that fell within the same sampling area (within 500 m of the tower). The intensive plot category was comprised of the 12 intensive BigFoot plots that did not fall within the tower measurement area (more than 500 m away from the tower).

Plot measurements of stand characteristics such as tree frequency, basal area, and carbon content were normally distributed and compared between the three plot groupings with an ANOVA. I also divided the trees in each plot group by species and size-class. These data were not normally distributed, due to the patchy spatial distribution of such stand characteristics, and thus were compared among the plot groups according to bootstrapped 95% confidence intervals. For the bootstrap, 1,000 random samples were drawn with replacement from the range of plot measurements of each stand characteristic (Efron and Tibshirani, 1997). Uncertainty was calculated as the difference between the 2.5 or 97.5% confidence interval and the reported mean, where the largest difference was reported. Calculated uncertainties represent estimates of sampling and measurement uncertainty only, and do not represent other sources of uncertainty, such as those contained in biomass equations.

RESULTS

Methods Comparison

A one-way ANOVA among stand characteristics from fixed- and variable-radius BigFoot plots in 2004, as well as variable-radius BigFoot plots in 2002 projected to 2004, demonstrated that at least one of the three plot types yielded significantly different estimates of tree frequency, basal area, and carbon-content ($p < 0.01$) (Table 2). The difference in basal area estimates demonstrates that the difference in carbon-content estimates is not due to errors involved in scaling to weight with biomass equations.

Variable-Radius Plots: 2002 vs. 2004

During the 2004 variable-radius BigFoot plots survey, I did not encounter 6% of the trees that were in the BigFoot plots in 2002 and assumed that they died between the two measurement years. On the other hand, I added 27% more trees in 2004 to the variable-radius BigFoot plots than were counted in 2002. A 6% mortality rate and a 27% recruitment rate are both unlikely representations of natural patterns, according to the approximate annual mortality and recruitment rates of 1% in the tower plots (E. Hammond Pyle, personal communication).

The large number of added trees is the source of the difference between the variable-radius estimates of tree frequency, basal area, and biomass from the two measurement years. Back calculations with species-specific growth rates reveal

Table 2. Mean tree frequency, basal area, and biomass estimates yielded by
variable-radius and fixed-radius BigFoot plots in 2004. The first variable-radius
estimate is that of the original survey in 2002, projected to 2004 using
species-specific growth rates. Numbers in parentheses represent a 95% confidence
interval. A one-way ANOVA among all three plot types demonstrates that they
each yielded significantly different tree density, basal area, and biomass estimates
($p < 0.01$).

	Trees/ha	**Basal area (m^2/ha)**	**Carbon-content (Mg/ha)**
Variable-radius, projected	654 (± 92)	27 (± 3)	73 (± 8)
Variable-radius	953 (± 116)	32 (± 4)	85 (± 10)
Fixed-radius	1016 (± 100)	38 (± 4)	108 (± 12)
F-value	14.32	10.02	12.68
P-value	0.00	0.00	0.00

that 82% of the trees added in 2004 likely fell in the BigFoot variable-radius plots in 2000, but were missed during the original survey, and that an even larger portion of the 2004 additions should have been included in 2002.

Fixed-Radius vs. Variable-Radius Plots

Despite the addition of missed trees from the original survey to variable-radius estimates in 2004, a paired t-test comparing fixed-radius and variable-radius tree frequency, basal area, and carbon-content estimates demonstrates that they all remain significantly different, although the level of significance decreased ($p < 0.05$). Comparisons of the tree size-classes captured by each method demonstrate that the discrepancy between the two methods' tree frequency estimates increases as larger size-classes are added to the comparison (Fig. 15a). Cumulative carbon-content estimates from each sampling method diverge even more (Fig. 15b) because of the greater relative contribution of large trees to total carbon-content.

In variable- and fixed-radius plots, both basal area and carbon-content estimates are multiplied by tree frequency estimates when projected over area. Therefore, whatever error is involved in estimating tree frequency is carried through all other calculations that are equalized by area. Fixed-radius plots provide a more accurate measurement of tree frequency than variable-radius plots do because the probability that a tree will be selected in a fixed-radius plot is directly proportional to its frequency of occurrence (Grosenbaugh, 1957). In this case,
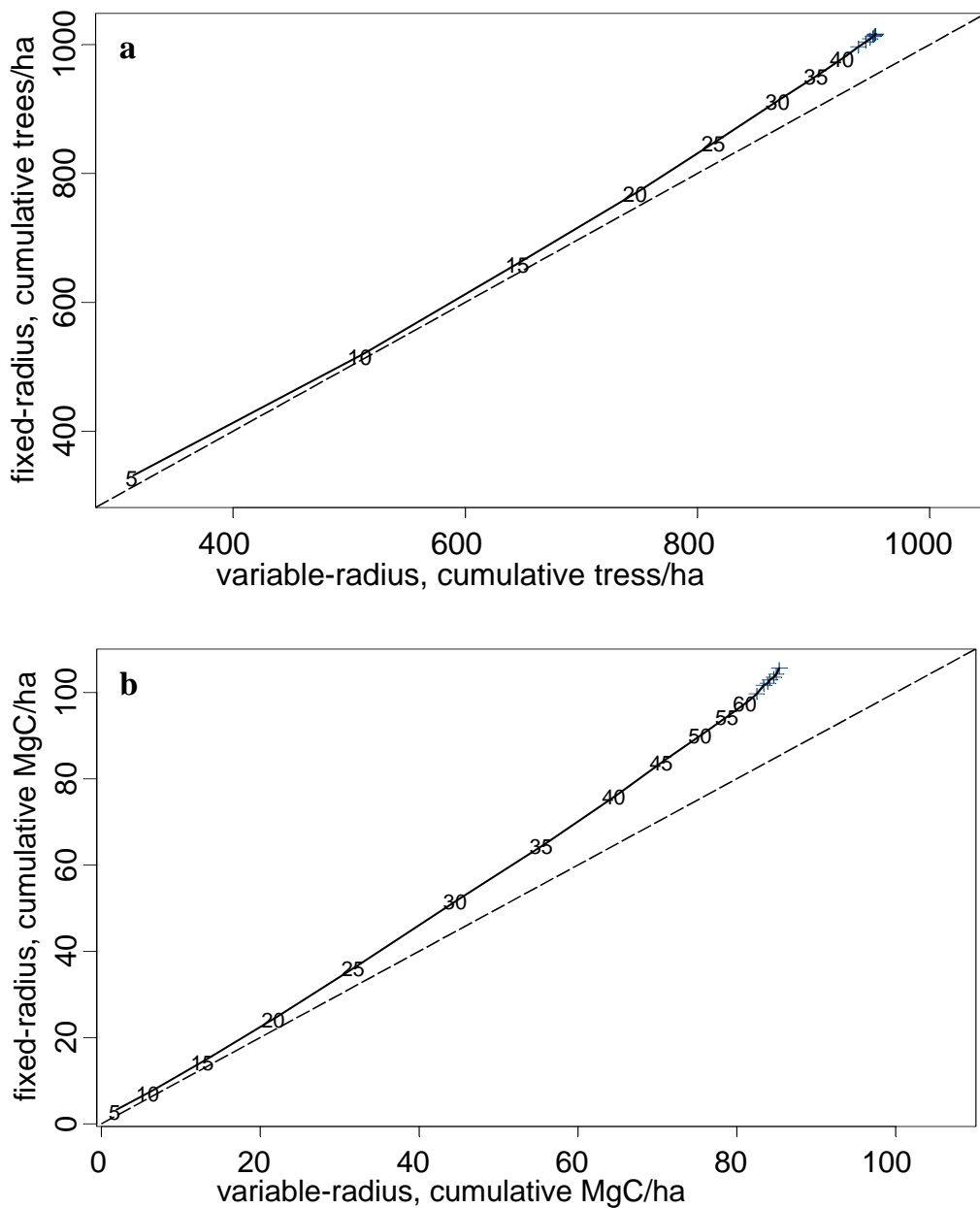
Figure 15. Variable- versus fixed-radius plot estimates of (a) cumulative trees per hectare and (b) megagrams of carbon per hectare for each size-class of tree. Size-classes are divided into increments of five, beginning with 5 cm DBH. Numbers along the solid line represent the smallest possible tree DBH in each size-class. Size-classes between 45 and 95 cm DBH are depicted as "+" for visual clarity. If tree density estimates between the two plot methods were equivalent, the line representing their comparison (solid) would closely follow the one-to-one line (dashed).

