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An Investigation of Root Biomass in Forested Ecosystems

By

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Professor Paul V. A. Fine

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by

Benjamin Thomas Caldwell

Abstract

An Investigation of Root Systems in Forested Ecosystems

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Professor Kevin O'Hara, Chair

The root systems of forest ecosystem are both important and understudied. Roots function as the critical organs of nutrient uptake and anchor tree stems against wind throw and aboveground disturbance. Roots are also an important terrestrial reservoir of carbon and play an important role in global climate. Conversion or disturbance of forest lands can result in an emission of carbon dioxide to the atmosphere, and so quantifying the amount of carbon in root biomass is of interest for forest scientists and the climate policy their research informs.

This dissertation contributes to the science of root biomass measurement and modeling, providing techniques and approaches to improve those estimates, and models for leaf area that can be used to estimate root biomass. It focuses on techniques to improve measurement of root biomass using ground penetrating radar, an emergent method to measure root biomass. First, I investigate what above-ground metrics might best be used to model and predict root biomass and distribution and I develop new models relating basal area to leaf area for quaking aspen (*Populus tremuloides)* in the Sierra Nevada. Second, I investigate root biomass and distribution in coast redwood (*Sequoia sempervirens*), and how water acquisition may drive the allocation to roots in redwoods.

Ground penetrating radar is shown to have considerable utility for the measurement of coarse root biomass. Above ground biomass is shown to be an excellent predictor of coarse root biomass in Sierran ecosystems. Leaf area, which is predicted by pipe model theory to have a tight relationship with fine root biomass, is shown to have some predictive power for root biomass, and my model represents an improvement over other reported metrics. Finally, I conclude that global root biomass estimates have not been based on reliable or unbiased data to date and I contribute A plan to correct this gap in future global estimates.

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Introduction

Science is an empirical pursuit. Inference is bounded by what we can observe and measure. As such, there are typically many more questions posed than we can collect data to answer. New technologies and techniques that allow us to answer open questions, and prompt the cycle of improved understanding, are therefore often responsible for breakthroughs in science. The study of tree roots represents a black box in ecology, needing methods that will allow us to see with greater clarity in a largely opaque medium (Vogt, Vogt, & Bloomfield, 1998). As roots are costly in both time and resources to directly study, there has been a relatively large body of work that attempted to understand what we can infer about roots based on observation of above-ground organs (Cairns et al. 1997, Brown 2002, Mokany et al. 2006). The theory that grounds these investigations is optimum allocation theory and pipe model theory (Shinozaki et al. 1964a, Coutts 1983, Canham et al. 1996), but the execution of the models is primarily empirical and statistical. As long as that is the case, sufficient measurement precision of both above and below-ground tree components will be necessary to make inference for whole trees. The ability to make such inference would be of use and interest in both forest yield models and in greenhouse gas accounting and climate modeling (Brown 2002, Landsberg and Sands 2010). Finally, a global dataset on root and shoot allocation would be fascinating to interpret in the light of optimal allocation theory as science moves to inform climate change adaptation efforts (Chapin et al. 2010).

Tree roots are known to function as organs of water and nutrient uptake. They also provide structure and support to the stem, preventing or ameliorating the effects of windthrow and flood, anchoring the tree in the medium of the soil (Mitchell 2012). Tree roots can serve as a reservoir for nutrients (Chapin III et al. 1990, Shibuya et al. 2006) and an organ for regeneration after disturbance via sprouting (Bond and Midgley 2001, Schwilk and Ackerly 2005). All these functions provide competitive advantage to the organism, but come at a cost. These costs can be divided into direct costs, those costs which are a result of the production and respiration costs of roots, and indirect costs, in the form of forgone allocation to above-ground organs (Chapin III et al. 1990). Researchers approaching apportionment between roots and shoots have typically attempted to make sense of this allocation in terms of the long-term competitive environment, typically the genetic and phenotypic makeup of an organism, and also an organism's phenotypic plasticity in response to different disturbance environments (Ackerly et al. 2000, Craine 2005) in the competitive context of co-occurring species in a particular set of moisture, temperature, edaphic and disturbance gradients (Ackerly 2003, Fine et al. 2005, Majdi et al. 2005). There is also recognition that allocation strategies vary with ontogeny, as a plant will typically have very different allocation priorities during different phases of development (Coleman et al. 1994). In the framework of this theoretical background, then, it seems reasonable to assert that a plant species' relative allocation to above and below-ground organs will be strongly influenced by the context of past competitive and environmental pressures, and the success that species have had at different stages of development.

In the broader context of the evolutionary environment's influence on different species' range of variability, variation observed within a particular species is often better explained using functional or physiological theory, which can help extricate and explain the influence of a given environment on the expression of the more limited genetic palette found in a given species (Landsberg and Sands 2010). The link between roots and leaves as sources and sinks of water and carbohydrate is such an example. This relationship, and its correlation to stem conductive tissues, is conceptualized through the pipe model theory posited and modeled by Shinozaki, Yoda, Hozumi, & Kira in1964 and further developed by Waring, Schroeder, & Oren in 1982. Since leaves and roots are complementary organs, linked by xylem and phloem (sapwood) through the stem, there should be a direct and quantifiable functional relationship between the organ systems and the sapwood. Sapwood has been used to effectively model leaf area and growing space occupancy in forested ecosystems worldwide (Waring et al. 1982, Valentine 1985, Mäkelä 1986, O'Hara and Berrill 2010).

While less studied, the obvious link between modeling fine roots as the organs of water uptake using a pipe model was formally explored by Valentine (1988), although the focus of the model was that of describing leaf area and basal area development from stand-replacing disturbance to stand-replacing disturbance. Those models were extended to model nutrient transport interactions between the different organs (Thornley 1991, Dewar 1993). These posited relationships are difficult to translate to implementable process models, however, because of the difficulties in parameterization of the model's inputs for mature trees and stands (Lacointe 2000, Landsberg 2003). The difficulties of process modeling notwithstanding, there are theoretical grounds to expect fine root biomass to be quite tightly related to leaf area. As fine root biomass, turnover and distribution has been consistently difficult to predict (Kurz et al. 1996, Vogt et al. 1996, Cairns et al. 1997, Vanninen and Mäkelä 1999), there would be utility in a statistical, empirical allometric model between tree leaf area and fine roots, even if it could not be extended to a process model as yet.

For some of the same reasons which have limited the use of process models to predict fine root biomass, coarse root biomass has been most successfully modeled using allometric relationships between above- and below-ground biomass (Brown 2002). However, the lack of empirical data has greatly impeded efforts to implement these models (Brown 2002, Mokany et al. 2006). Because of the effort required and the destructive nature of sampling necessary to collect data on root biomass with traditional excavation of roots, the datasets that can be used to related root biomass to that aboveground biomass are fairly limited (Mokany et al. 2006, Chapter 3). Modern techniques, particularly ground-penetrating radar (GPR) provide the opportunity to augment these data to the extent required (Butnor et al. 2003). However, the breadth of the applicability of this technology across the range of physical and biological conditions found in forested ecosystems is still unclear.

Quaking aspen and coast redwood, two tree species endemic to California, make an interesting and useful test case for the utility of leaf area to estimate fine roots and ground penetrating radar to measure coarse roots. They are also interesting from a carbon-allocation perspective as two examples of tree species with evolutionary success partially as a result of their prolific resprouting ability (Lieffers et al. 2001, Bond and Midgley 2001, Ramage et al. 2011). The species commonly occur on very different soils, an important factor in GPR's reported efficacy (Daniels 1996, Hirano et al. 2008). There are also complementary knowledge gaps for each species; aspen roots are relatively well-studied (Barnes 1966, DesRochers and Lieffers 2001b), while coast redwood roots are not; sapwood-leaf area models have already been developed for coast redwood (Berrill 2003) but had not for quaking aspen in the Sierra Nevada before this dissertation. Both face conservation threats under future global climate changes (Johnstone and Dawson 2010, Anderegg et al. 2012).

These forested ecosystems were chosen to explore the principal gaps in the state of knowledge about root biomass and test how to most efficiently fill that knowledge gap. Chapters 1 and 2 focus on examining the relationship between above-ground components of Sierra Nevadan quaking aspen and Californian coast redwood, respectively. Chapter 3 examines the way root biomass is currently estimated on a global scale. These chapters have an applied focus, and use empirical models as the most practical near-term approach to answer pressing questions. Ultimately empirical models of root biomass will be supplanted by process models that represent more complete understanding of the ecophysiological and evolutionary allocation strategies of trees and plant communities (Lacointe 2000, Craine 2005). This level of understanding will never be reached without data to inform inquiry, however, and as there is currently a paucity of root data the approaches outlined in these chapters will have utility for those ends as well.

1 The utility of leaf area and above-ground biomass for the prediction of fine and coarse root biomass for *Populus tremuloides* in the central & southern Sierra Nevada

Introduction

Quaking aspen (*Populus tremuloides*) is one of the most widely distributed tree species in the world (Lieffers et al. 2001 p. 311, Shepperd et al. 2006). It grows across Canada and as far south as Mexico. It is at the southern and western extent of its range in California's Sierra Nevada. The species only locally abundant in any given location in California, and restricted to relatively small stands on mesic, high-elevation sites. Nonetheless, quaking aspen plays an important role for wildlife, water quality and conservation, and floral diversity in Sierran ecosystems, and has been a species of considerable interest for management and for study by climate-change ecologists (Shepperd et al. 2006, Berrill and Dagley 2012, Anderegg et al. 2012).

Aspen is fire-adapted species with the unusual ability to regenerate by suckering after disturbance. This vegetative regeneration originates in the roots; suppressed hormonally in the presence of healthy leaves and stems, the roots will produce suckers if the above-ground component of the tree is damaged or removed (Frey et al. 2003). Healthy stands of quaking aspen will sucker prolifically after such an above-ground disturbance, with sucker densities reaching 250,000 stems/ha in the first year (Alban et al. 1994). These shoots self-thin as the stems mature (Bond and Midgley 2001). Suckering has proven to be an important part of a competitive set of physiological adaptations. This heavy reliance on vegetative regeneration also allows some aspen clones to achieve a superlative status among living organisms for age and size. Aspen may therefore represent both the world's largest and longest-living organism (Lieffers et al. 2001, Mitton and Grant 2009).

For these reasons, the quaking aspen root system, as the site of vegetative regeneration, has been the object of serious study for several decades. Many studies have focused on description of the root system itself, using hydraulic excavation to reveal the extent and distribution of clonal root systems (Barnes 1966, DesRochers and Lieffers 2001b, Landhäusser et al. 2012). The authors of early studies noted that aspen roots are prolific, interconnected, and shallowly distributed. These data, combined with the observation that aspen clones are large and persistent, led to speculation that nutrient transfer might occur via the roots within stems of a single clone. This was subsequently confirmed using chemical tracers, which indicated the transfer of water and carbohydrates between stems in a given clone via connected root systems (Byle 1964).

More recent research has focused on aspen clone persistence in the face of rapid anthropogenic change of temperate ecosystems. Studies on these phenomena have focused on fire suppression and the impact of climate warming on water availability, as well as increase pressure from insect pests (Romme et al. 2000, Shepperd et al. 2001, Frey et al. 2004, Anderegg et al. 2012). As land managers in the Sierra Nevada consider options for quaking aspen regeneration, one key issue is how to promote its regeneration, which historically was probably driven by fire, to management and political realities in which allowing or intentionally starting stand-replacing fires may not be an option (Krasnow et al. 2012). Fire suppression is thought to reduce aspen competitiveness because without fires intense enough to kill off the overstory, more shade-tolerant species have the opportunity to invade aspen stands and overtop aspen (Shepperd et al. 2001). A second consideration is the influence of climate change, and the increasing water stress in ecosystems as a result (Moser et al. 2009, Alexander and Allen 2013). Indeed, some authors have studied the effects of climate change on aspen communities elsewhere in the American west (Anderegg et al. 2012). These studies have shown that chronic water stress can lead to catastrophic cavitation of the xylem of an aspen clone. Since a given clone is likely composed of multiple stems, and water stress is experienced by all stems due to interconnected roots, catastrophic water stress can affect many stems simultaneously, leading to so-called “Sudden Aspen Death” (Anderegg et al. 2012). Aspen control of water loss by the leaves is limited compared to conifers, and in locations like the Sierra Nevada this may contribute to it being most commonly found on mesic sites (Kaufmann et al. 1982, Shepperd et al. 2006). Aspen is therefore of considerable ecological interest, has been very competitive and may be faced with a contracting range due to anthropogenic ecosystem impacts. Further study of aspen is thus both worthwhile for its unusual suite of physiological adaptations and timely as its range begins to shift, potentially rapidly, north.

Ecophysiology, as the study of physiological adaptation to changing environmental conditions, provides tools to study quaking aspen’s response to climate change. Understanding how quaking aspen leaves and roots respond to changes in historic disturbance regime will be key information as land managers try and keep aspen as an ecosystem component. A major gap in an ecophysiological approach to the problem however is the ability to predict the size or the extent of the root biomass in question. Also lacking are regional models to estimate leaf area and biomass from commonly taken measurements like basal area (although one has been built for a part of Alberta, (DesRochers and Lieffers 2001a) . From an applied standpoint, an understanding of aspen root and leaf connection and extent would improve rapid assessment of stand health. From a theoretical standpoint it would also be interesting to estimate the proportion of a stand below-ground, in the context of optimal allocation theory (Bloom et al. 1985). Distinct from, but related to applications in restoration management, leaf area estimates have applications for prediction of below-ground biomass, which is useful for estimating below-ground carbon sequestration in an ecosystem (DesRochers and Lieffers 2001a, Davis et al. 2004).

The pipe model theory is the theoretical framework that describes the implication for plant form of the connectivity between roots and leaves via the xylem (Shinozaki et al. 1964a, Waring et al. 1982). Since the water necessary for photosynthesis must pass through the xylem, there is a strong basis for empirical models of leaf area based on the cross-sectional area of functional xylem, or sapwood, tissue in the bole. Applications of pipe model theory in forest management and ecology range widely, but include estimating leaf area to guide management for timber, water quality, and complex stand structures, as well as measurement of growing space efficiency and total growing space occupancy (Waring et al. 1980, O’Hara et al. 1999, Stancioiu and O’Hara 2005b, Gersonde et al. 2005, Berrill and O’Hara 2007). As an ecophysiological metric, LAI (leaf area per ground surface area, a unitless measure) is a key descriptor in ecology. Furthermore, it is highly scalable from the ecosystem level (where it can be used to estimate net primary productivity and ecosystem transpiration) down to the stand level (where it can be used to manage growing space) (Gholz 1982, Nemani and Running 1989, Vertessy et al. 1995, O’Hara et al. 1999). Interestingly, while the prediction of leaf biomass and leaf area from sapwood area is well-described, the obvious counterpart, prediction of the roots, is not. This is unfortunate but not unexpected, as root biomass prediction and mensuration represent a key gap in our knowledge of forested ecosystems (Waisel et al. 2002).

Functionally, coarse roots serve to buffer tree stems from windthrow (Coutts 1983). They also serve as the site of fine root attachment, allowing roots to extend to greater distances and depths (Pregitzer 2002). Finally, they are the location where most of the below-ground forest biomass is sequestered. For aspen, the coarse roots are the sites of vegetative regeneration and a site of carbohydrate storage for suckering (Frey et al. 2003). Fine roots, on the other hand, are the site of nutrient and water uptake (Pregitzer 2002). They are also important as the source of root exudates to the soil. Fine root turnover represents a significant flux of carbon and other nutrients to the soil, the size of which is not fully understood (Hendricks et al. 1993).

The opportunity is then to use pipe model theory to develop an empirical model that links leaf area to root biomass. To do this, both data on root biomass and leaf area is required. I predict that leaf area would correlate well with fine root biomass, and that above-ground biomass could be used to model below-ground biomass with a high degree of fidelity. Finally, tree basal area, a proxy for connective tissue, should have good predictive ability for leaf area and root biomass. Developing a method that ties the basal area of quaking aspen, and other Sierran conifers, to leaf area and fine roots is of interest, as part of an effort to gauge the utility of different methods and metrics to estimate whole-ecosystem carbon stocks (Chapter 3). This study thus serves as a complement to existing models for basal area-based estimates of leaf area in Sierran conifers (Gersonde et al. 2004, 2005).