variable-radius plots likely underestimated tree frequency, an inaccuracy that was carried through basal area and carbon-content estimates. Based on this evidence, fixed-radius sampling provided a more accurate estimation of carbon-content in the BigFoot plots, as is further examined in the discussion.

Spatial Comparison

Because variable-radius and fixed-radius plots did not yield equivalent measurements of stand characteristics, I only used fixed-radius BigFoot and tower plot estimates from 2004 for the spatial comparison. Comparisons of tree frequency, basal area, and carbon-content estimates among three spatial groups of increasing distance from the eddy-flux tower demonstrate that there is no discernable difference between these aggregated estimates ($p < 0.05$) (Table 3). These results demonstrate that the tower footprint plots are representative of the greater forested region, at least at a scale of 25 km^2, most importantly in terms of carbon-content.

The variability detected in individual stand measurements largely reflects the natural heterogeneity of the forest. The highest degree of variability consistently occurs with estimates yielded from the intensive plot group because it is comprised of the smallest sample size ($n = 12$). Also, although carbon-content is a function of both tree frequency and basal area, neither estimate is an absolute predictor of carbon-content because carbon storage also varies with tree species and size-class. Notice, that no single plot group consistently yields the highest or lowest estimates for all measured parameters (Table 3). The inconsistencies

Table 3. Mean estimates of tree frequency, basal area, and carbon-content from three spatial groupings of plots in 2004. Footprint plots are closest in proximity to the flux tower whereas extensive plots are the farthest. Numbers in parentheses represent a 95% confidence interval. F- and p-values are the result of one-way ANOVA comparisons of each parameter among plot groups. None of the parameters differ statistically among the footprint, intensive, and extensive plot groups ($p > 0.05$).

	Trees/ha	Basal area (m^2/ha)	Carbon-content (Mg/ha)
Footprint plots (n = 46)	964 (± 81)	37 (± 3)	119 (± 10)
Intensive plots (n = 12)	1040 (± 232)	42 (± 9)	115 (± 30)
Extensive plots (n = 20)	975 (± 160)	35 (± 5)	99 (± 17)
F-value	0.29	1.28	2.03
P-value	0.75	0.28	0.14

between relative tree frequency, basal area, and carbon-content estimates between plot groups appear to be associated with differences in the overall species and size-class composition of the three groups.

Figure 16 displays the species distribution in trees per hectare, basal area per hectare, and carbon-content per hectare among footprint, intensive, and extensive plot groups. The only significant difference between the three plot groups in terms of species distribution are with oak, hemlock, and white pine species. The most significant and consistent difference between the plot groups is with oaks, which contribute significantly more basal area in the footprint plots than in the intensive and extensive plots (Fig. 16b), and significantly more carbon in the footprint plots than in the intensive plots (Fig. 16c). Hemlocks contribute significantly more carbon in the intensive plots than in the extensive plots (Fig. 16c). White pines contribute significantly more basal area in extensive plots than in intensive plots (Fig. 16b). No other differences according to the 95% confidence intervals are detectable, demonstrating that the species distribution among the three spatial plot groups is not significantly different for the majority of species.

Figure 17 displays the size-class distribution in trees per hectare, basal area per hectare, and carbon-content per hectare among the three plot groups. No differences among the three spatial plot groups in terms of size-class distribution are discernable.
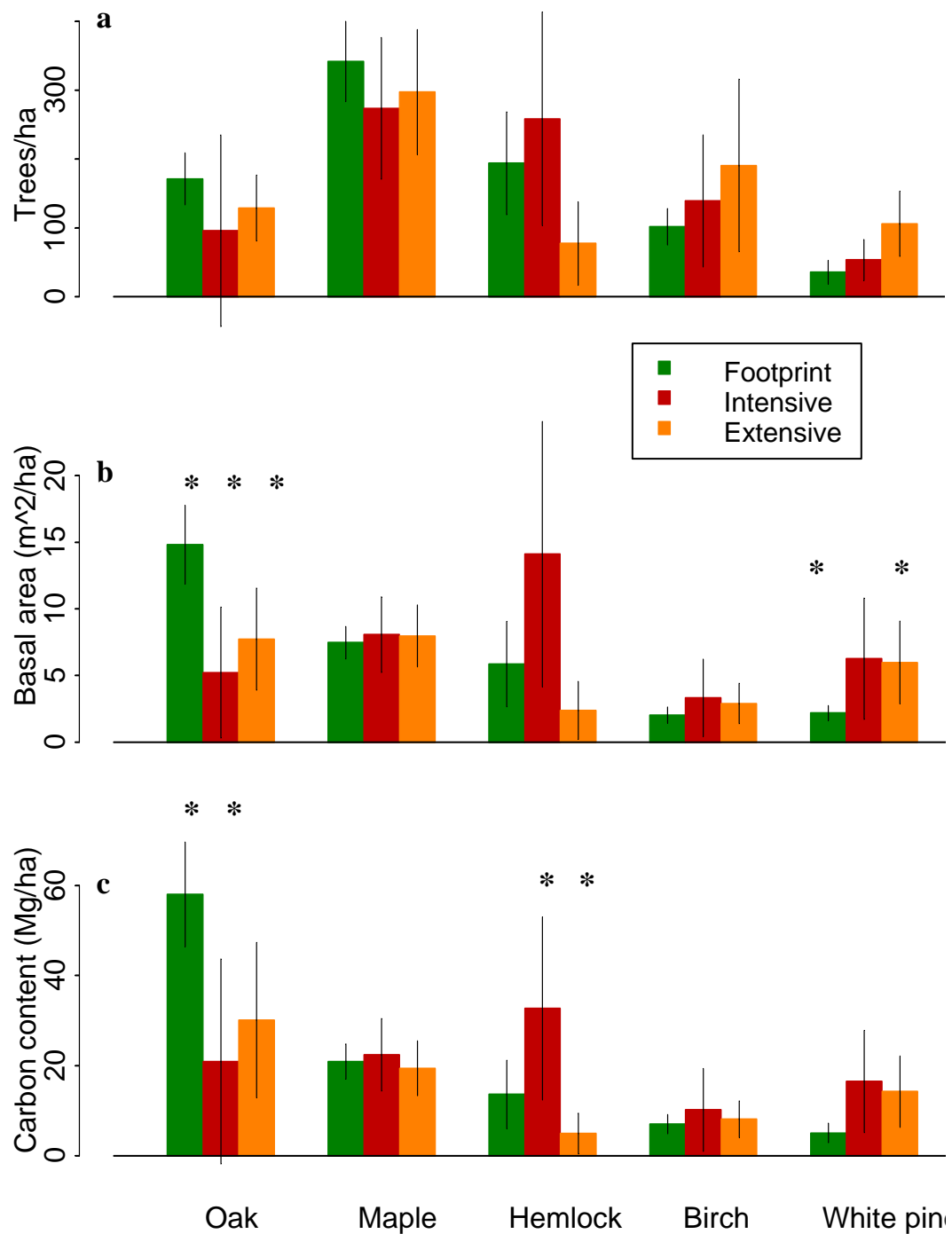
Figure 16. Mean (a) tree frequency, (b) basal area per hectare and (c) carbon-content per hectare estimates of trees in five main species groups in footprint, intensive, and extensive plots. Error bars represent 95% confidence intervals. Refer to Appendix C for species contained in each species group.
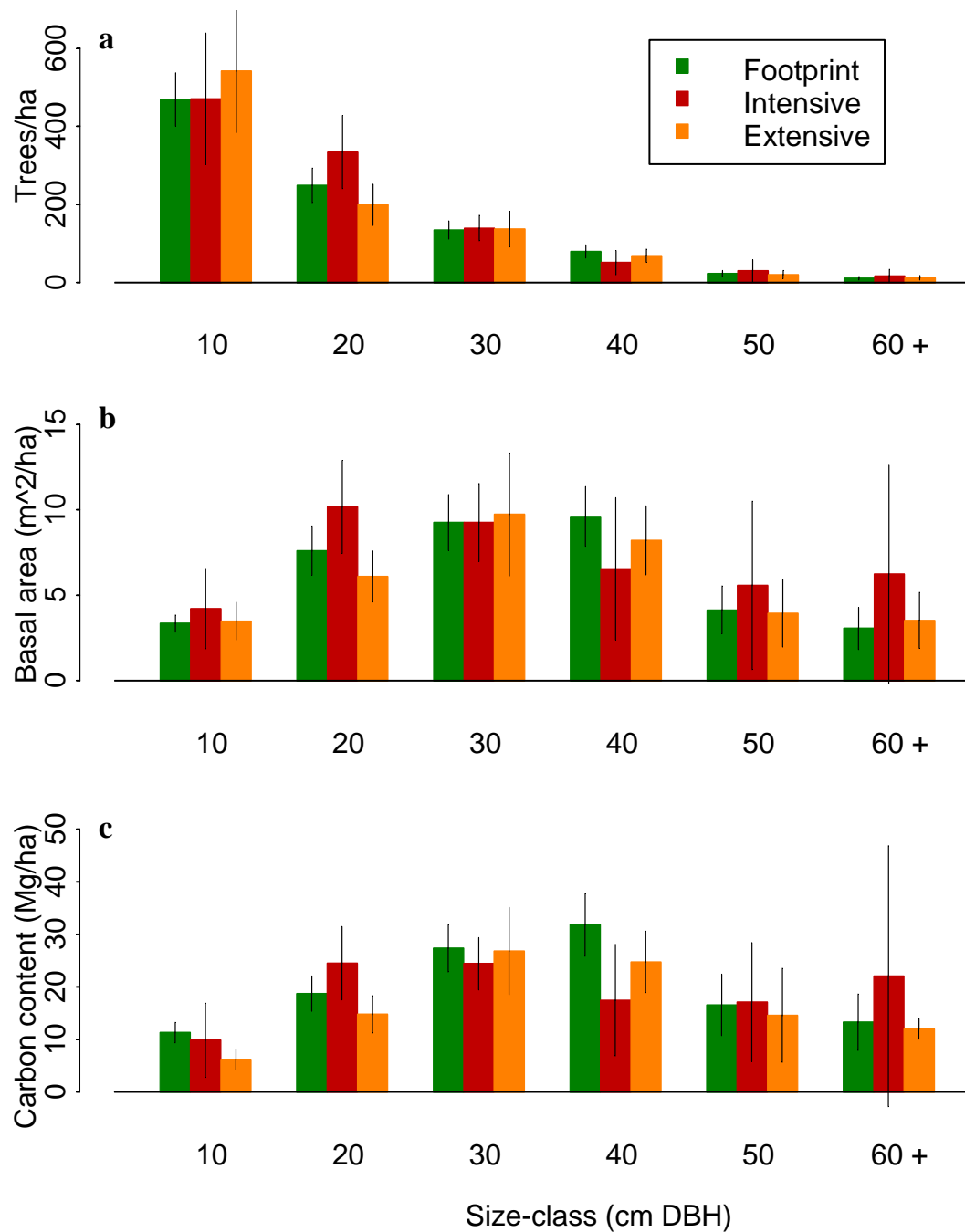
Figure 17. Mean tree frequency (a), basal area (b) and carbon-content (c) estimates of trees separated by size-class in footprint, intensive, and extensive plots. Size-classes are divided by increments of 10 cm DBH. The number representing each size-class is the median sized tree in each category, except for the latter category, which includes all trees 55 - 105 cm DBH.