Methods

Sampling locations

Three different sites in the southern and central Sierra Nevada on public and private lands, were selected for sampling (Table 1, Figure 1). Stand selection occurred with the intent to cover as broad a range of tree diameters and stand basal areas possible, as well as including both mesic and more xeric sites. Plots were randomly located within sites. The number of plots in each site ranged from one to three, depending on the variability observed in each site. Plot sizes ranged from 0.02 to 0.04 ha. Within each plot, sampling was focused on measurements of leaf area, fine roots using root cores, and coarse roots using trenches and ground-penetrating radar.

Each plot center was recorded using a WAAS-enabled GPS and marked with a tree tag or flagging. In each plot sampled, diameter at 1.4 meters (diameter at breast height or dbh) for all stems was measured using a diameter tape to the nearest mm. Stems were mapped using a laser rangefinder with a digital compass (LaserAce^{TM}). For a subset of stems, heights and height to the base of the live crown was also measured using the same instrument. Stems included in the subset were selected randomly, with at least five sampled in each plot. If there was a high degree of variance observed in the crown heights or diameter-height relationship, additional height measurements were taken as time in the field allowed.

Leaf area estimation

Methods for direct measurement were largely the same protocols used in Kenefic and Seymour (1999). However, because quaking aspen is a diffuse-porous species with dispersed sapwood I thought it inappropriate to develop a sapwood –leaf area relationship for the species (Bréda 2003, but see Kauffmann and Troendle for results to the contrary (1981)). Instead, important independent variables measured were stem and branch diameters and the cross-sections calculated from these metrics.

In the field, selected stems (n=12) were felled, and diameters were measured at ground level, at breast height, and at the crown base. Stems were selected to cover a range of tree sizes and crown positions. Only healthy stems without major structural damage were selected for sampling. The crown was subdivided into thirds, and stem diameter was also measured at the base of each third. Stem disks were removed on the main stem at one-third and two-thirds of the crown's length. Total height and height at the base of the live crown was also recorded. The diameter at the base of every branch and branch length were recorded. At least three branches from each third of the live crown were removed from the stem. Leaves and petioles were stripped from the branch, bagged separately in paper bags, and placed on ice in a sealed container.

In the lab, a subset of all leaves was collected from each tree for scanning. Each tree crown was divided into thirds and three branches from each third of the crown had all leaves scanned, for a total of nine branches per tree. All leaves from the selected branches were scanned and the leaf area calculated using WinFolia, software produced and maintained by Regent Instruments, Inc. After mass was measured leaves were placed in a drying oven at 70^0C. Dry mass was recorded after a stable mass was reached (usually after 72 hours). Dry and wet mass for all leaves was recorded; measurements of the scanned subset of leaves were kept separate for subsequent analysis.

The crown of the largest tree sampled shattered on impact with the ground and all the leaves fell to the ground, making it impossible to relate a given leaf to a given branch. I was able to locate all leaves, though, as they lay close to the crown of the tree; the approach used was to estimate the tree's leaf area without using branch-level measurements or estimates, but based on estimated biomass of all the leaves next to the fallen tree. It was not possible given field conditions to collect all the leaves from the tree. Rather, a protocol was devised to sample the shattered crown of the tree, stratifying on the observed distribution and density of the leaf biomass around the shattered crown. The total area for each stratum (i.e. portion of the area around the tree's crown that contained leaves) was measured, and two to four 50 cm radius plots set up in each stratum. All leaves from each plot were collected and processed in the lab as above.

Coarse root biomass

Methods for coarse root biomass followed those described in Chapter 2. Briefly, coarse root biomass was estimated using a combination of direct measurements from trenches in each plot and indirect measurement of root biomass using a ground-penetrating radar (GPR). Returns from the radar were regressed on the measurements from the trenches to determine the relationship between the GPR returns and root biomass. The more extensive measurements from GPR were then used to estimate root biomass for that area.

Fine root biomass

Fine root biomass (diameter <5 mm) was measured in each site using root cores (n = 140) taken at 10, 20 and 30 cm depth. Root cores were extracted using a quantitative corer and brought back to the lab for analysis (Ryals and Silver 2013). Rather than exhaustively extracting the fine root biomass from every root core, root biomass for each root core was estimated by determining the best model form (Michaelis-Menton or logistic) for the cumulative biomass of roots extracted from the core at set time intervals (Metcalfe et al. 2007). To do this, a subsample of root cores were extracted at set time intervals until root biomass was exhausted in each. The models were then tested for goodness of fit to the cumulative extraction over time from the cores. At 40 minutes per core, the amount of biomass predicted by the logistic model had an acceptable level of error compared to the actual biomass extracted (<10%, no detectable bias). For the rest of the cores, roots were extracted for 40 minutes, and a logistic model fit to the cumulative biomass extracted to arrive at the root biomass in each core. Since a logistic function approaches its asymptote at infinity, a cutoff time was used when the derivative of the slope was <1%, (i.e. there was less than a 1% change in the biomass predicted by the model) (Metcalfe et al. 2007). Cores that had model slopes, intercepts or standard errors that were outliers were removed, for a sample size of 118. Fine root biomass was calculated for a per-area basis (density) using the volume of the core extracted.

Modeling and analysis

Leaf area

From the relationship between estimated scanned leaf area and dry leaf area, specific leaf area for a given branch was estimated. A regression between branch leaf area and branch cross-sectional area was found for all trees (Figures 4 and 5). Inclusion of branch length in the model did not offer significant improvement in the model, so only cross-sectional area was used. Whole-tree leaf area was then estimated by taking the sum of measured and estimated direct measurements on each tree. For the largest tree sampled, leaf area was estimated based on the sample of total leaves taken from the crown. Leaf area for each plot within strata was calculated, and for each stratum the mean multiplied by the stratum area was used as the estimate of the stratum’s total leaf area. The estimated leaf area for all strata were then summed and used as the estimate of whole-tree leaf area for that tree. All analysis was conducted in R (R Development Core Team 2013). Non-linear model forms were explored in the nls package, but ultimately all models selected were OLS regressions analyzed using lm() in R’s base package.

Belowground biomass estimation using above-ground data

Multivariate models to predict fine and coarse biomass with measured above-ground metrics were tested, and the most significant variables used to reduce the models to ones with the best predictive power. Linear relationships were explored between variables of interest using visual inspection of the data to remove outliers and determine whether the assumptions of OLS regression were met (Quinn and Keough 2002). R base and the ggplot2 package were the primary tools used for this analysis (Wickham 2009, R Development Core Team 2013). Once the model form and assumptions were confirmed, adjusted r^2 and p values were used to assess the utility and significance of tested correlations, again using lm() in R base. First-order polynomials were found best explain the relationship between tested dependent and independent variables, and were used throughout the analysis. In all cases, there was a single strong predictor that was used in the best model.

Results

Leaf area estimation

The specific leaf area relationship found for stems was approximately 8.77 ± .30 m^2kg^{-1}. The relationship between wet and dry leaf biomass exhibited very little variation, with a slope of 0.5 and an intercept very close to zero (adj. r^2 .93, Table 3, Figure 3).

The estimated relationship between branch leaf area and cross-sectional area was

$$B_{LA} = .12 + .05\mathrm{A}_{\mathrm{Br}} \quad [1]$$

Where

$$B_{LA}: branch\ leaf\ area\ (m^2)$$

$$A_{Br}: Branch\ cross\ sectional\ area\ (cm^2)$$

The model for branch leaf area predicted by branch diameter was

$$B_{LA} = -.31 + 0.029D_{Br} \quad [2]$$

Where

$$B_{LA}: branch\ leaf\ area\ (m^2)$$

$$D_{Br}: branch\ diameter\ (cm)$$

Branch-level leaf area was moderately well predicted by both branch diameter and branch cross-sectional area. Both independent variables provided an approximately equal goodness of fit to the leaf area data (table 5 and in figures 4 and 5).

Several different independent variables were explored to determine which provided the best estimate of leaf area (based on a comparison of adj. r^2 values and visual examination of the regressions and residuals). As branch cross-sectional area was a slightly better predictor of leaf area at the branch level than diameter, I used tree cross-sectional area at breast height to estimate the tree-level leaf area. For the entire dataset, the predictor for leaf area was the tree cross-sectional area, with an adjusted r^2 of .89. Inclusion of tree height in the model increased the residual standard error and lowered the coefficient of determination; so, only tree cross-sectional area was retained as an independent variable. The tree leaf area to cross-sectional area at breast height was estimated to be

$$A_L = -2.065 + 0.05BA \quad [3]$$

Where

$$A_L: tree\ projected\ leaf\ area\ (m^2)$$

$$BA: tree\ cross - sectional\ area\ (cm^2)$$

Without inclusion of stem 12, the large stem that shattered the model estimated was

$$A_L = 7.175 + 0.03BA \quad [4]$$

Inclusion of the largest stem in the dataset did not result in a dramatically different model estimate over the range of values in the sample and subsample, although the sampling protocol for the large stem was different than the other stems (Figures 6, 7) .The best fit models and those considered most ecologically meaningful are presented in table 4, with their appropriate descriptive statistics. A model which used diameter at base of live crown as the independent variable is presented for comparison because, while it often is the metric with the best predictive power, it did not prove to be in this case.

LAI

For the five plots in which aspen was predominant, calculated LAI for the aspen stems ranged from 1.6 to 2.5 , and for the site from 1.6 to 9.5 (Table 6).

Coarse root biomass

Basal area and LAI were very strong predictors of coarse root biomass. Adjusted r^2 exceeded .97 for these models (Table 7). GPR scans of the soil show a highly interconnected mat of roots between quaking aspen stems, confirming results from other studies that relied on excavation.

Root biomass was observed to be concentrated in the upper 50 cm of the soil, with approximately 80% of total biomass found in the top 50 cm, on average (Figure 8). Root biomass decreased unimodally with depth (Figure 9).

Fine root biomass

LAI was a highly significant predictor of fine root biomass in these ecosystems as well, and predicted the majority of the variation in fine root biomass (Table 7, Figure 10). While the goodness of fit of this model was somewhat lower than for other models used, this model explained more variation in the data than other models in the literature which have sought to predict fine root biomass empirically (Chen et al. 2004, Finér et al. 2011).

Discussion

Specific leaf area

There have been very few previous studies that have reported values for specific leaf area for quaking aspen. Bond-Lamberty et al. (2002) reported SLA of 5.82 ± 1.91 m^2kg^{-1} in northern Manitoba, Canada; Kaufmann and Troendle (1981) reported 10.97 m^2kg^{-1} (no report of variance) near Fraser, Colorado. My sampled value of 8.77 ± .30 m^2kg^{-1} falls within this range (Table 3). The more extreme climatic conditions and shorter growing season in Canada may lead to a lower SLA there.

Leaf area

While some studies have found that including crown parameters tended to improve tree-level estimates of leaf area in other species (Dean et al. 1988, Nowak 1996), these terms did not improve models tested in this study. One possible inference is that the relationship between leaf area and the stem cross-sectional volume is relatively constant across different light environments for quaking aspen. This may be a result of the relatively low tolerance to poor light conditions of quaking aspen, which are observed to decline rapidly when overtopped in the Sierra Nevada (Shepperd et al. 2001). *Populus tremula*, a closely related species from Europe, Asia and north Africa, has been noted to change leaf inclination to manage water stress and light availability (Niinemets 2010), but the species does not change the physiology of its leaves in response to the light regime, as many shade-tolerant species do. As a consequence, quaking aspen probably exhibits less plasticity in the mass ratios of its component parts than many of the firs studied by Dean et al. (1988). Data on quaking aspen physiology is relatively scarce compared to other congenerics. As there has been relatively little published on the above-ground adaptability of quaking aspen to different water and light conditions, this area of study deserves more attention.

Kaufmann and Troendle (1981) presented leaf area - sapwood relationships from quaking aspen in Colorado, but did not report diameters for the stems measured. Assuming the range of diameters sampled was comparable, the leaf area estimates from that study and this one are at least on the same order of magnitude and range. In the most directly comparable study, Kaufmann et al. (1982) reported a leaf area – basal area relationship for destructively sampled aspen in Colorado. They reported a quadratic model for aspen leaf area as explained by basal area. Their results were complicated, however, by the fact that large aspen stems in different site conditions in their study appeared to exhibit very different basal area/ leaf area relationships. Two large stems on ‘moist south slopes’ have leaf area/basal ratios approximately four times that of three other stems in the same size range located in a cooler more xeric sites. The authors report that the stems on the xeric sites suggested a quadratic model form, and the other two stems a linear form to the model. They attributed that difference to water availability and excluded the two stems that suggested a linear model from their analysis. The quadratic model developed by Kaufmann et al. exhibited symptoms of over-fitting, however, and inspection of their graph suggests that an asymptotic model may have been more appropriate. That aside, it is unclear whether the linear model form that I report would hold for quaking aspen on xeric sites. As most quaking aspen stands in the Sierra Nevada are found on mesic sites, a linear model seems to best explain the diameter-SLA relationship for Californian aspen. Specific application of the pipe model theory indicates sapwood cross-sectional area would provide better predictions of tree leaf area. Sapwood/heartwood differentiation is very difficult in aspen and previous studies have used tree diameter or basal area. The difference in sapwood to heartwood ratios, particularly in larger trees, is a likely source of error in predicting leaf area using only basal area or diameter.

LAI for sites sampled was relatively low compared to reported from aspen sites in Alberta, Canada and Northern Wisconsin (Ruark and Bockheim 1988, DesRochers and Lieffers 2001a) which may lend support to the contention that some stands in the Sierra may be marginal for quaking aspen. Relatively low LAI values may indicate poor site quality that may not be able to support vigorous growth. Whether this is due to fire suppression (Romme et al. 2000, Shepperd et al. 2006, North et al. 2007), climate effects (Frey et al. 2004, Anderegg et al. 2012), or some other cause is unclear. It may simply be that sites in the Sierra Nevada, located at higher elevations on average and with lower water availability than those sampled by Ruark et al. and DesRochers and Lieffers, have always been marginal for quaking aspen (1987, 2001a). More data would thus needed if there is a convincing case that quaking aspen is under unusual stress on these sites. LAI and SLA, as well as the root/shoot ratio for the stand, would be excellent physiological metrics to compare in order to begin to make that case (Lieffers et al. 2001).

Modeling below-ground biomass based on above-ground data

Root biomass and distribution: the efficacy of GPR

Coarse root density (kg m^{-3}) was observed to peak in biomass at 20-30 cm below the ground's surface, with a monotonic decline in root density with increasing depth thereafter (Figure 9). GPR readings were able to obtain a reliable signal relatively deep in this ecosystem, reaching a median of 1.7 meters depth. In the Sierra Nevada, quaking aspen generally occurs on sites with fairly mesic conditions, and this was also the case in the sites sampled. Relatively superficial availability of water may explain some of this pattern of root concentration on the soil surface. Quaking aspen is generally considered a shallow-rooted species, with excavations in sites across North America confirming this root distribution (Shepperd et al. 2006). For example, excavated aspen in Alberta had root biomass only to 70 cm (DesRochers and Lieffers 2001a) while excavation of roots in Utah revealed the majority of the root biomass concentrated in the upper 1.5 meters of the soil (Gifford 1966).

Fine roots

Fine root biomass estimated at the stand level was comparable to other values in the literature (Vogt and Moore 1983, Gower 1987, Vogt et al. 1987). It was highly variable both within sites and between sites in Sierran ecosystems.

Model efficacy and comparisons to other studies

Based on this analysis above-ground metrics, particularly basal area and LAI, do provide useful empirical models for below-ground biomass. While sampling took place across a range of site conditions, there are likely regional and climatic effects that were not captured in this study.

A study of quaking aspen in Alberta, reported a strong relationship between leaf area and root biomass (DesRochers and Lieffers 2001a), which I also found on my sites in the Sierra Nevada. The slope of the models was quite different, however, at 3.58 in Alberta and 1.27 in the Sierra, an indication that the LAI: coarse root relationship, at least, is regional. More importantly, the relationship is probably dependent on the disturbance history of the stand, a stable relationship achieved between LAI and root biomass once the stand matures., The LAI present in quaking aspen immediately after stand-replacing disturbance is strongly influenced by stand health and carbohydrate storage prior to disturbance. DesRocher and Lieffer's study was in a stand that had recently undergone a stand replacement disturbance. Since sucker LAI and LAI of mature stems are probably differently related to root biomass (i.e. root biomass might in fact be a better predictor variable for LAI in recently-disturbed aspen stands) the relationship may not be comparable. As a result, the relationship in Alberta is more indicative of a stand immediately post-disturbance, that maintained much of its pre-disturbance root biomass.