Figure 18 depicts the proportion of carbon in each plot group that is attributed to the three main species groups and most frequent size classes. The data contained in Figure 18 have sample sizes that are too small for statistical comparisons, so no differences among the three spatial groups in terms of the size-class distribution of carbon in particular species can be detected nor rejected. Figure 18 is, however, useful for non-statistical comparisons of the contribution of each species and size-class to carbon-content within and among spatial groups, which are addressed in the discussion section.
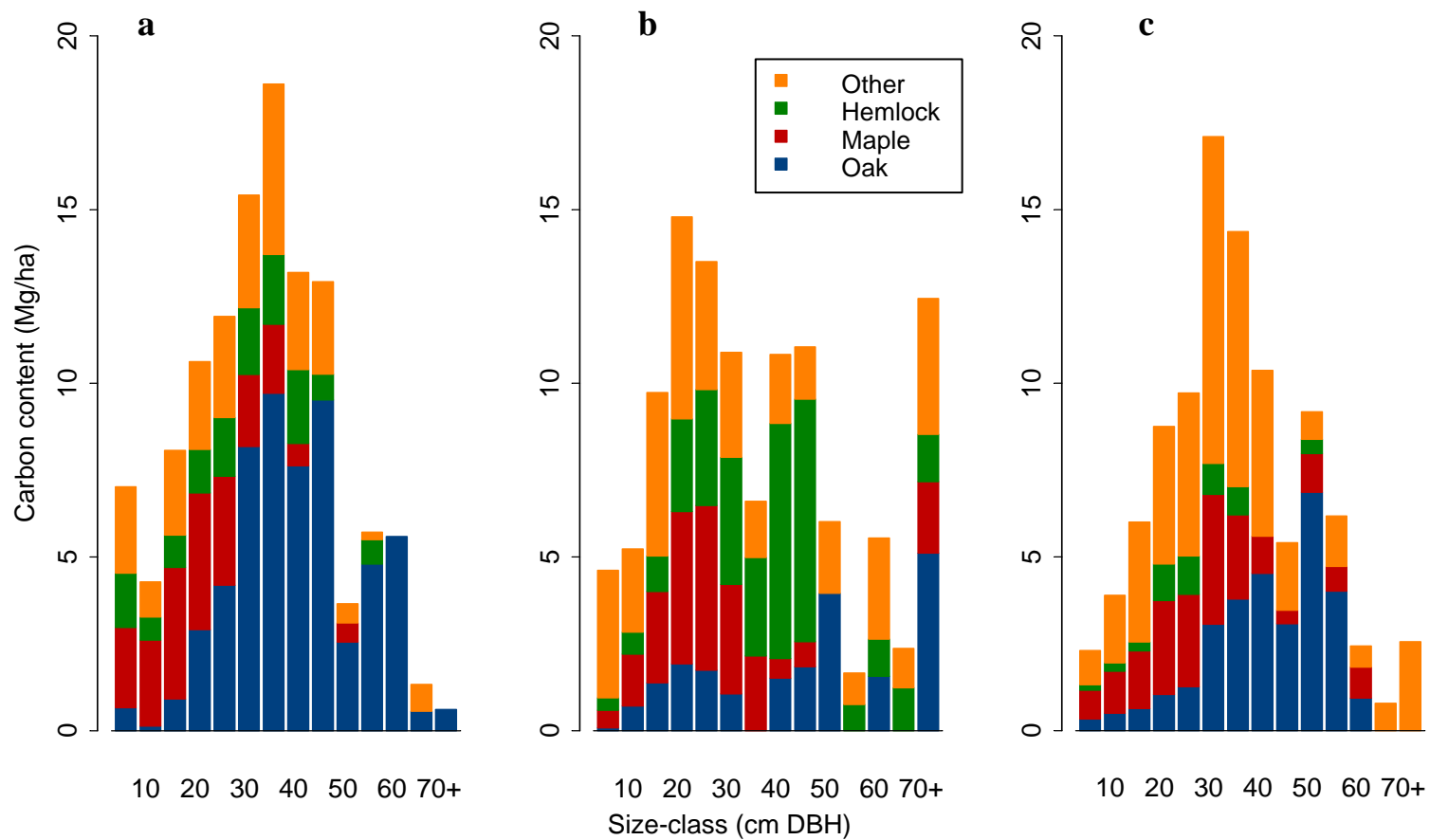
Figure 18. Mean basal area per hectare in each size class for the three major species groups in (a) tower footprint, (b) intensive, and (c) extensive plots. Size-classes are divided by increments of 5 cm DBH. The last bar represents all trees 70 cm in DBH and greater. Species contained in each species category are listed in Appendix C.

DISCUSSION

Methods Comparison

Problems with Borderline and Missed Trees

The discrepancy between variable-radius estimates from the original survey in 2002 and the resurvey in 2004 is the result of a difference in investigator judgment about tree inclusion. The most obvious source of the high proportion of missed trees from the original survey is the BigFoot group's treatment of borderline trees. Protocol of the variable-radius method requires investigators to measure borderline trees' distance from the sampling point to determine with certainty their status as "in" or "out" of the plot (Bell and Dilworth, 1993; BC Forest Service, 2004). The BigFoot group counted roughly half of the borderline trees (A. Kirschbaum, personal communication) without measuring their distance to the sampling point. Evidence from the 2004 survey suggests that many more than half of the borderline trees from the 2000-2002 surveys should have been included in the BigFoot plots.

The large number of previously missed trees that were counted in the 2004 survey may also be partially attributed to the advantage that access to data from the previous survey provided, where reference to these data helped prevent missed trees. The BigFoot group lacked this advantage because they only surveyed their plots once in 2000, and all subsequent measurement of tree growth included only the trees they found "in" in 2000. This is also the reason that the number of trees that the group potentially missed increased over time from 2000 to 2002. While the

absence of a resurvey did not affect the BigFoot group's estimates of NPP, it does cause problems for accurate carbon accounting of live biomass, which requires annual assessment of recruitment and mortality.