Fine roots are consistently hard to estimate using above-ground metrics (Kurz et al. 1996, Vogt et al. 1996, Chen et al. 2004). Some new explanatory variables such as site class, and novel metrics such as a per-tree estimate of fine roots have been tried with greater success (Vanninen and Mäkelä 1999, Chen et al. 2004). The strength of the relationship between LAI and fine roots in these Sierran stands was thus unusual. A variety of above-ground metrics are used in the major studies on fine root modeling above, but LAI estimated from below-ground metrics has not previously been attempted. Two important factors in the strength of the leaf area to fine root model are the physiology of the species and the spatial and temporal availability of the water resources to the trees in the stand. The physiology of the species will affect the form and the coefficient of the model used; for example, in a species with poor regulation of water loss would expect to allocate relatively higher fine root biomass per unit mass of leaf area compared to a species with better regulation of water loss. The species' efficacy at water uptake, of course, would also affect that ratio.

If, however, trees on a given site are accessing groundwater at depths below those sampled for fine roots (often only sampled to 30 cm) then the function of superficial fine roots' principal on that site may be the uptake of nutrients from the litter and organic soil. In locations with seasonal precipitation, root distribution and physiology would be predicted to optimize needs across the year or multiple years. Whatever the case, understanding water availability in time and space should make significant progress towards landscape -scale empirical leaf area/fine root models when comparing the leaf area/fine root relationships of similar species.

Root/shoot ratio

The measured coarse root/shoot ratio for Sierran sites measured ranged from 0.3 to 1.9, with the highest ratio in a recently disturbed, nearly pure quaking aspen stand. In general, I found the highest root/shoot ratios in stands where aspen dominated by basal area, and where there had been recent disturbance. This is an expected consequence of quaking aspen's suckering regeneration strategy; aspen roots persist after disturbance when the above-ground parts of the stand may be destroyed. This surviving root system provides the regeneration mechanism and carbohydrate reservoirs for new suckers after disturbance (Shepperd and Smith 1993, Landhäusser and Lieffers 2002). Other studies have found similarly high or higher root/shoot ratios in aspen, particularly in stands with active suckering (DesRochers and Lieffers 2001a). The root-shoot relationship for aspen may also reflect the long-term carbohydrate balance in the stand, conifer competition and disturbance history, and the water balance for the whole aspen stand, as aspen roots graft (DesRochers and Lieffers 2001b, Di Orio et al. 2005, Rehfeldt et al. 2009, Anderegg et al. 2012).

Root biomass estimation and measurement continues to represent a significant challenge to measure and estimate in forested systems. The resources required to obtain unbiased data to a reasonable degree of precision are relatively large. In consequence these data are relatively limited. The methods used here support the utility of the new techniques and methods to measure and estimate root biomass. They also support the efficacy of modeling fine and coarse root biomass using above-ground data, as a way to further improve estimates of NPP and biomass at large spatial extents.

Conclusions

Aspen regeneration and stand health assessments

In California, quaking aspen has been the subject of considerable concern as a species potentially in decline as a result of climate change and fire suppression (Shepperd et al. 2006, Anderegg et al. 2012, Krasnow et al. 2012). Aspen, a shade intolerant, disturbance-adapted species is often overtopped by conifers in the absence of fire and clones may eventually become carbohydratestarved and unable to regenerate after disturbance (Bartos and Jr. 1998, Shepperd et al. 2001, Calder et al. 2011). Aspen roots in declining stands are observed to exhibit decay and decline in root shoot ratio as compared to healthy stands (DesRochers and Lieffers 2001b, Anderegg et al. 2012). Encroachment in aspen stands by conifers is easily observed using imagery or a standard timber inventory. GPR and biomass surveys will probably have less application in this field. The one exception might be an assessment of root biomass coupled with measurements of carbohydrate reserves in roots to determine whether aspen is likely to regenerate vigorously after disturbance.

Implications for modeling root biomass at the landscape level

Ground penetrating radar does appear to have applications for estimation and refinement of root shoot ratios, particularly in ecosystems where roots are fairly shallow. While GPR has limits in terms of the depth to which it can penetrate, it also has clear advantages in its non-destructive nature and potential to allow repeated measurements in the same area.

The strong relationship between aspen LAI and below-ground biomass lends support for modeling above- and below-ground relationships to arrive at better estimates of below-ground biomass and root/shoot allocation at the stand and landscape level. If a similar relationship could be developed for other forested ecosystems, it would provide a basis to improve these below-ground estimates across ecosystems. Challenges include the measurement or estimation of below-ground biomass of deeply rooted trees, as the theoretical lower limit for GPR measurement of something the size of a root is in the range of 4 meters deep in ideal conditions. There are also significant technical challenges to measuring LAI precisely with existing remote sensing techniques, or applying values estimated from direct measurement to a landscape scale (Asner et al. 2003, Bréda 2003, Potter 2012, Ganguly et al. 2012). Nonetheless, these methods provide advantages over excavation or the application of general root/shoot relationships based on very small, possibly biased samples. They also represent an opportunity to advance the field of allocation theory and estimates of the carbon reservoir in below-ground biomass. GPR scans should be used in combination with whole-tree root excavations and excavation at the plot level to overcome the shortcomings of each method used in isolation.

Quaking aspen leaf area shows good correspondence to both fine and coarse root biomass. Coarse root biomass is a key factor in aspen regeneration, and fine root biomass of key importance in water uptake and availability. The possibility of an assessment of root biomass using leaf area allows scalable assessments, from those based on ground-based measurement to those based on remotely-sensed imagery (Ganguly et al. 2012). These options add to the toolbox of land managers and those interested in forecasting the future effects of climate changes in the Sierra Nevada. In order to use this information to inform management decisions, it will be important to create or adapt existing models for leaf area-based assessments and integrate these diameter/leaf area models with those for Sierran conifers (O’Hara et al. 1999, Gersonde et al. 2004).

Figures and Tables

site	Management history	latitude	longitude	soil order	suborder	mean elevation(m)
BM	Restoration thinning	39.41	-120.18	Alifisols	Xeralfs	1700
LYBLM	Unmanaged	39.67	-120.15	Mollisols	Xerolls	1670
SAG	Unmanaged	39.43	-120.28	Alifisols	Xeralfs	2500
SN	Unmanaged	37.61	-118.83	Mollisols	Xerolls	2200
SPI	Timber	39.47	-120.52	Inceptisols	Unbrepts	2100

Table 1: Sampling locations.

Tree	leaf area - diameter	leaf area - csa	tree height (dm)	base diameter (cm)	DBH (cm)	Diameter BLC (cm)	Diameter 1/3 height (cm)	Diameter 2/3 height (cm)
1	4.06	7.91	90.22	12.80	14.02	10.06	7.62	3.35
2	34.73	34.46	29.60	41.10	31.60	23.90	20.40	10.60
3	36.78	41.52	13.05	30.70	24.20	19.60	14.80	4.00
4	22.97	25.66	12.08	23.20	15.60	15.50	9.40	5.80
5	15.57	15.29	9.23	16.60	13.20	13.20	10.40	4.80
6	8.34	8.53	8.50	13.90	10.90	10.70	7.75	3.50
7	21.42	23.82	14.00	21.30	18.20	17.30	9.60	3.90
8	10.76	10.37	80.30	19.40	12.60	9.90	1.20	4.30
9	22.88	21.79	127.00	27.10	21.60	14.30	10.20	5.10
10	22.04	20.63	143.00	31.40	19.70	14.20	10.30	5.80
11	10.98	10.82	130.60	20.60	13.60	10.50	8.00	4.60
12	124.81	124.81	55.60	55.60	44.00	24.20	15.10	NA

Table 2: Compiled tree-level data used to develop leaf area models. This is the aggregated, tree-level data compiled for individual trees. Data in leaf-area diameter and leaf area csa columns is estimated from branch cross-sectional area to branch leaf area models developed as a part of this study. Other data presented were directly measured.

	Adj. R^2	DF	SE(m)	Intercept	slope	p-value
SLA	0.93	91	0.2929	0.021	8.77	2.00E-16

Table 3: Specific leaf area (m^2kg^{-1}) for sampled stems.

	Adj. R^2	DF	SE(m)	Intercept	slope	p-value
Leaf area~CSA	0.89	10	0.0049	-2.065	0.05	2.57 E-06
Leaf area~ DBH	0.82	10	0.4257	-31.950	3.05	3.07E-05
Leaf area~ d.BLC	0.56	10	1.2600	-45.680	4.88	0.00318
Leaf area~ DBH w/o stem 12	0.68	9	0.3193	-6.380	1.49	0.00117
Leaf area~CSA w/o stem 12	0.60	9	3.1662	7.175	0.03	0.00127

Table 4: Tree-level models for leaf area. All models are in terms of leaf area in meters squared. The three independent variables are diameter at breast height and diameter at base of the live crown for all stems, and diameter at breast height with stem 12 removed from the analysis. All independent variables are in terms of cm.

	Adj. R^2	DF	SE (m)	Intercept	slope	p-value
Leaf area ~ CSA	0.538	75	0.0053	0.12	0.05	1.95E-14
Leaf area ~ branch diameter	0.553	75	0.0030	-0.31	0.029	5.46E-15

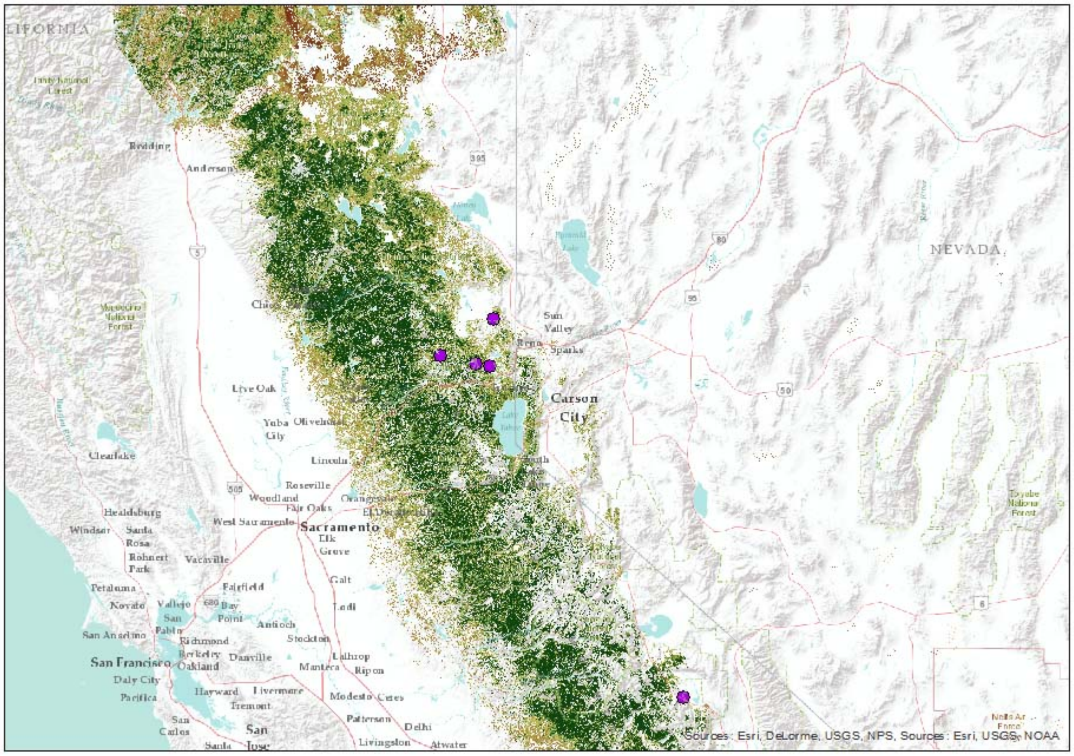
Table 5: Leaf area models at the branch level. All models use leaf area in terms of meters squared as the dependent variable. The independent variables are branch cross-sectional area and branch diameter, respectively. They are in terms of cm^2 and mm, respectively.

Plot	LAI
1	1.047458
2	1.64398
3	2.216311
4	2.21727
5	2.518608

Table 6: LAI for five aspen stands mean = 1.9, sd=.59.

model	adj.r2	p value
Coarse Root~LAI	0.9718	0.00131
Coarse Root~basal area	0.896	0.00267
Fine Root~coarse Root	0.8405	0.00639
Fine Root~basal area	0.6185	0.00728
Fine Root~LAI	0.5895	0.00955

Table 7: Model significance and fit for fine and coarse roots to selected above-ground metrics.



Sources: Esri, DeLorme, USGS, NPS, Sources: Esri, USGS, NOAA

Figure 1: Plot map of sampled Sierran stands.

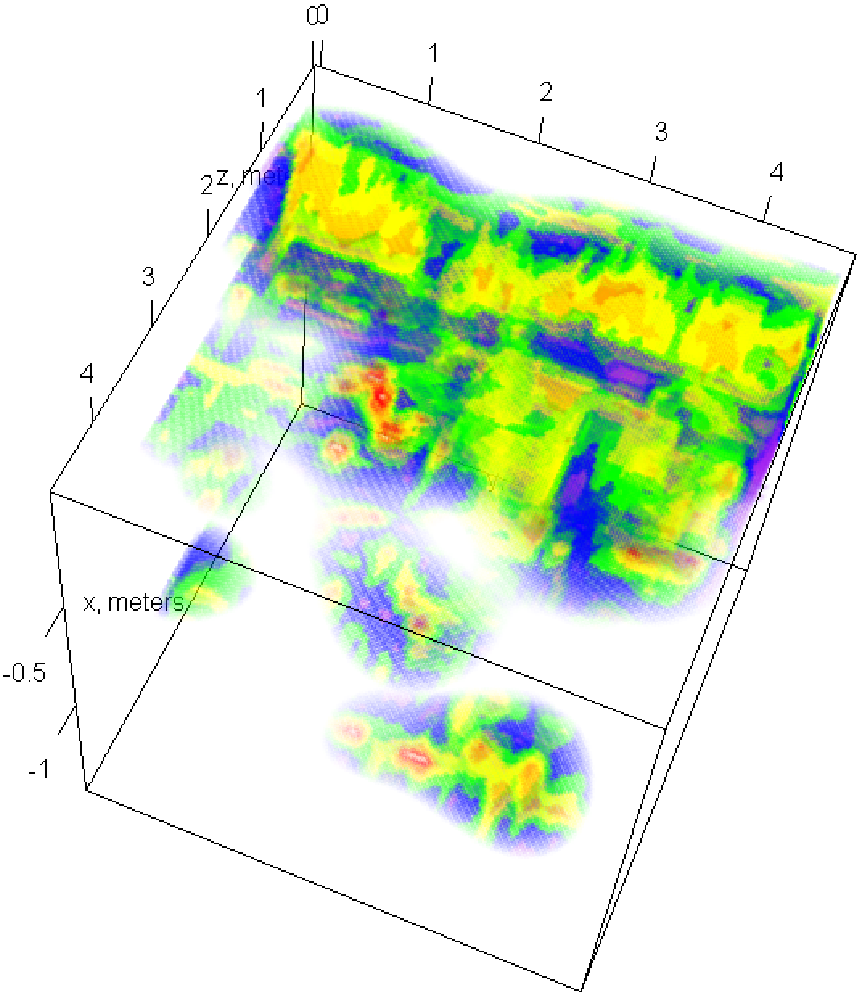


Figure 2: Enhanced three dimensional plot of GPR radar returns.

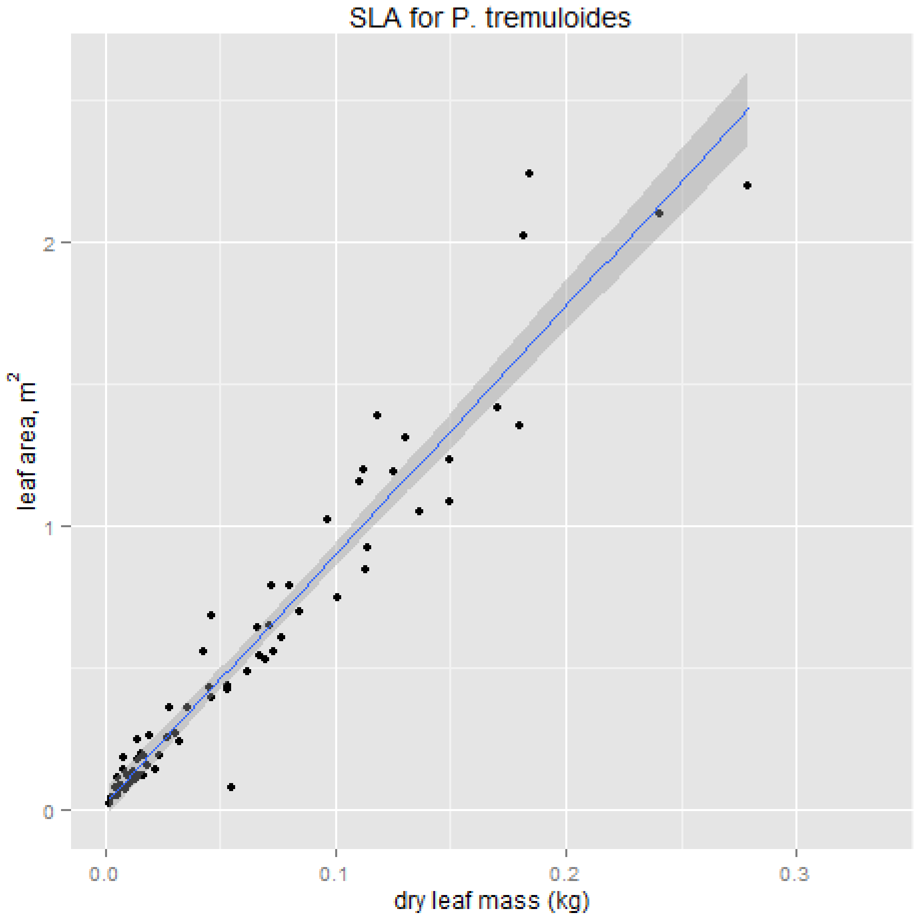


Figure 3: Specific leaf area for *P. tremuloides* found for sampled stems. Modeled relationship is a linear OLS model. Confidence bands are set at 95% se of the estimate. Model parameters are found in table 3.

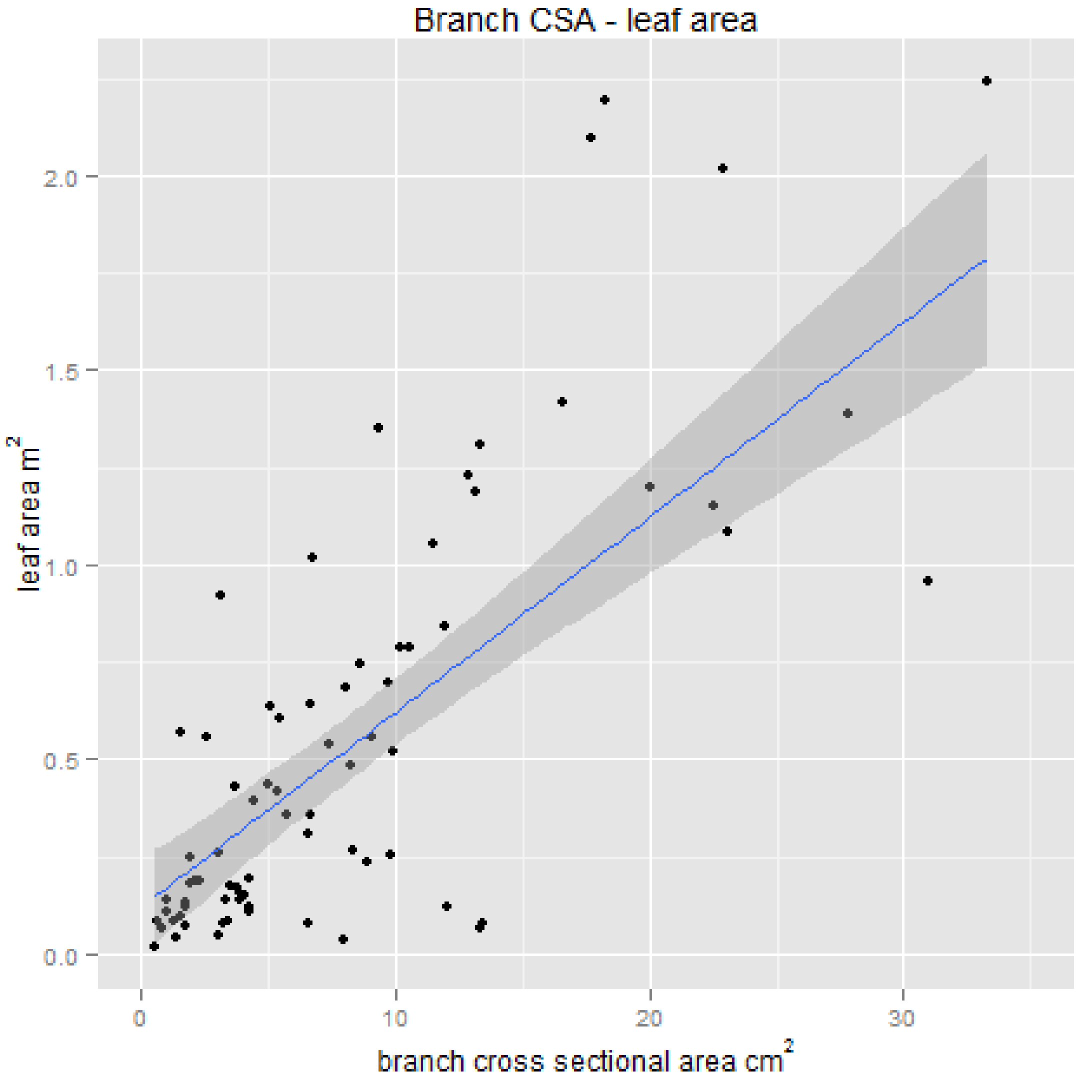


Figure 4: Branch cross-sectional area and leaf area modeled. Modeled relationship is a linear OLS model. Confidence bands are set at 95% se of the estimated slope. Model parameters are found in table 5.

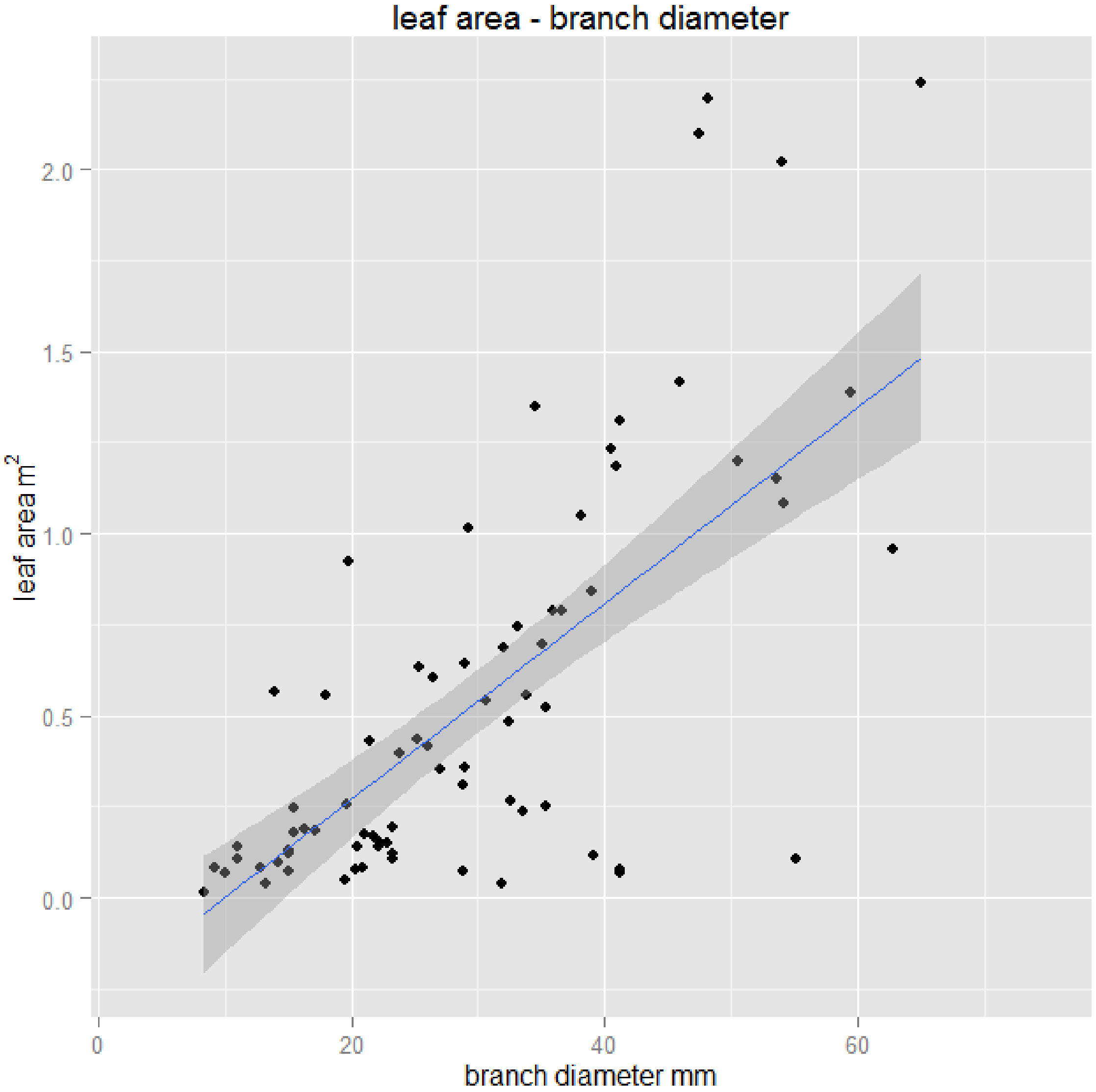


Figure 5: Branch diameter and leaf area relationship for all sampled branches. Modeled relationship is a linear OLS model. Confidence bands are set at 95% se of the estimated slope. Model parameters are found in table 5.

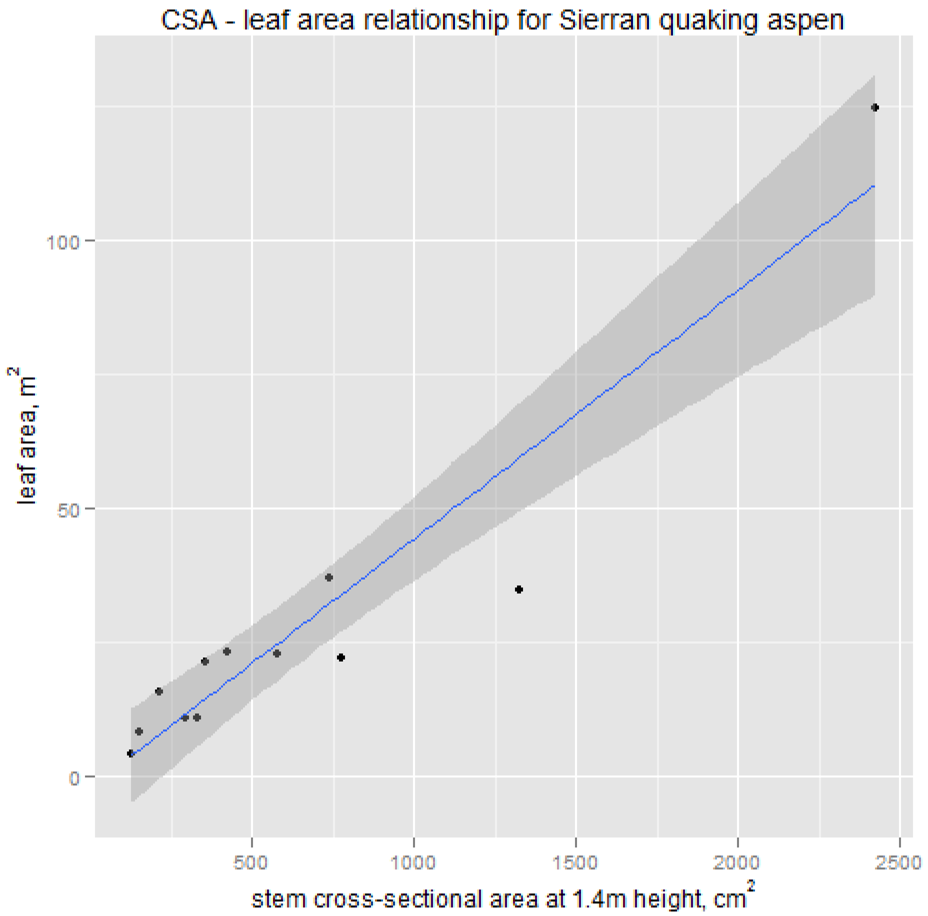


Figure 6: Tree-level leaf area~ cross-sectional area relationship. Modeled relationship is a linear OLS model. Confidence bands are set at 95% se of the estimated slope. Model parameters are found in table 4.

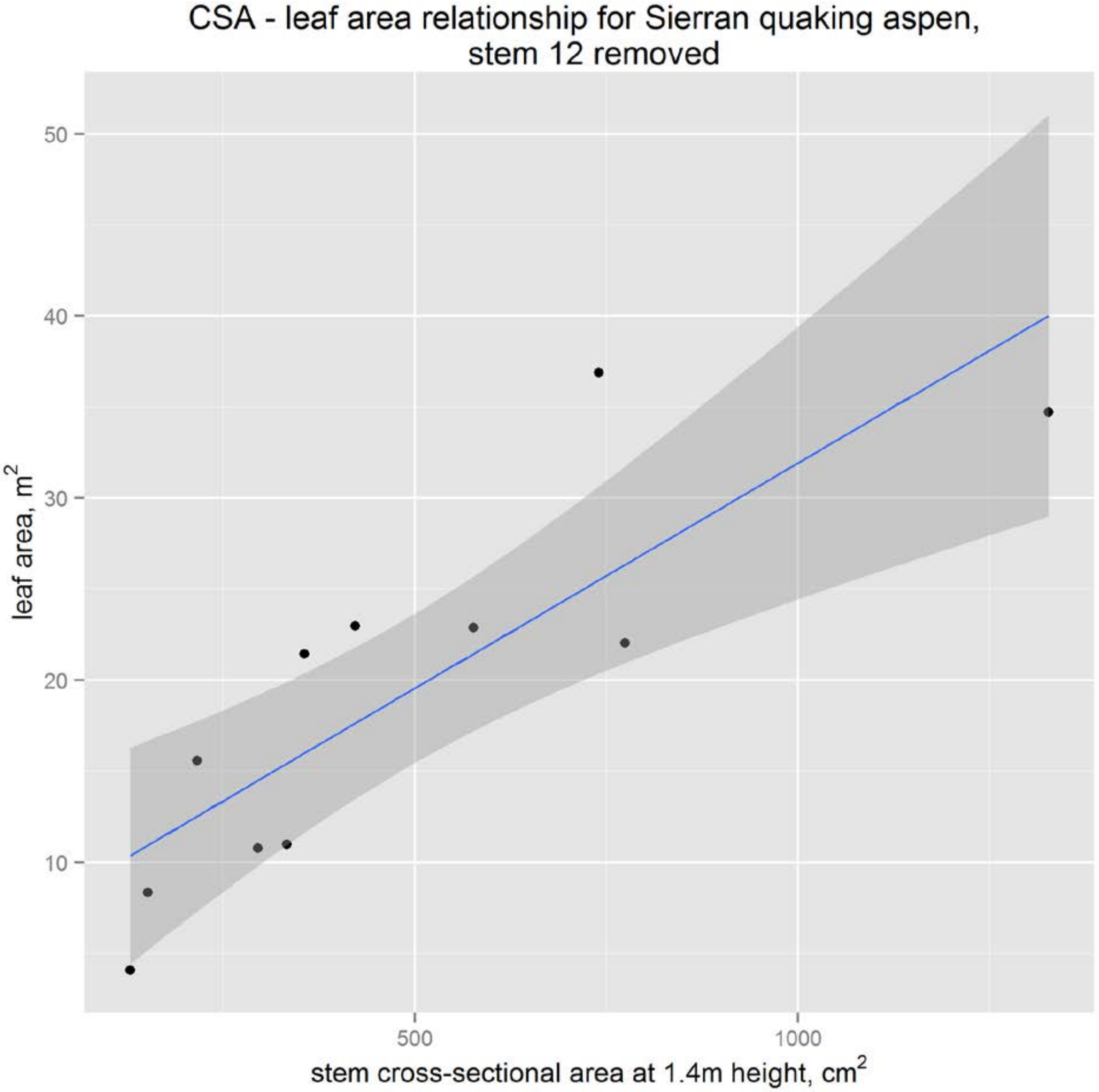


Figure 7: Tree-level cross-sectional area and leaf area relationship without stem 12. Modeled relationship is a linear OLS model. Confidence bands are set at 95% se of the estimated slope. Model parameters are found in table 4. Stem 12 was the largest stem sampled in the study.