Questioning the Speediness Assumption

One of the strongest arguments in favor of the variable-radius sampling method is its speediness. However, the additional attention that borderline trees require (Bell and Dilworth, 1993) may reduce variable-radius sampling's time advantage over fixed-radius sampling. The number of questionable trees will vary depending on stand conditions and instrument gauge. In the literature, authors report that borderline trees make up as much as 10% of the sample although the authors of this finding also stated that this is not a large enough portion to detract from the method's time advantage (Bell and Dilworth, 1993). Conversely, in the field situation of this project, I found that questionable trees were so frequent that the measurement of their distance had a significant impact on the time required by the method. Stage and Rennie (1994) likewise pointed out that claims of the method's facile implementation in the original literature (Grosenbaugh, 1952) have proved illusory for most inventory applications.

Visibility Problems

Visibility problems caused by dense stands and/or heavy understory can also decrease the time advantage of the variable-radius method. Moreover, decreased visibility can increase the likelihood of missing trees because the

investigator's line-of sight is blocked. The author of the only field analysis of the variable-radius method in a forest with a similar composition to the Harvard Forest was quick to note that intervening vegetation frequently made it impossible to see large, far away trees that he should have counted in (Husch, 1955). Consequently, he recommended only using the variable-radius method during leaf off, yet this would severely reduce the ease of species identification and would make it almost impossible to recognize tree mortality. Other authors (Bell and Dilworth, 1993) suggested brush cutting to improve one's visibility of a borderline tree; however this tactic would clearly be inappropriate for a scientific study. I found that the need to look through thick brush, scrutinize trees far into the distance, and step away from the sampling point to improve my vision of a given tree made implementation of the variable-radius method awkward and mentally taxing.

Requirements of Investigator Judgment

Problems with missing trees and determining their status as "in" or "out" highlight the most conspicuous logistical difference between fixed- and variable-radius methods. The undefined plot border of the variable-radius plot increases the need for surveyors to make repeated judgment calls about tree inclusion. Similar decision-making requirements for the fixed-radius method are relatively rare and not nearly as demanding. The inconsistency in variable-radius estimates, both between years and in comparison with fixed-radius estimates, is indicative of a larger disadvantage specific to the implementation of variable-radius plots in the field.

Evidence in the Literature

The amount of error reported in the literature for variable-radius sampling is sometimes high (Husch, 1955; Dietschman, 1956; Afiensev, 1958 – See Table 1). Other authors responded to these findings that the variable-radius method could result in large errors and was consequently not equivalent to the fixed-radius method with the conclusion that differences between the two methods can only be attributed to measurement bias (Grosenbaugh and Stover, 1957; Afensieve, 1958; Kirby, 1965) or type I error (Sukwong et al., 1971) (i.e. false rejection of the null hypothesis that fixed- and variable-radius methods are equivalent). Even so, the relatively large amount of error found in many comparative studies is evidence of the variable-radius method's vulnerability to bias and difficulties in field implementation. For these reasons, I found that the variable-radius method was inadequate for our purposes of long-term carbon accounting.

Economic Considerations

The error that is sometimes involved in variable-radius sampling may go largely unmentioned because forestry studies comparing the two methods often focus on the economic cost of the method relative to the worth of the stand. Husch (1955) summarized this idea with his comment that "it is important that the cost of obtaining information… be kept at a minimum or at least commensurate with the value of the timber." However, the sampling accuracy required by scientific measurements potentially precludes any economic cost of implementing those

methods. As Avery (1965) put it, "[Fixed-radius plots] might be given preference in high value sawtimber stands where cruising reliability completely overshadows time and cost considerations." Indeed, in light of the immense costs of associated measurements such as eddy-covariance and remote sensing, ground validation measurements are so important that methodological reliability and appropriateness for the question and ecosystem at hand far outweigh the time and cost that may be involved in the method's implementation.

Spatial Comparison

In the intensive and extensive plot areas, I observed and sampled a much wider variety of forest types including stands that were recently logged and stands that were entirely flooded with water, none of which are represented in the tower footprint plots. It is notable that these observed differences were not reflected in overall tree frequency, basal area, and carbon-content estimates (Table 3), indicating that in terms of these stand characteristics, tower plots are representative of the surrounding region, at least as sampled by plots across a 25 km^2 area.

Spatial plot groups were also indistinguishable in terms of the species and size-class distribution of tree frequency, basal area, and carbon-content measurements, except for with oak species and some small differences with hemlocks and white pines (Figs. 16 and 17). The lack of significant differences in species and size-class composition among plot groups is partially attributable to the high variability of single estimates, which are largely a reflection of the patchy growth patterns that are inherent to forest composition in the Northeast (Foster,

1992). The near absence of significant differences is also attributable to the particularly high degree of variability associated with most intensive plot group means, which is the result of the group's small sample size (n = 12). Despite the absence of significant differences, observed, yet non-significant, differences also deserve attention to tease apart differences in stand composition among the spatially separated plot groups.

Species Composition among Spatial Plot Groups

The tower footprint shows a significantly higher contribution of oak to whole stand basal area, and carbon (Figs. 16b and c, and 18a). The majority of oak at the Harvard Forest is red oak (*Quercus rubra*), a mid- to late-successional species (Foster, 1992). Furthermore, in the intensive plots, much of the basal area and carbon composition are comprised of hemlocks (*Tsuga canadensis*) (Figs. 16b and c, and 18b). The high incidence of hemlocks in the intensive group is largely attributed to an old-growth hemlock stand, referred to as "Hemlock Hollow" by researchers at the Harvard Forest (McLachlan et al., 2004), that was sampled by two intensive plots. This kind of hemlock stand was not present in the extensive plot group although it does occur infrequently outside of Prospect Hill (McLachlan et al., 2004). The larger proportion of hemlocks outside of the footprint may have especially important implications for the tower's ability to capture changes in the rate of carbon accumulation and total carbon storage if and when hemlocks decline due to the invasion of hemlock wooly adelgid (*Adelges tsugae*).

Birches (Fig. 16) and small to medium maples (Figs. 16 and 18) were more uniformly distributed throughout all plot types, although birches contributed the least amount of basal area and carbon out of all the species groups. Red maple and birch species are early to mid-successional hardwoods (Foster, 1992), although they will continue to grow in somewhat older forests alongside longer-lived oaks and hemlocks. Although maples and birches are important to modern forests, they were uncommon prior to European settlement (Fuller et al., 2004). They often grow with other "poor hardwoods" in cut-over, old-field, planted white pine stands and on land that was once in pasture (Foster, 1992). White pines (*Pinus strobus*), which occurred at their highest frequency in extensive plots (Fig. 15a), but which occurred with their highest basal area and carbon-content in intensive plots (Figs. 15b and c), are often the remnants of planted, old-field stands and also grow naturally in old pastures (Foster, 1992).

Stand Age among Spatial Plot Groups

Prior to European settlement, forests in the Northeast were dominated by shade-tolerant, disturbance-intolerant, late successional species such as hemlock and oak species (Fuller et al., 2004). The higher incidence of oaks and hemlocks in footprint and intensive plots suggest that the forest in those plots, all of which are located on Prospect Hill, is of an overall older age than the forest sampled by the extensive plots. This is also supported for the footprint by the plot group's peak in carbon-content in comparatively larger size-classes (Fig. 17c).

However, it is also notable that the basal area and carbon in the intensive plots is distributed more toward smaller size-classes (Fig. 17b and c, and 18b). This may indicate that some of the plots in the intensive group are of a younger age than the plots sampled in the footprint and extensive plots. The presence of younger stands in the intensive group is also supported by the plot group's higher tree density estimate (Table 3) because as stands grow older, their tree count often decreases. The possible younger age of stands sampled by the intensive plot group may not be reflected in the carbon-content estimate (Table 3) because of the presence of a few very large trees (Fig. 17b and c, and 17b) that are heavily weighted in the carbon estimate.

The extensive plot group has more trees in the smallest size-class than any other plot group (Fig. 17a), suggesting that the forest sampled by these plots are also at an earlier growth stage. Additionally, the extensive plots have more carbon in "other" species than any other plot group (Fig. 18c, Appendix C), and a potentially higher species richness. Previous research has shown that as Northeastern temperate forests age, their species richness decreases (Motzkin et al., 2004) which also supports the possibility that the extensive plots are overall younger.

Disturbance and Potential Future Trends

These qualities also reflect the increased amount of disturbance and management activities that remain common on land outside of the footprint of the tower, and especially outside of the Harvard Forest. In fact, in the intensive and

extensive groups, three of the plots (numbers 9, 91, and 92) that I sampled were located in stands that were selectively logged sometime in the past five years; two plots had small paths or roads running through them (numbers 9 and 62); and one plot (number 95) suffered from so much roadside disturbance that the average DBH was 9.5 cm (compared to an overall average of 17.4 cm DBH in the extensive plots) and the tree density was ~1400 trees per hectare (compared to the average of 1040 trees per hectare in the extensive plots (Table 3)). (See Figs. 10 and 11 for plot locations.)

This observation indicates that an important difference between the tower footprint at the Harvard Forest and the surrounding forested land may lie in current management practices and the influence they have on stand composition. All of the intensive and footprint plots fall within the Prospect Hill tract at the Harvard Forest, land that has been protected from development and major harvesting activities for the last 50-70 years (Motzkin et al., 2004). Although the land-use and disturbance history of Prospect Hill is representative of the greater forested region (Foster, 1992), current land-use practices of private and publicly owned forest will obviously differ from that of a research forest.

These differences in management choices may affect patterns of carbon sequestration over the long-term, as is implied by the slightly higher carbon-content estimates of the plots that occur on Prospect Hill (Table 3). As the forest on Prospect Hill continues to grow without management, and parcels of forest outside the footprint continue to be managed, differences in their rates of

carbon sequestration and overall carbon storage capacity may further diverge over time. So, while the tower footprint is currently representative of regional trends, most importantly in terms of carbon storage, persistent differences in the management and disturbance regimes between the Harvard Forest and surrounding forests could result in discrepancies at the landscape level in the long-term that are not captured by the eddy-flux tower. Continued measurement of extensively placed plots in differently managed forests, will provide useful information about the future representativeness of the tower data.

*Scales of Heterogeneity within and around Harvard Forest*

Intensive plots are located much nearer to the tower footprint than are extensive plots (Figs. 10 and 11). Intensive and footprint plots likewise yield more similar standing carbon estimates than extensive plots (Table 3). This observation suggests that spatial proximity may be an important predictor of the carbon composition of forest stands. However, the similarities that exist between the footprint and intensive plots do not carry through basal area and tree frequency estimates (Table 3), nor to species and size-class distributions, where footprint and extensive plots appear more similar (Fig. 18).

It is possible that the land-use history and composition of forests such as these are so "exceedingly complex and variable in scale and intensity over time" (Foster, 1992) that spatial proximity is not a relevant indicator of similarities and dissimilarities. Indeed, patchiness in soil type and drainage, forest age, and land-use history occur on a scale of 50-200 m (Fig. 19) (Foster, 1992). This is small enough that two individual plots, which are several hundred square meters in area, could vary just as much or more from one another as two spatially distinct groups of plots could.