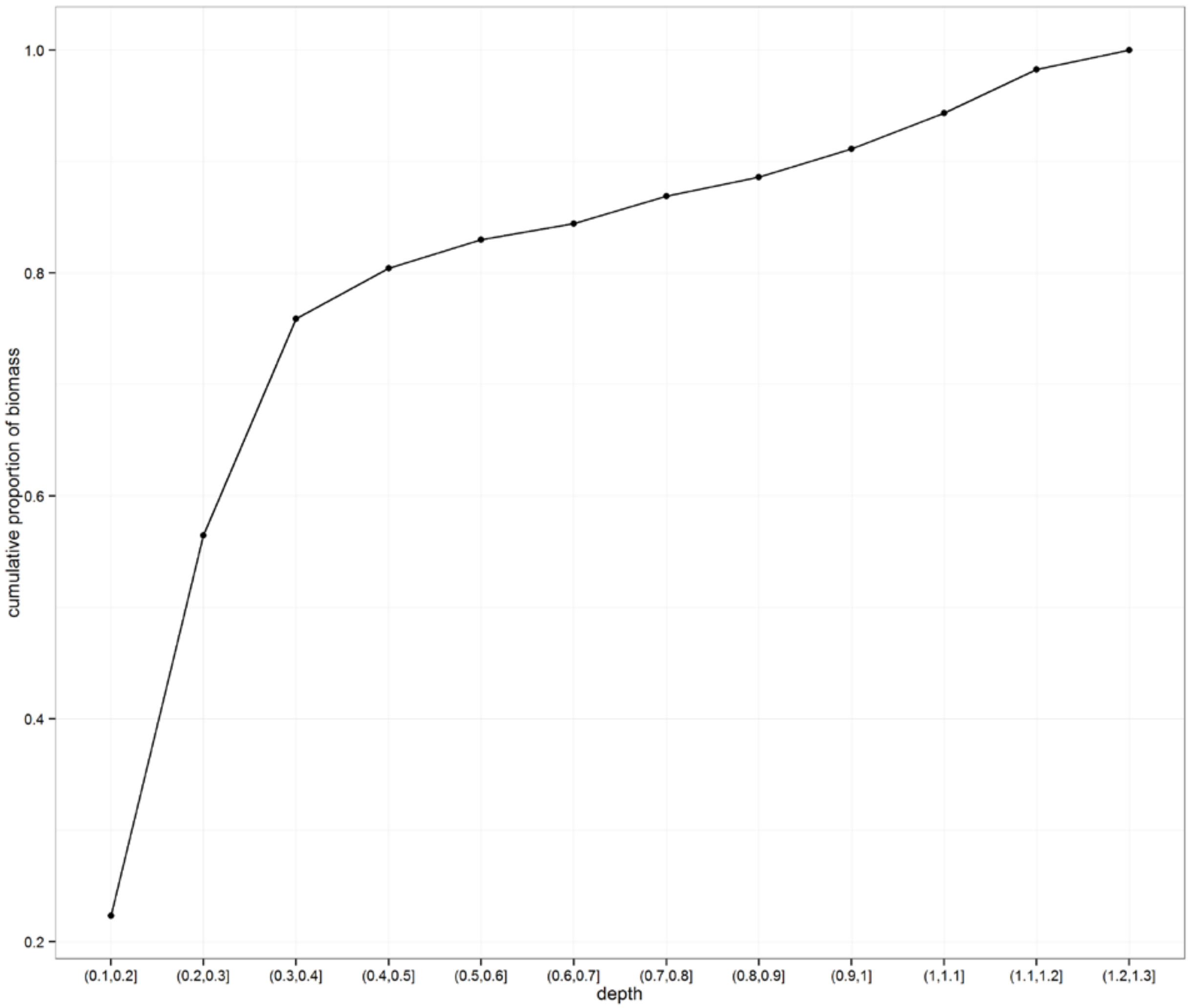


Figure 8: Cumulative proportion of biomass by depth.

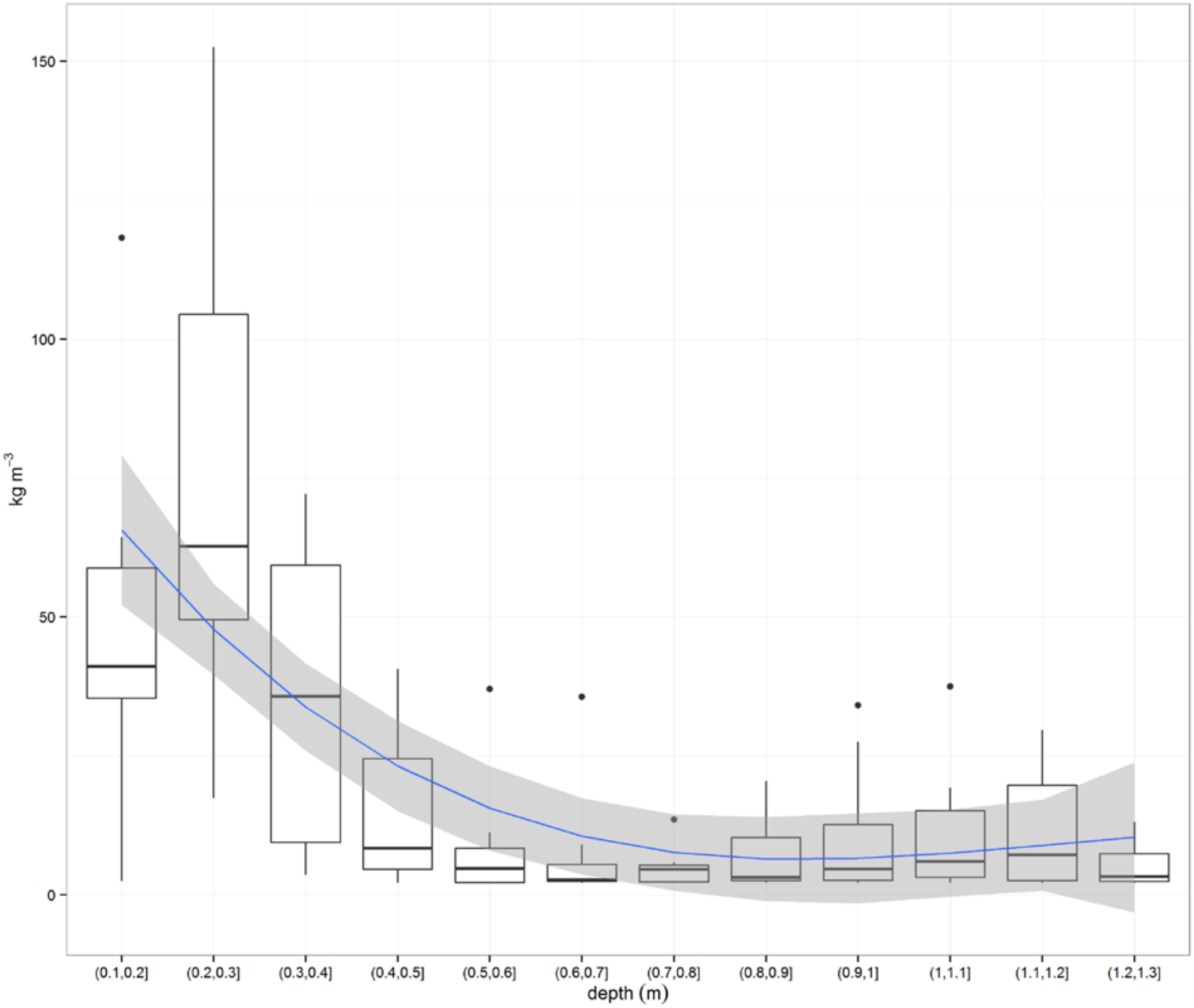


Figure 9: Coarse root density estimated from GPR returns by depth.

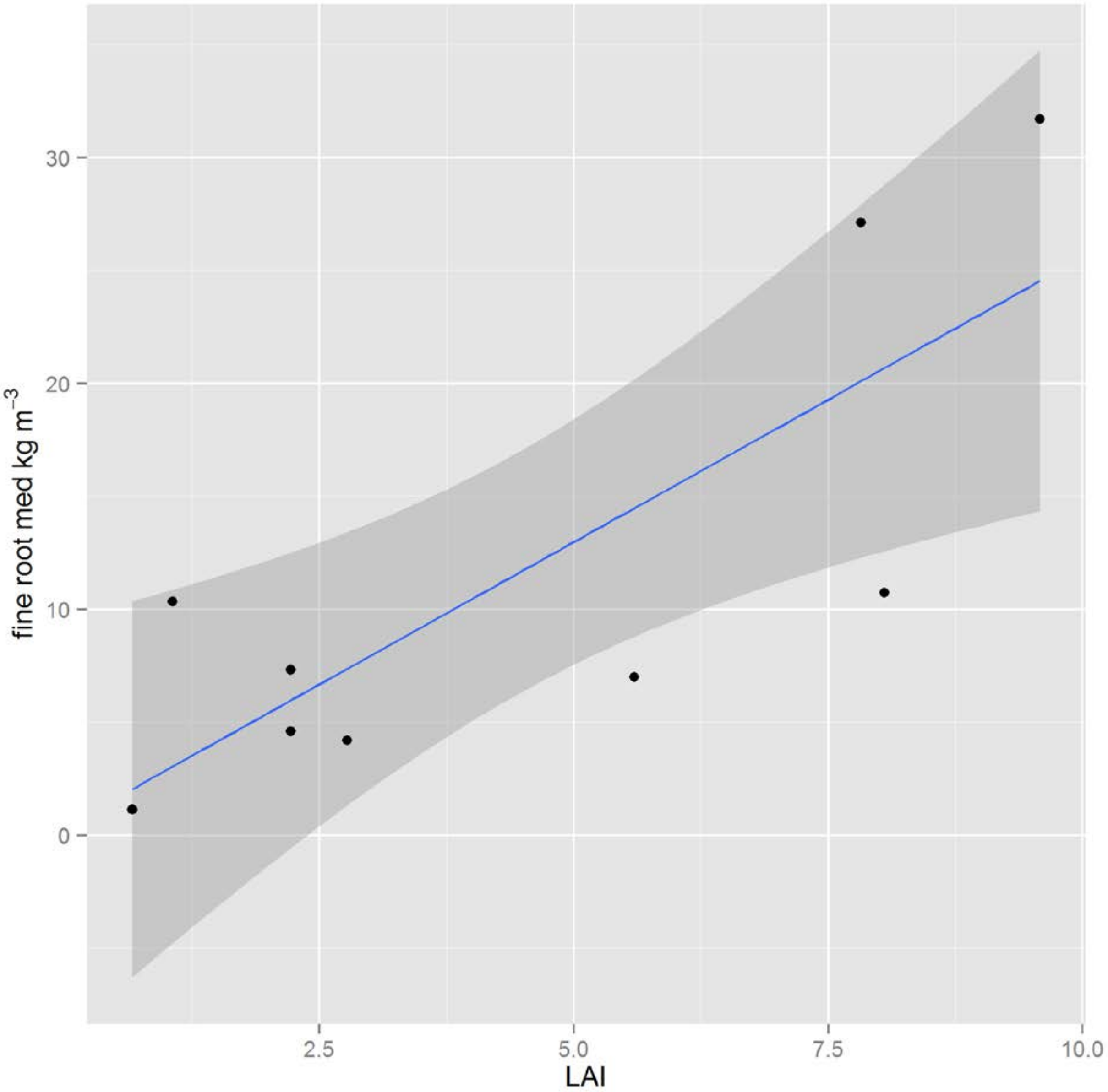


Figure 10: Model for fine root biomass density based on LAI. Adj. r^2.59, p=.01.

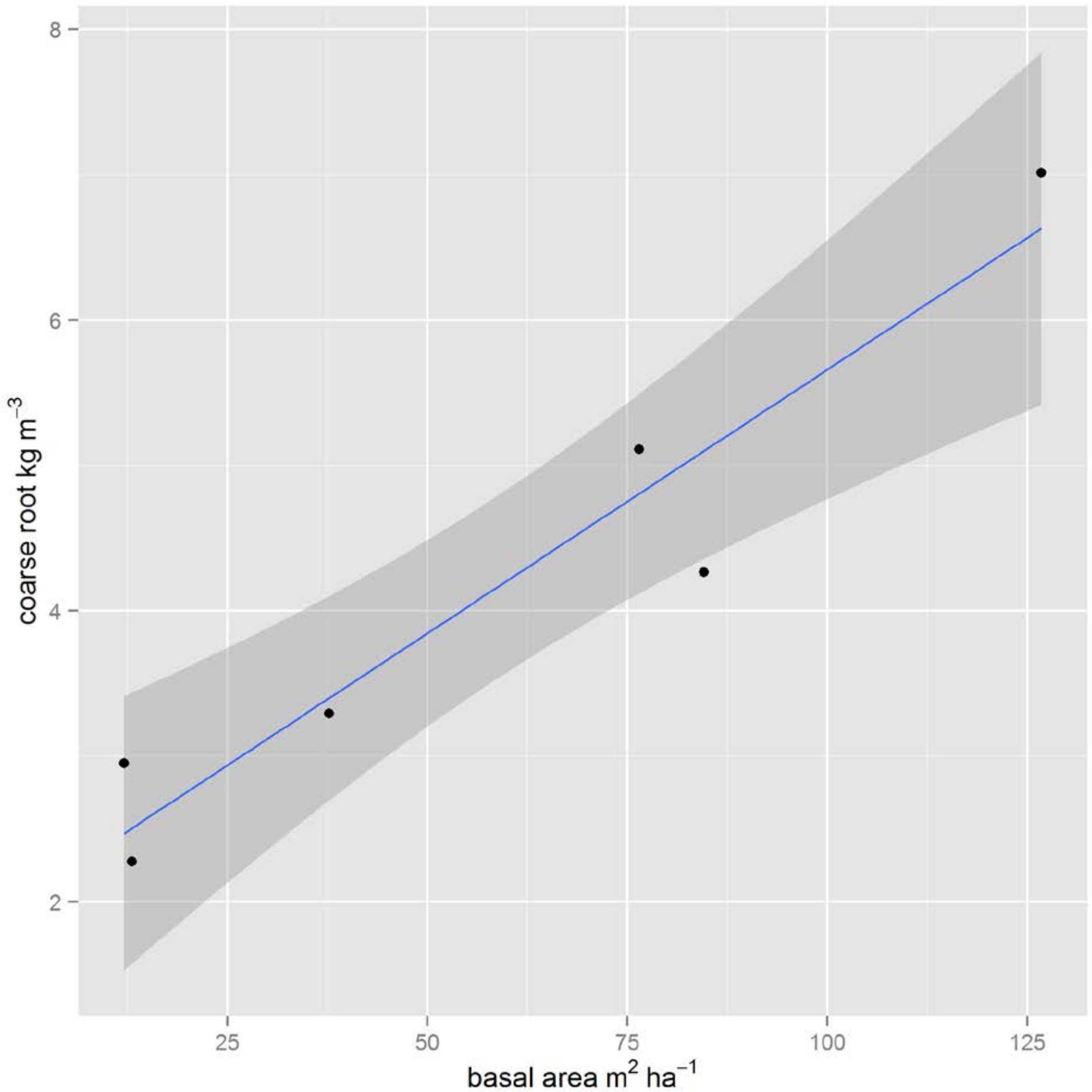


Figure 11: Model for coarse root biomass density based on basal area. Adj. r^2 .9, p = .002.

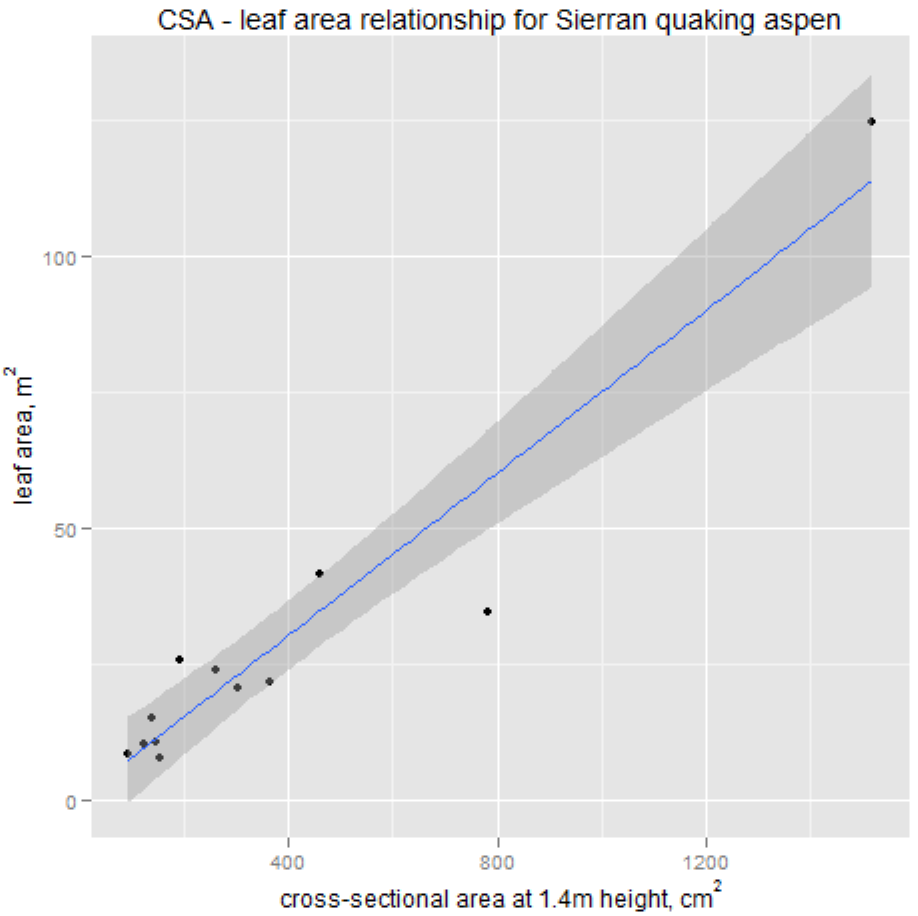


Figure 12: Tree-level leaf area ~ CSA at breast height relationship. Modeled relationship is a linear OLS model. Confidence bands are set at 95% se of the estimated slope. Model parameters are found in table 4.

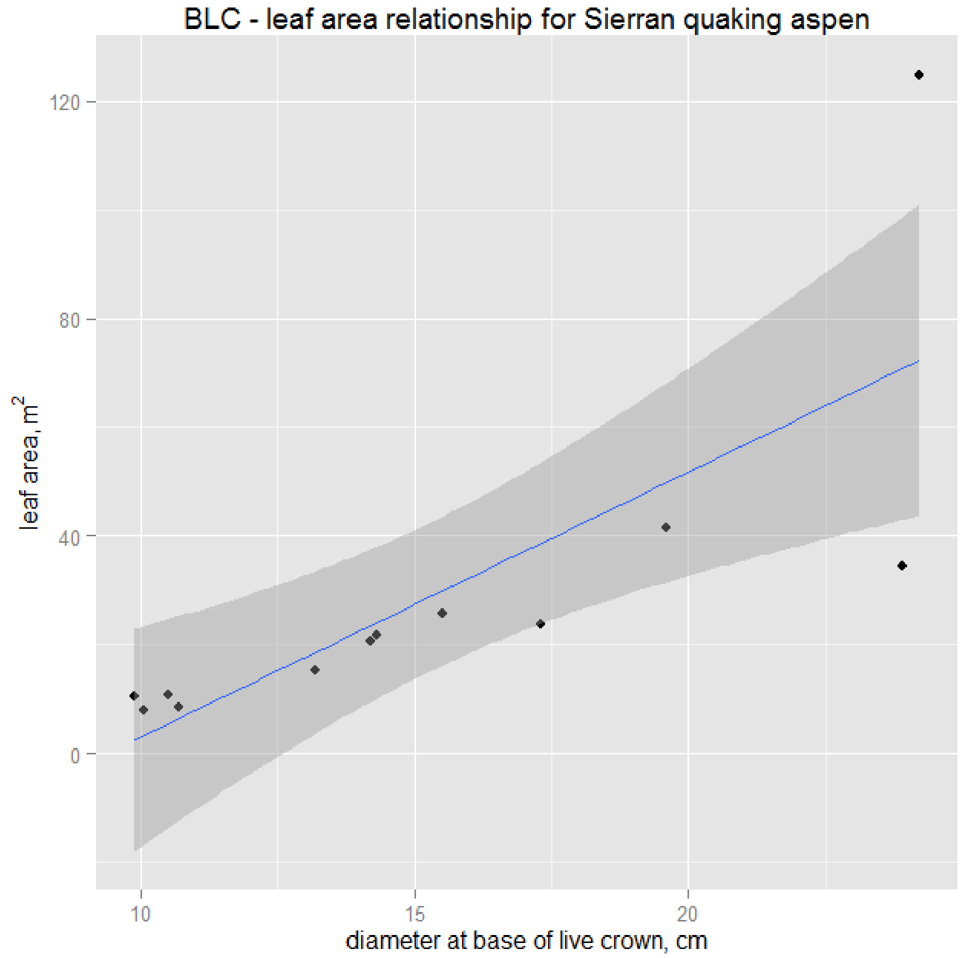


Figure 13: Base of live crown (BLC) to leaf area relationship. Modeled relationship is a linear OLS model. Confidence bands are set at 95% se of the estimated slope. Model parameters are found in table 4.

2 Water relations and root distributions in coast redwood ecosystems

Introduction

Coast redwood (*Sequoia sempervirens* D. Don) is the iconic tree of California. Superlatives for the species are many, but the first mentioned is often that the tallest tree is a coast redwood (Van Pelt 2002). Coast redwoods are the only hexaploid conifer, one of four surviving narrow endemic species of a once more extensive family (Ahuja 2008). The species' oldest specimens are large enough and structurally complex enough to support extensive epiphyte and faunal biomass in the canopy, which is rare in temperate forests (Sillett and Van Pelt 2007). It is little wonder then that attention on these majestic trees has focused on the above-ground components; the size, appearance, and value of the bole and branches have few parallels.

While the above-ground organs of coast redwood are deserving of the attention received, the complete story for the species includes the below-ground organs, the fine and coarse roots and burls. Coast redwood is known for its prolific success as a vegetative regenerator, which affords it exceptional ability to persist and survive after disturbance (Ramage et al. 2011). Indeed, a single redwood clone is apparently able to persist almost indefinitely in a single location by resprouting after an assortment of disturbances (Tredici 1999). Taken with its long life, and the low viability and limited dispersal ability of its seeds (Olson et al. 1990), coast redwood's ecological niche can be aptly described as that of persistence, *sensu* Bond and Midgley (2001). Observed on the scale of human lifetimes, coast redwood seems almost indestructible, able to recover from severe fires that burn all the foliage on a stem (Ramage et al. 2011), floods which partially cover the bole with sediment (Zinke 1988), and logging and complete removal of the stem (Olson et al. 1990).

At the end of the 19th century redwood's primary threat in its native range seemed to be from logging and demand for its valuable wood (Ingersoll 1883, Tredici 1999). Today, however, a rapidly changing climate and a dryer California will likely put severe stress on coast redwood, which is a highly water-demanding species (Johnstone and Dawson 2010, Limm et al. 2012). Locations that were historically suitable for coast redwood may no longer support these majestic stems, and there is thus considerable interest in determining where the species may come under threat of extirpation.

To understand the potential of coast redwood to access subsurface water and its ability to sprout after disturbance, it is important to better describe the roots, which have received relatively little attention to date. While believed to be widely and shallowly rooted, with no taproot (Olson et al. 1990), there is little to no data on the extent, biomass, or depth of coast redwood root systems. Published descriptions of coast redwood roots are limited to Fritz's description of a root system partially uncovered when the parent stem fell over (Fritz 1995), published as a pamphlet by the Save the Redwoods League, and a page in Zinke's chapter on coast redwood (1988). The diagrams from these authors are of fairly large root systems, incorporating the legacy of the stem's submersion under sediment and subsequent root re-sprouting.

Fritz (1995) describes the root system of a stem that was approximately 1200 years, old located in the Richardson grove on alluvial flats. The stem fell naturally in 1933, in the process upturning much of root system and exposing it to inspection above ground. Fritz estimates that the root system extends to 14 feet below the surface, with a strong legacy of successive burial by flood silts, followed by re-sprouting of the root system at the new level of the soil. What is on first inspection structurally similar to a taproot Fritz describes as the dead stem at the original level of the ground, 11 feet below the surface. This implies that dead buried wood from this tree had resisted decay for over a millennia. The living and functional root system depicted in the diagram is connected to the main bole between two and six feet below the soil surface. Zinke's (1988) description is of stems in Rockefeller forest, but it is unclear from the text or the diagram how the roots were uncovered or examined, and gives no depths or scale for the root systems. He also describes root generation at the new level of the soil after partial stem burial by flooding, referencing Fritz (1995).

Description of redwood roots is thus quite limited. We have available to us only two descriptions, both quite terse, of five coast redwood stems found on alluvial soils. The authors' primary conclusion is that redwood generates new roots in response to flooding. The major inference is that redwood is fairly shallowly rooted, with a very limited below-ground biomass compared to the stem. However, since the sample size is so small, and not representative of up-slope or mid-slope coast redwood, it cannot be said to be representative of the species. A more complete description of coast redwood roots would therefore be an interesting complement to the comparative wealth of information on above-ground organs, and would provide some needed information for the discussion on redwood conservation. I predicted that redwood stems on mid-slope positions will have structurally different root systems than those on alluvial soils, as upslope stems will not be subject to the same flood disturbance. Also, stems on these higher slope positions may have deeper roots in order to anchor the stem on steep hillsides and access deeper subsurface water.

Methodological approach

Linking below-ground to above-ground components

The premise of this study is that above and below-ground tree organs are linked, and that the characteristics of one should predict the other, given other important covariates. This is supported by the pipe model theory, which provides a formal mathematical relationship and mechanism for relating leaf area to sapwood cross-sectional area. Since the water resource carried to the leaves comes, to a large extent, from the roots, it follows that both root and leaf area should be predictable based on each other and on sapwood area. In coast redwood, leaf area is predictable from sapwood area (Stancioiu and O'Hara 2005a). Such a model has not been described for coast redwood roots, however.

This study undertook measurement and description of coast redwood roots to augment the limited information available, and test the viability of sapwood-root models. Relatively new methods of measurement and modeling roots were attempted to determine their utility in these systems.

Root estimation using ground-penetrating radar (GPR)

Direct measurement of below-ground biomass is difficult, particularly for larger tree stems. It is time consuming, particularly if roots must be excavated. Moreover, excavation is fatal for the stem excavated and destructive to the site where the measurements are made.

However, there have been a series of recent methodological advances and new approaches to root biomass measurement (Nadezhdina et al. 2003, Zenone et al. 2008, Ellis et al. 2013). Among them, ground penetrating radar (GPR) has generated considerable interest as a tool for the measurement of roots in forest systems. The use of GPR has a long history in geophysical studies and archeology. In these applications, its uses have varied from detection of the thickness of ice to the determination of the edge of buried artifacts (Daniels 1996, Conyers and Goodman 1997). GPR is based on detection of differences in dielectric conductivity between substances. As electromagnetic waves pass through a medium, a portion of those waves emitted from the radar are reflected to the receiver. The speed and relative intensity of the returns can then be used to determine the size and location of objects located in solid materials such as soil, rock, and ice (Daniels 1996). GPR has been applied to the measurement of root biomass in pine plantations in the southeastern United States (Butnor et al. 2003, Stover et al. 2007) and Hawaii (Samuelson et al. 2010). It has also been successfully employed in estimating below-ground biomass in a California oak savanna system (Raz-Yaseef et al. 2013). Although it has limitations related to slope, soil types, and measurement depth, ground-penetrating radar does permit non-destructive measurement of the roots of large trees. Methods and approaches for root measurement with GPR are still being developed, with previous research on this topic concerned with the goodness of fit of direct biomass measurements and radar returns (Hruska et al. 1999, Butnor et al. 2001, 2003, Fourcaud et al. 2002, Nadezhdina et al. 2003, Barton and Montagu 2004, Stover et al. 2007, Zenone et al. 2008, Hirano et al. 2008, Samuelson et al. 2010, Hebsur et al. 2010, Ehret 2010, Raz-Yaseef et al. 2013). The approach used in these studies has been to couple root cores or root biomass excavated from trenches with radar returns collected from the same location. Regressions are then fitted to determine the viability of a method for a given site, and to determine the relationship of root biomass to radar returns (Butnor et al. 2003, Hirano et al. 2008, Raz-Yaseef et al. 2013).

A new approach to root measurement with GPR

I built on this work in three novel ways. First, my study involved two different soil types that have not yet been investigated for root density using ground-penetrating radar. This both broadens the scope of ecosystems that have been successfully measured using GPR, and allows me to refine techniques that may be generally applicable for all sites. Second, I present here a new metric for the radar/root relationship that is both more flexible and allows the user to optimize a root/biomass regression across sites and plots. Third, software for three-dimensional interactive visualization of GPR returns is not widely available. I used open-source software to create interactive representations of GPR data in 3 dimensions. I also used generalized additive models (GAMS) to smooth radar data and make objects, such as root structures, more discernible to the human eye (Wood 2011).

Methods

Site selection and below-ground measurements

Measurements took place in the summer of 2011 and 2012. Fixed- radius measurement plots were established in forested in the North Coast of California in coast redwood forests (35- 65 kilometers inland, on average). Plots ranged from 0.02 to 0.10 ha in area, scaled to the height of the dominant stems on the site. All trenches and GPR grids were placed within the fixed-radius plots.

Sampled coast redwood stands had a history of timber management, as is characteristic of the majority of coast redwood forests in California. Sites were located based on access and permissions, and covered a representative range of soils, elevations, and management histories (table 1). The oldest coast redwood site sampled received a selection cutting in 1940, while some plots were in stands thinned as recently as the 1990s. Each plot center was recorded used a WAAS-enabled GPS and marked with a tree tag. In each plot sampled, diameter at 1.4 meters (dbh) for all stems was measured using a diameter tape to the nearest tenth centimeter. Stems were mapped using a laser rangefinder with a digital compass (LaserAce^{TM}). For a subset of stems, heights and height to the base of the live crown in units of 0.1 meter was also measured using the same instrument. Stems included in the subset were selected randomly, with at least five sampled in each plot. If there was a high degree of variance observed in the crown heights or diameter-height relationship, additional height measurements were taken as time in the field allowed. Sapwood measurements were taken using an increment borer on a subset of the coast redwood stems to the nearest mm. Bark thickness measurements were taken using a bark gauge to the nearest mm.

Coarse root biomass

Ground-penetrating radar measurements correspondence to directly measured root biomass was used to increase the volume of soil explored for roots and to reduce destruction of the site that would otherwise be necessary for root biomass measurement. Rectangular grids for GPR measurement were laid out within each plot, with at least one per plot and as many as four in larger plots. Two antenna amplitudes were used in the course of sampling; one emitted at a frequency of 1000 MHz and one at 450 MHz. Regular intervals were marked on the grids, ten cm apart for the 1000 MHz radar and 25 cm apart for the 450 MHz radar antenna used. These were the end points for transects within the grid. A representative grid can be seen in Figure 2. The GPR, a Noggin SmartTow™ (Sensors and Software Inc., Ontario CA) was then pulled across transects, and data collected as a grid using the commercial software bundled with the GPR (Sensors and Software 1999). Sensors and Software's software was used in the field to apply autogain (inverse decay of the GPR signal for a given depth), and determine the speed of the signal for a given site to determine the depth of a reflector. Those transects were used to locate objects and confirm that they were roots. Use of grids and transects also aided in the interpretation of the measurements.

After radar surveys, one to two trenches were excavated beneath each area surveyed. Trenches were excavated by hand, and measured approximately 30W x 60D x 200L cm unless a rock layer impenetrable using hand tools was encountered (n=2). The exact measurements for each trench were recorded using a tape measure at multiple locations in the trench. In each trench, the excavated trench was divided into two layers based on depth, divided at the mean depth for the trench. For each layer, all excavated material was placed on a tarpaulin. Coarse roots (>5mm diameter) were hand-separated and place in sealed plastic bags. Bags were placed on ice, and returned to the lab for drying and measurement.