Plot Placement and Regional Representation

The assembly of complex land-ownership regimes in the forest surrounding the Harvard Forest prevented the BigFoot group from placing extensive plots on land other than that owned by the Harvard Forest, the state, or a single private party (Fig. 12) (A. Kirschbaum, personal communication). It is possible that the forests on these parcels have land-use histories and experience management that is not representative of other differently-owned parcels of land. Because they were not randomly placed across all surrounding forested parcels, the extensive plots actually represent a subset of the surrounding forested land, rather than the entire surrounding 25 km^2 region.
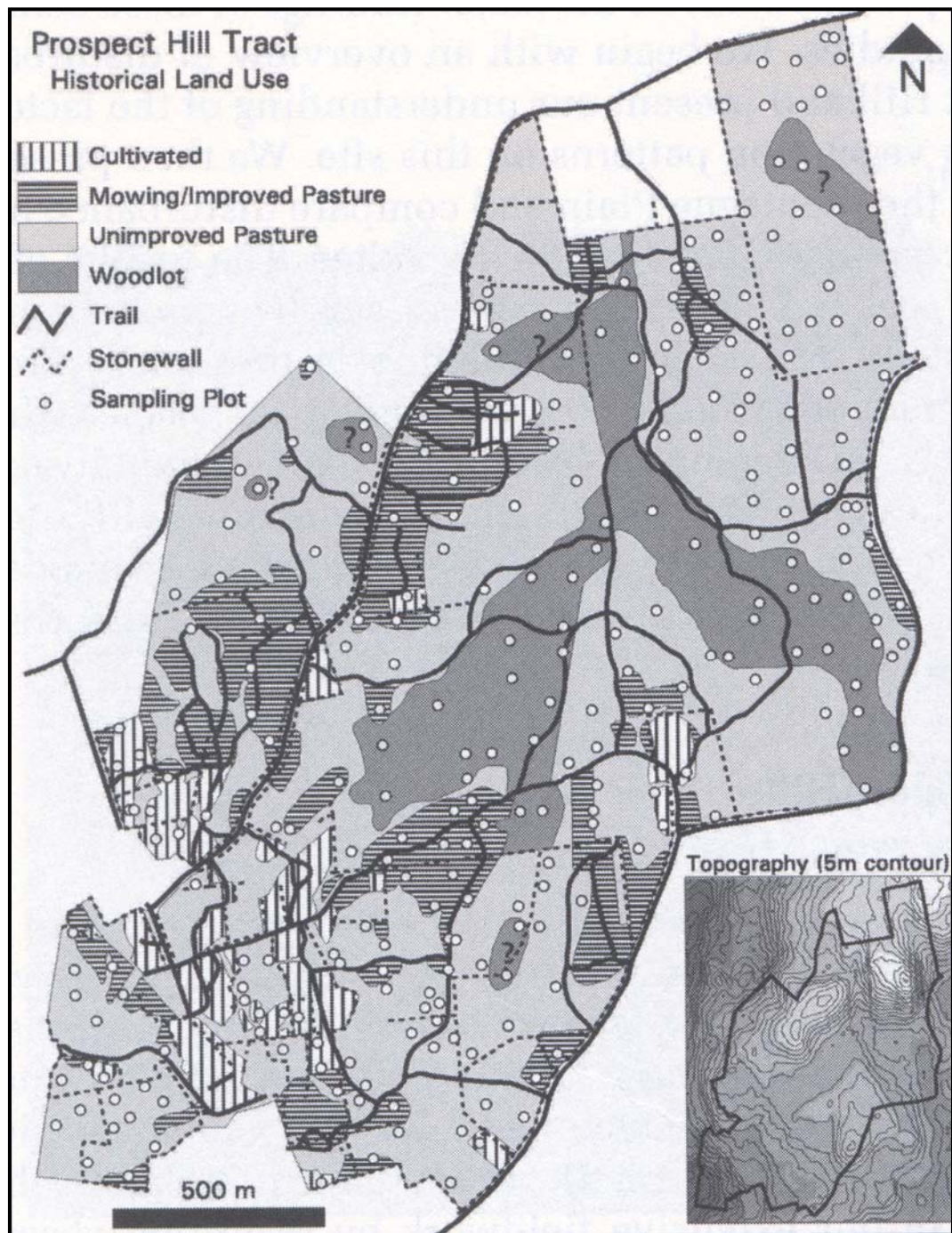
Figure 19. Map of Prospect Hill tract at the Harvard Forest indicating historical land-use. Note the scale and patchy distribution of the differently-used types of land, a variability that continues to influence trends in forest characteristics today. Reproduced from Motzkin, 2004.

Future Explorations

Ground validation measurements are not the only tactic for evaluating the spatial accuracy of eddy-covariance. By combining remotely sensed images from sensors like the Moderate Resolution Imaging Spectroradiometer (MODIS) with eddy-flux data, researchers hope to improve the regional scaling of micrometeorological measurements.

Researchers' ability to estimate ecosystems' gross primary production (GPP) using remote sensing techniques is advancing at a rapid pace (Xiao et al., 2004). The Vegetation Photosynthesis Model (VPM), which is conceptually based on the partitioning of photosynthetically active vegetation and non-photosynthetically active vegetation, uses the Enhanced Vegetation Index (EVI) to estimate GPP (Xiao et al., 2004). EVI is a function of reflectance data of blue, red, and near infrared bands (Heuete et al., 2002; Xiao et al., 2004), and is thus related to vegetative greenness or photosynthetic capacity. At Harvard Forest, the EVI was more strongly correlated with GPP than the more widely applied Normalized Difference Vegetation Index (NDVI) (Running et al., 2004; Xiao et al., 2004).

Although EVI correlates well with GPP, its relationship with overall ecosystem biomass is not well understood. As a final exploration for the validation of eddy-covariance measurements, I sought to test the utility of the MODIS EVI data for intra-site biomass comparisons at the Harvard Forest. Comparisons between these two datasets, however, yielded no correlation.

The BigFoot plots are arranged across the 25 km^2 in such a way that several plots fall within the same pixel thereby not taking full advantage of the maximum amount of pixels available. For 43 BigFoot plots there were 25 EVI pixels (because many pixels contained two or more plots), but within those 25 there were only eight unique EVI values. Most plots (24 out of 44) fell within only four pixels. Moreover, the potential relationship between EVI pixel and BigFoot plot values is unclear because the BigFoot plots may not in fact be a good representation of the surface area captured by the MODIS data. The BigFoot plots are not randomly distributed across the entire 25 km^2 region and are limited in the land-cover type that they represent (A. Kirschbaum, personal communication). Increasing the number of plots that fall within a single pixel, such as was done with the intensive BigFoot plots (Fig. 11), may reduce this representation error. Intra-site comparisons may be possible at locations where issues of land-ownership are less complex and a larger portion of the parcel of interest is available for sampling. Also, differences in EVI values between several sites may be large enough to conduct meaningful inter-site comparisons. Future advancements in the resolution of the MODIS data may also increase the utility of biomass and vegetative index comparisons. This project will continue to seek to improve the relevance of remote sensing vegetative indices for the spatial validation of whole-stand carbon-content.

Conclusion

In summary, comparison of the variable- and fixed-radius methods for measuring tree biomass demonstrated that the former method was inappropriate for our questions of long-term carbon accounting. Carbon-content, basal area, and tree frequency estimates from two spatially distinct groups of plots outside the tower footprint provide evidence that the tower footprint is representative of the greater forested region. The forest in the tower footprint is, however, composed of unusually high numbers of oak. While measurements from the tower footprint provide reliable estimates of forest carbon storage for forests of a similar type, periodic re-measurement of stands outside of the footprint will continue to be useful for the validation of footprint data. Additional explorations surrounding the possibility of coupling ground-based measurements with remote sensing vegetation incidences may prove useful for making regional-scale estimates of forest carbon sequestration.

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Appendix A. Prism factors used for each BigFoot, variable-radius plot.

Plot	Prism Factor	Plot	Prism Factor
0	2.5	77	2.5
5	3	79	2.5
9	2.5	80	2
22	3	81	2
23	3	82	2
27	2	83	2.5
28	2	84	2
30	2	85	2
32	3	86	3
33	3	87	2
35	2	88	2
39	2	89	2.5
40	2.5	90	2
44	3	91	2
54	3	92	2
55	3	93	2
62	3	94	2
63	3	95	1
66	2	96	2.5
68	2.5	97	2
71	3	98	2.5
74	2	99	2

Appendix B. Species-specific biomass equations for calculating the weight of trees using their DBH. All DBHs are in inches and weights in pounds, unless otherwise indicated. Those species for which no biomass equation could be located were included under the most taxonomically similar species.

Acer rubrum (Red maple) (Young et al. 1980)
ln (weight) = 0.9392 + 2.3804 ln (DBH)

Acer pennsylvanicum (Striped maple)
ln (weight) = 1.2451 + 2.3329 * ln (DBH) (Young et al., 1980)

Acer saccharum (Sugar maple) (Young et a. 1980)
ln (weight) = 1.2541 + 2.3329 * ln (DBH)

Betula alleghaniensis (Yellow birch) (Young et al. 1980)
ln (weight) = 1.1297 + 2.3376 ln (DBH)

Betula lenta (Black birch) (Brenneman et. al 1978)
weight = 1.6542 * DBH ^ 2.6606

Betula papyrifera (Paper birch) (Young et al. 1980)
ln (weight) = 0.4792 + 2.6634 ln (DBH)

Betula populifolia (Gray birch) (Young et al. 1980)
ln (weight) = 1.0931 + 2.3146 ln (DBH)

Carya spp. (hickory spp.) (Brenneman et al. 1978)
- includes *Carya glabra* (Pignut hickory) and
  Carya ovata (Shagbark hickory)
weight = 2.0340 * DBH ^ 2.6349

Fagus grandifolia (American beech) (Young et al. 1980)
ln (weight) = 1.3303 + 2.2988 * ln (DBH)

Fraxinus americana (White ash) (Brenneman et al. 1978)
weight = 2.3626 * DBH ^ 2.4798

Hamamelis virginiana (Witch-hazel) (Telfer 1969)
weight = [0.001 * 10 ^ (-3.037 + 2.900 * log10 (DBH * 10))] –
         [0.001 * 10 ^ (-2.729 + 2.162 * log10 (DBH * 10))]

Ilex verticillata (Winterberry) (Telfer, 1969)
weight = 53.497 * (DBH) ^3.340
- weight in grams
- DBH in centimeters

Kalmia latifolia (Mountain-laurel) (Day and Monk 1974)
weight = 0.001 * 10 ^ (2.1533 + 2.0017 * log10 (DBH)

Ostrya virginiana (Eastern hophornbeam)
- used *Ulnus americana* (American elm) (Perala and Alban, 1994)
weight = 0.0825 * (DBH) ^ 2.460
- weight in kilograms
- DBH in centimeters

Picea abies (Norway spruce) (Jokela et al., 1986)
weight = 0.2722 * (DBH) ^ 2.1040
- weight in kilograms
- DBH in centimeters

Picea rubens (red spruce) (Whittaker et al., 1974)
weight = 0.2066 * (DBH) ^ 2.1830
- weight in kilograms
- DBH in centimeters

Picea glauca (white spruce) (Perala and Alban, 1994)
weight = 0.1643 * (DBH) ^ 2.480
- weight in kilograms
- DBH in centimeters

Pinus resinosa (Red pine) (Young et al. 1980)
ln (weight) = 0.7157 + 2.3865 ln (DBH)

Pinus strobus (white pine) (Young et al. 1980)
- Includes *Pinus sylvestris* (scotch pine)
ln (weight) = 0.4080 + 2.4490 ln (DBH)

Prunus serotina (Black cherry) (Brenneman et al. 1978)
- Includes *Crataegus* spp. (hawthorn spp.)
weight = 1.8082 * DBH ^ 2.6174

Prunus penslyvanica L. (pin cherry) (Young et al., 1980)
weight = 0.1556 * (DBH) ^ 2.1948
- weight in kilograms
- DBH in centimeters

Quercus alba (White oak) (Brenneman et al. 1978)
weight = 1.5647 * (DBH) ^ 2.6887

Quercus rubra (Northern red oak) (Brenneman et al. 1978)
- Includes *Castenea dentate* (American chestnut)
weight = 2.4601 * DBH ^ 2.4572

Quercus velutina (Black oak) (Bridge 1979)
ln (weight) = -0.34052 + 2.65803 * ln (DBH)
- weight in kilograms

Sorbus decora (showy mountainash)
- used equation for *Sorbus americana* (American mountain-ash) (Roussopoulos and Loomis, 1979)
weight = 44.394 * (DBH) ^3.253
- weight in grams
- DBH in centimeters

Tsuga canadensis (Eastern hemlock) (Young et al. 1980)
ln (weight) = 0.6803 + 2.3617 ln (DBH)

Vaccinium spp. (blueberry) (Telfer, 1969)
- Includes *Pyrus arbutifolia* (chokeberry)

Appendix C. Species contained in species plotting categories for Figs 16 and 18.

<u>Figure 16:</u>
Oak
- o *Quercus alba* (white oak)
- o *Q. rubra* (red oak)
- o *Q. velutina* (black oak)

Maple
- o *Acer pennsylvanicum* (striped maple)
- o *A. rubrum* (red maple)
- o *A. saccharum* (sugar maple)

Hemlock
- o *Tsuga Canadensis* (eastern hemlock)

Birch
- o *Betula alleghaniensis* (yellow birch)
- o *B. lenta* (black birch)
- o *B. papyrifera* (paper birch)
- o *B. populifolia* (gray birch*)*

White pine
- o *Pinus strobus*

Figure 18:
Hemlock
- o *Tsuga canadensis* (eastern hemlock)

Maple
- o *Acer pennsylvanicum* (striped maple)
- o *A. rubrum* (red maple)
- o *A. saccharum* (sugar maple)

Oak
- o *Quercus alba* (white oak)
- o *Q. rubra* (red oak)
- o *Q. velutina* (black oak)

Other
- o *Betula. alleghaniensis* (yellow birch)
- o *B. lenta* (Black birch)
- o *B. papyrifera* (paper birch)
- o *B. populifolia* (gay birch*)*
- o *Carya glabra* (pignut hickory)
- o *C. ovata* (shagbark hickory)
- o *Castenea dentate* (American chestnut)
- o *Crataegus spp.* (hawthorn)
- o *Fagus grandifolia* (American beech)
- o *Fraxinus americana* (white ash)
- o *Hamamelis virginiana* (witch hazel)
- o *Ilex verticillata* (winterberry)
- o *Kalmia latifolia* (mountain-laurel)
- o *Ostrya virginiana* (eastern hophornbeam)
- o *Picea abies* (Norway spruce)
- o *P. glauca* (white spruce)
- o *P. rubens* (red spruce)
- o *Pinus resinosa* (red pine)
- o *P. strobus* (white pine)
- o *Prunus penslyvanica* (pin cherry)
- o *P. serotina* (black cherry)
- o *Sorbus decora* (showy mountain-ash)