Directly measured root biomass

On return to the lab, roots were placed in a freezer for storage. Afterwards, coarse roots were oven-dried to a stable mass at 70^{O} C and the dry biomass recorded. Using volume for each trench and the dry biomass, I calculated biomass density for each trench and depth.

Fine roots

Fine root biomass was estimated in each plot using root cores. Multiple cores were taken on each plot. Core contents were stored in a freezer in sealed bags. Root biomass was extracted following methods in Metcalfe et al. (2007) and fully described in Chapter 1.

Modeling and analysis

Basal area per hectare for each plot was calculated using the diameter measurements for the stems in each plot. Sapwood area at breast height was calculated as the remainder of stem cross-sectional area after subtracting bark and heartwood area for coast redwood stems with a sapwood measurement.

Leaf area at the tree level was estimated using allometric regressions constructed from direct measurement of leaf area (Watson 1953). The estimation approach that was taken balanced the accuracy of sapwood area-based leaf area estimation with the increased measurement efficiencies of allometric relationships based on basal area. Site-specific redwood sapwood area to leaf area relationships were readily available (Stancioiu and O'Hara 2005a). Sapwood is readily distinguished from heartwood in the field for coast redwood. Accordingly, I measured sapwood area for a subset of the coast redwood stems. For the remainder of the stems in the study I used basal area-based allometry available in the literature to estimate leaf area (Kaufmann and Troendle 1981, Gersonde et al. 2005). If the tree was a coast redwood and sapwood measurements were available, I used sapwood area as the independent variable to estimate leaf area. If the tree was coast redwood and sapwood measurements were not available, I used a site-specific linear model developed from this dataset. To fit this model I used the leaf area estimated from the sapwood to leaf area model as the response variable, and basal area as the predictor (n=180, adj. r^2=.86 for the pooled data). Because the linear model had a negative intercept and the sapwood/leaf area estimate exhibited nonlinearity at the lower end of the diameter range, a logistic model was used for the lower end of the range of diameters (stems with a diameter of less than 14 cm), a piecewise model.

In order to compare above ground to below-ground biomass, above ground biomass was also estimated at the plot level. To avoid destructive sampling, estimation used species-specific equations for the appropriate forest inventory and analysis national program (FIA) super section (Jenkins et al. 2003, Woodall et al. 2011). These equations are diameter and height-based. As I did not have heights measured for all stems (n=802) heights for a subset (n=263) were estimated with species-specific regressions using basal area as the predictor from trees measured in this study.

After these measurements were taken and metrics estimated as necessary, correlations between a matrix of basal area, LAI, coarse root biomass, and fine root biomass were investigated using the lm() package in R base (R Development Core Team 2013).

Multivariate models to predict fine and coarse biomass by species class were tested, and most significant variables used to reduce the models to ones with the best predictive power. Linear relationships were explored between variables of interest using visual inspection of the data to remove outliers and determine whether the assumptions of OLS regression were met (Quinn and Keough 2002). R base and the ggplot2 package were the primary tools used for this analysis (Wickham 2009, R Development Core Team 2013). Once the model form and assumptions were confirmed, adjusted r^2 and p values were used to assess the utility and significance of tested correlations, again using lm() in R base. First-order polynomials were found best explain the relationship between tested dependent and independent variables, and were used throughout the analysis. In all cases, there was a single strong predictor that was used in the best model.

GPR data

Coarse root biomass was estimated by regressing directly-measured root biomass from the excavation of trenches on radar returns from a ground penetrating radar. Once this regression was constructed, the scans from the radar could be used to determine mean biomass per unit soil volume in a much more extensive area within each plot than would have been possible via excavation. The entire sub-surface area of each plot was not scanned, but that area scanned from the radar grid or grids measured in each plot was extrapolated to the plot level to estimate the plot-level below-ground root biomass per unit volume (root density).

In addition to the signal processing applied in the field, data was post-processed for low frequency noise removal (DEWOW) and to further enhance the signal using a Fourier transformation (Bandpass) (“EKKO View Enhanced” 2012). Individual depth slices were then exported as .csvs to facilitate import into R (R Development Core Team 2013).

In an R environment and using functionality from the ggplot2 and plyr packages in R, I wrote scripts to plot slices of radar returns for each grid (Figure 5) (Wickham 2009, 2011). These were useful aids in determining the greatest meaningful depth for each site (defined as the greatest depth to which a meaningful radar return was obtained) and in eliminating spurious readings (typically in the first 10-15 cm in each site, caused by poor coupling between the radar and the soil surface) (Daniels 1996). In addition to these graphs, I used standard histograms to compare the distribution of amplitudes in the horizontal and vertical dimensions to the 2-dimensional plots of the radar returns.

I also wrote scripts in R to visualize radar returns in the three spatial dimensions and return amplitude (Adler and Murdoch 2013). Because GPR best detects objects with a primary axis perpendicular to the radar transect, there are often missing data between high-amplitude returns (Butnor et al. 2001, Raz-Yaseef et al. 2013). To better visualize that missing data and map root nets, missing data between high-amplitude returns was interpolated using a spline smooth in the R package mgcv (Wood 2011) (Figure 7).

GPR and coarse root biomass prediction

Data from root excavation was regressed to radar data for each site. GPR data exist as an amplitude at a given location in space, constrained by the dimensions of the grid, the greatest depth of radar penetration and the range of amplitudes for each grid. The majority of those data points are background noise or returns. Also, the relationship between GPR data and root biomass is condition-specific. With the intent of flexibility to account for these two facts, a new approach to the standard regression between root biomass and GPR radar return was developed.

The first major contribution to this approach is an improvement to the metric itself. A measurement on a per unit area basis is desirable in order to aid inference to variable soil volumes. Only a proportion of the radar data - that above a given amplitude threshold - indicates the presence of an object, with the rest of the signal representing background noise or an indication of a relatively uniform medium (e.g. a single soil horizon). The metric used, therefore, was the proportion of amplitudes above a threshold for a given volume, hereafter referred to as "radar reflectance."

One approach when developing this metric is to assume a single threshold across all sites and ecosystems. A second is to allow the threshold to vary by site to allow for differences in site conditions. Both approaches were implemented for comparison. When using a single threshold, first the slice plots were reviewed to arrive at a preliminary indication of which thresholds seemed to indicate a meaningful object or pattern. Using linear models (1st and 2nd order polynomials) root biomass was then regressed on radar reflectance across thresholds. The threshold that gave the lowest residual standard error was selected (R Development Core Team 2013). For the second approach, a matrix of all possible combinations of thresholds for each site was created, and then linear models were iteratively fit as above to every possible combination of threshold amplitudes. A threshold combination was selected that minimized residual standard error and AIC (in this case, they were the same combination).

Using the regression for radar amplitude on a root biomass, the root biomass was estimated for the entire volume measured in the GPR grid. Since trench measurements explored a much smaller soil volume than the GPR grids, it was also possible to make the comparison between estimated root biomass from trenches and roots, restricting the comparison to those depths which overlapped for the GPR and the trenches.

Results

Plots measured had a wide variety of tree densities, diameter ranges, and species mixtures. These reflected both the management history and the species mixture of each site. A small-plot effect was tested by comparing both estimated LAI and the standard deviation of DBH against plot size (area, m^2) at the species level. There was not a significant effect of plot area on the LAI estimated. The standard deviation of DBH decreased. Neither relationship was significant.

Median basal area for plots in coast redwood stands was 103 m^2ha^{-1}. The majority of the basal area was represented by coast redwood, with some Douglas-fir *(Pseudotsuga menziesii*) and tanoak (*Notholithocarpus densiflorus*) also present (Figure 5).

In the GPR to biomass models a 1st order polynomial was selected based on review of scatterplots of the data and a comparison of residual standard error of the different model forms. All parameters and the whole model were significant for both the single and multiple threshold approaches to radar reflectance. The model with multiple thresholds (Figure 8) had a higher coefficient of variation than that fit with a fixed threshold (Figure 9) (R^2 of .80 and .69 respectively). Higher biomass was found at shallower depths in both directly and indirectly measured datasets (Figure 10). Using the dataset from the GPR, root biomass was estimated across depths and sites. Biomass continued to attenuate with depth, although there was a slight increase in mean biomass at the 1-1.3 meter range. In measurements with a 450 MHz antenna, the signal attenuated to the point of unreliability at approximately 1.5 meters. This signal attenuation is accelerated (i.e., shallower penetration) in clayey soils, limiting inference on some of those sites to depths 60 cm or less.

The result of the three-dimensional graph is an interactive, three dimensional root map of each grid, with a degree of confidence in the interpolated root map, a product which to date has not been produced. Still frames of such a representation can be seen in Figure 7. Use of GAMs to smooth data, and the use of 3-dimensional visualization considerably improved the interpretation of objects in the radar scans. Objects such as roots which were obscured by the granularity or noise of the radar returns were clearly apparent afterwards, and it was possible to clearly see and trace the course of roots and other objects in the scans.

The relationship between destructively sampled roots and roots sampled with the GPR established, the larger volume of roots measured by the GPR was compared to the mass of roots measured via excavation. Plots with higher basal area (defined as those greater than the mean basal area for the forest type), had larger differences between GPR measurements and trench measurements than did those with lower basal area (figure 6).

Discussion

Coarse roots in coast redwood

In all trenches excavated in coast redwood stands, I found large (> 3 cm diameter) roots at the lower limit of the trench, in the range of >50 cm depth. This appearance of larger roots in deeper soil horizons was also apparent after I analyzed the data, in an apparent bimodal or possibly multi-modal relationship in the biomass measured for coast redwood (Figure 10). There was an increase in the median biomass measured at around 1.3 meters in some redwood sites, after a steady decline from the root biomass measured at the surface. Due to the clayey nature of the soil and possibly due the associated compaction, GPR scans were unable to penetrate, on average, beyond 1.3 meters (see Zenone et al. 2008 for a description of clay's attenuation of a GPR signal). While the goodness of fit of the relationship between the radar return and excavated biomass was high (adj. r^2=.8), the radar may not have penetrated deeply enough to detect the majority of root biomass for coast redwood measured. Coast redwood forms a series of adventitious root collars after alluvial sediments cover the bole, so redwood roots may be located more deeply if the stems had been partially buried in the past (Zinke 1988). The site in this study on alluvial soils is young (<40 years old at the time of measurement) so this probably did not play a role in these results.

Another potential interaction is that larger trees may have more deeply distributed roots than smaller trees of the same species. For example, \ Fritz (1995) reported the root system of a 700 year old redwood to extend as deeply as 4.5 meters, with lateral roots that would have been measureable with a GPR beginning to emerge from the main bole at least 2 meters below the surface. The two redwood plots with the highest basal area also had the highest mean dbh, implying that the apparent measurement error was compounded by a difference in root distributions between the two sites. If this is the case, root biomass appeared to decline as above ground biomass increased because roots were more deeply distributed in these stands. Tested models supported this line of reasoning, as the regression slopes between basal area and roots had the opposite relationship than would be expected if root biomass remained at the same depth for all tree sizes, i.e. root biomass decreased in the layer of the soil measured with increasing basal area (Figure 11). Taking an accurate measurement of deeper, larger roots may be possible with a GPR that employs a lower-frequency antenna. Another approach would be to measure stands with a broader range of density or stand structure, and soils better suited to higher-frequency radar.

I was thus unable to conclusively demonstrate that upslope redwood has more deeply distributed root systems than those of the coast redwood located on alluvial sites described by Fritz (1995) and by Zinke (1988). However, these results do support the hypothesis that larger coast redwood stems have bigger, more widely and deeply distributed root systems than previously supposed.

Fine root models

As with models for coarse roots, there was not a clear relationship between leaf area and fine roots in coast redwood stands, although fine roots were measured by hand and observed to be concentrated in the superficial layers of the soil, and appear to be distributed more deeply in stands with larger trees (Figure 12). I suggest three possible explanations for the apparent decoupling between coast redwood leaves and roots. First, the majority of coast redwood plots in this study were on two sites that had experienced recent (< 20 years) harvest disturbance. The associated soil compaction and ecosystem recovery may have obscured any existing root-leaf relationship that may have otherwise been apparent. Soil disturbance and compaction as a consequence of timber harvest, although not ubiquitous, is a well-described phenomena in forest management for timber (Childs et al. 1989). However, the spectrum of consequences is large, and depends greatly on the size of the opening created, the way if any timber is removed from the forest, the slope, the type of soil, and the above-ground vegetation present before and after harvest (Fahey and Arthur 1994, Olsson et al. 1996, Ballard 2000). Moreover, our ability to make inference about harvest effects on soils is confounded by the timescale and complexity of the many other factors that can and do effect soils before and after harvest (Yanai et al. 2003). This has led to the dispute of general models which describe soil carbon loss and recovery over long timescales (Covington 1981, Yanai et al. 2003). On the other hand, the effect of harvest on fine root loss and turnover are thought to be correlated with the effects of compaction and its effect of reducing water infiltration and changing patterns of nutrient turnover (Olsson et al. 1996). Fine root distribution is also affected by the distribution of nutrients in the soil, which can cause a migration of nitrogen and phosphorus from surface to sub-surface soil horizons (but which vary with many site-specific factors) (Black and Harden 1995).

Second, coast redwood fine roots may be more decoupled from leaves than species without foliar water uptake. Mass flow theory predicts that there should be allocation to organs commensurate with the scarcity of the resource that organ(s) is involved in acquiring (Munch 1932, Lacointe 2000). Coast redwood and other flora in the same ecosystem can uptake moisture through foliage (Burgess and Dawson 2004, Limm et al. 2009). This would complicate the relationship assumed by pipe model theory, i.e. a source-sink relationship for water between roots and leaves connected by the sapwood (Oohata and Shinozaki 1979). As coast redwood continues to access water via the root system the postulated relationship would seem to hold, albeit potentially more weakly. Furthermore, as conductive tissue has been successfully used to model leaf area in the same stands sampled in this study (O’Hara et al. 1999), it seems highly unlikely that fine root biomass would be completely unrelated to leaf area (as this would imply that the two are completely decoupled for this species). However, it is possible that the two organ systems are more weakly coupled. If it could be confirmed that fine root biomass was in fact lower as a result of leaf uptake, this would be a key confirmation of the validity of mass flow theory in the regulation of nutrient allocation in plants (Munch 1932, Lacointe 2000).

A third explanation is that coast redwood, at least in some stands, is accessing subsurface water resources. Fine roots would be present at these depths, but since my core measurements went at most to 60 cm and did not reach ground water, this biomass would not have been captured in my dataset. Leaf area may thus prove to be a good predictor of fine root biomass in coast redwood, if a practical method of measuring fine roots in deeper soil profiles could be implemented. Alternatively, if the total water budget of a tree or stand could be calculated, the amount of water accessed through fog by the leaves, and the capacity of fine roots for water uptake estimated, it might be possible to back-calculate the biomass of fine roots in the stand. As there is likely to be significant uncertainty in this method, however, it would be preferable from that perspective to use direct measurements, at least on a limited basis, to corroborate the proposed estimate.

Further study on redwood fine roots should focus on increased sampling intensity in one location, preferably one that has not experienced serious disturbance for at least 40 years. An ideal set of experiments would be designed to distinguish sources of water uptake and use throughout the year with the goal of parsing the relative amount of water used from different soil profiles and from leaf water uptake, with enough temporal resolution to understand seasonal effects of that uptake (Dawson 1998, Ehleringer et al. 2000, Limm et al. 2009). A key challenge would be distinguishing water uptake from fog drip onto the surface and that from direct leaf uptake. This might be achieved, albeit imperfectly, by measurement of leaf and root response to water in the lab with clones taken from field measurement plots (Limm et al. 2009). Mass flow theory would predict increased allocation to fine roots on the surface in times and locations that fog drip is an important water source, and in deeper soil profiles when subsurface water is important (Munch 1927, Lacointe 2000). To discern whether this takes place for coast redwood, it would be necessary to resolve both fine root flux and fine root distribution in the soil profile, which would not be an inexpensive undertaking. However, if it were to be done what would be required is a nested multifactor experimental design which coupled high-temporal and spatial fine root cores to several meters depth with flux measurements in plots that could be assumed to be in a steady state (Vogt et al. 1998). This would allow the researcher corroboration of results from multiple measurement methods, a necessity for conclusive results in fine root study (Vogt et al. 1998).

Applications of GPR to root measurement

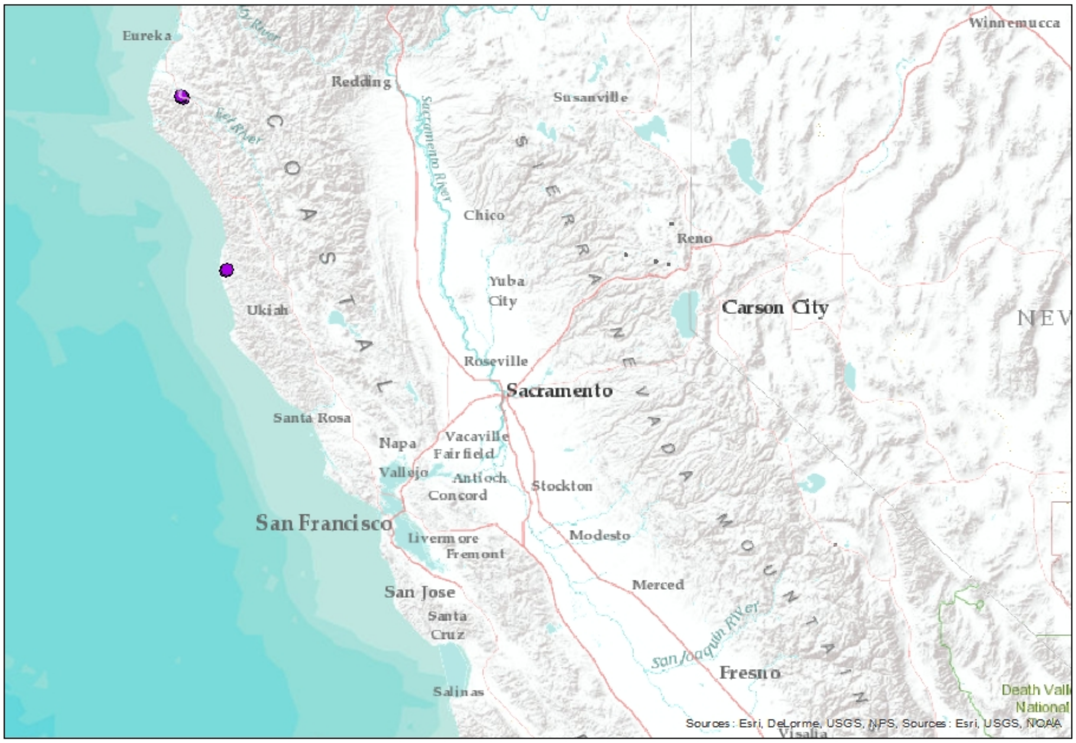
The techniques and software presented represent an efficient method and metric for measurement of root biomass at the stand level which can be applied across sites. Several significant areas for continued research are made available given this approach. The first is scaling up from the plot and stand level to the landscape level. It is impractical to measure root biomass in every stand in a managed forest, or every microsite in an unmanaged forest. To aid in the estimation of biomass at the landscape level, therefore, root data estimated from GPR must be tied back to metrics that existed in forest inventories or that can be estimated from satellite imagery. Basal area is one of the most common metrics estimated from forest inventories; likewise, leaf area estimation at the landscape scale is often a goal of remote sensing analysis (Gower et al. 1999, Chen et al. 2002, Bréda 2003).

Use of ground penetrating radar may have utility for coarse root studies in coast redwood, but probably will be limited to uncompacted soils with lower clay content than those in this study. Investigations using these methods in the one coast redwood plot that had not been harvested for 70 years and was located on loamier soils, produced returns that were much clearer. In old-growth stands coarse roots will presumably be larger to support the larger above-ground biomass (Zinke 1988, Fritz 1995). In these cases a lower-frequency antenna could also be used. The lower frequency would allow resolution of larger, deeper roots than were measured in this study. The trade-off for old growth stems, though, is that allometric relationships tend to hold more weakly in older larger organisms than their younger counterparts.

A major drawback of this method for measurement of roots is that GPR proved to have limited efficacy in the measurement of deeper roots in these soils. The use of the instrument for measurement of forest roots, at least in soils with a significant clay component, thus remains limited to superficial soil layers.

Limits notwithstanding, GPR can function as a useful and powerful technique among other techniques for studying roots, and will probably prove most useful for research on shallower roots or roots in sandier ecosystems, particularly when repeated measurements of root are of interest.

Figures and Tables



Sources: Esri, DeLorme, USGS, NPS, Sources: Esri, USGS, NOAA

Figure 14: Sampling locations; sites were selected in Mendocino, Humboldt, Mono, Placer, and El Dorado Counties.

site	Forest Type	Management history	latitude	longitude	soil order	suborder	mean elevation(m)
JDSF	Coast Redwood	Timber	39.37	-123.72	Ultisols	Humults	150
SCOTIA	Coast Redwood	Timber	40.45	-124.07	Entisols	Fluvents	28

Table 8: Sampling locations summary.

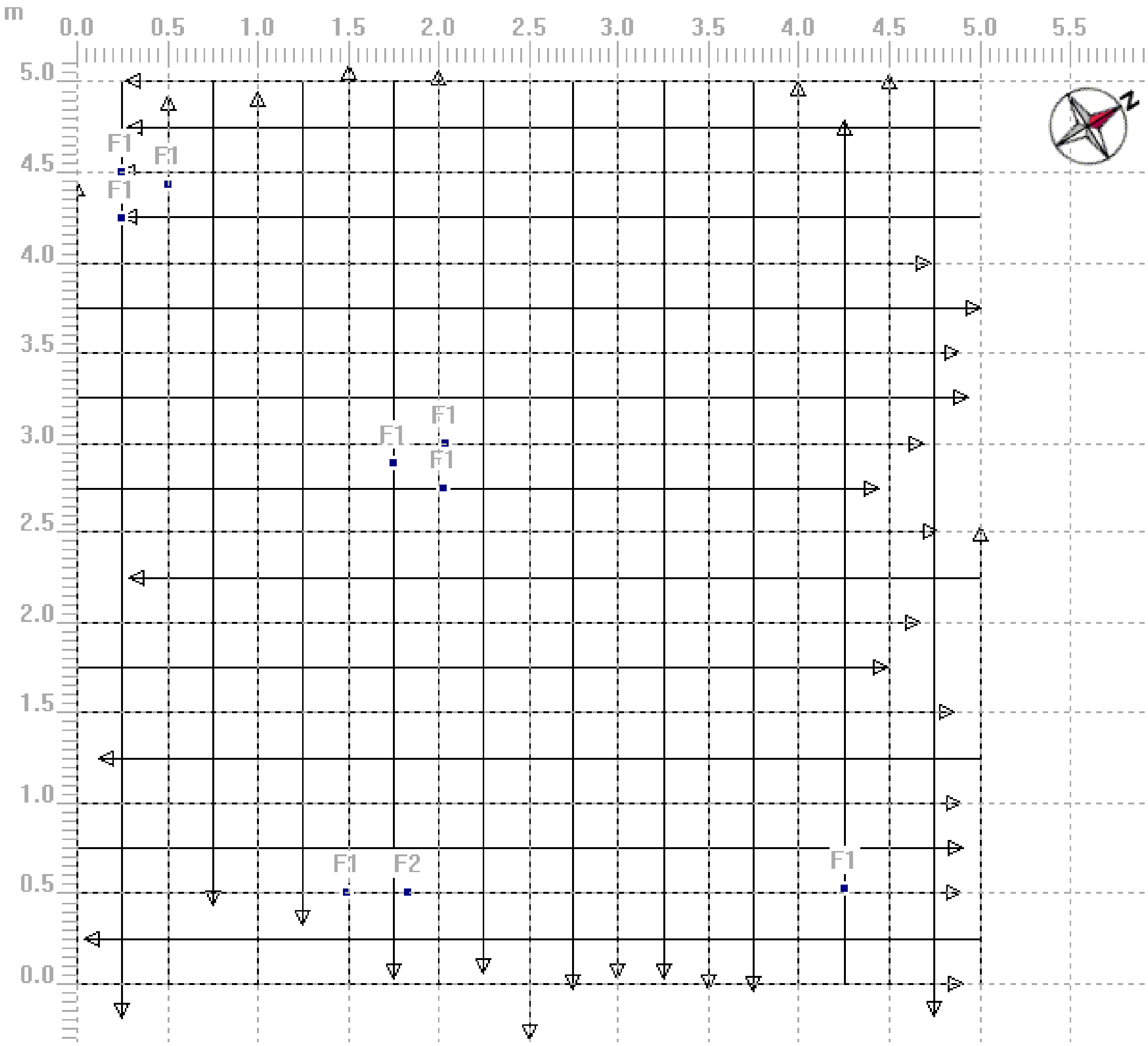


Figure 15: A representative GPR grid, as viewed from above

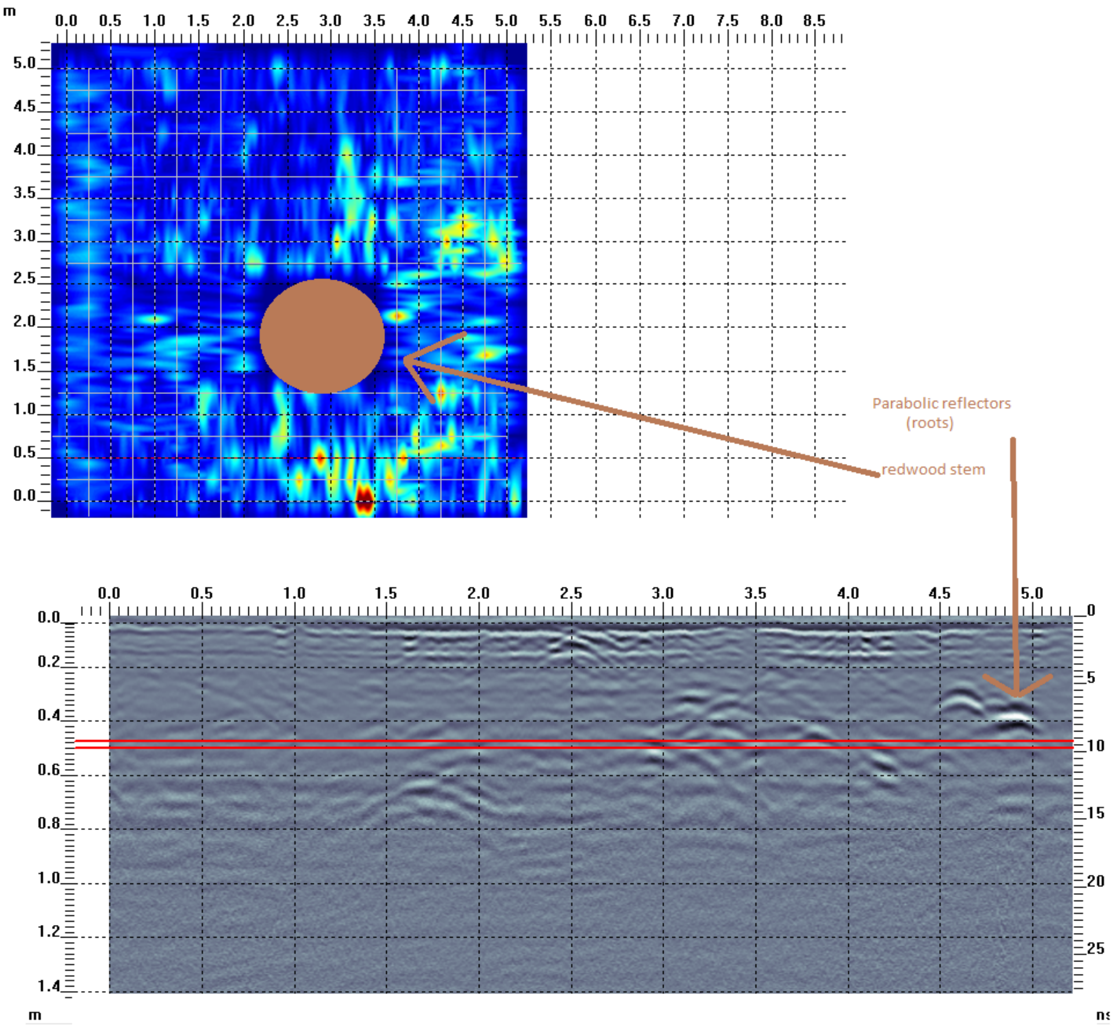


Figure 16: Viewing transects and grids measured using a GPR.

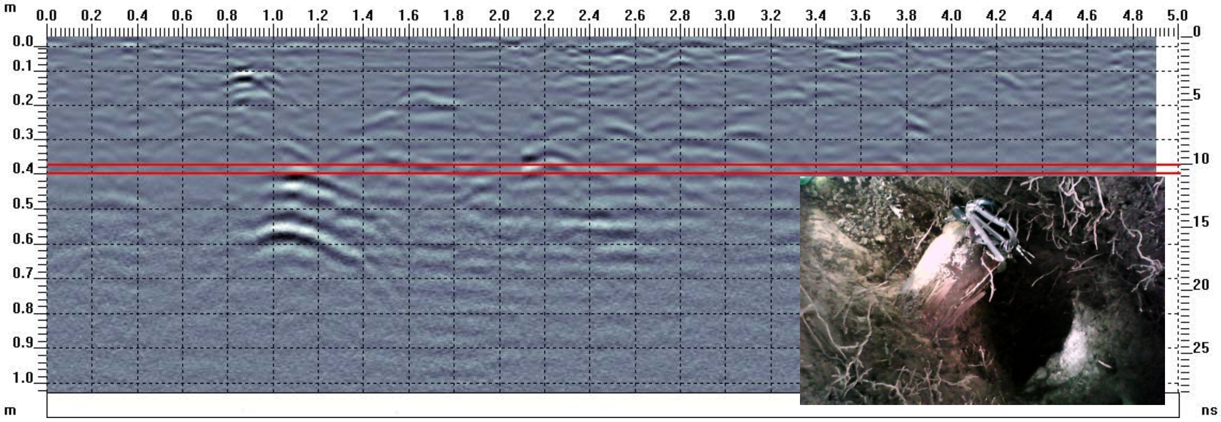


Figure 17: Parabolas generated from a single GPR transect, where the y axis is depth. Characteristic parabolas generated using a 1000 MHz antenna on a single transect. Objects are located at the apex of the parabolas. Roots were successfully located and excavated using these images. Parabolas are collapsed to the apex using Kirchove migration. Inset picture is the root at the apex of the largest parabola.

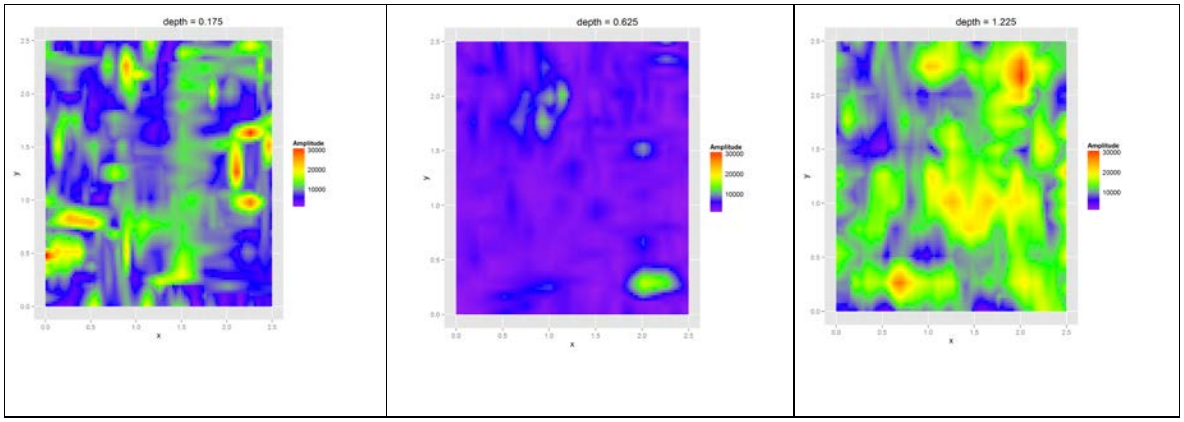


Figure 18: Two dimensional slices of radar data on the z (depth) axis from a coast redwood scan Warm colors indicate the highest intensity returns. Slices can be generated along the x, y, or z axis to aid the viewer in visualizing the data. Generated using scripts in ggplot2, plyr, and R base.

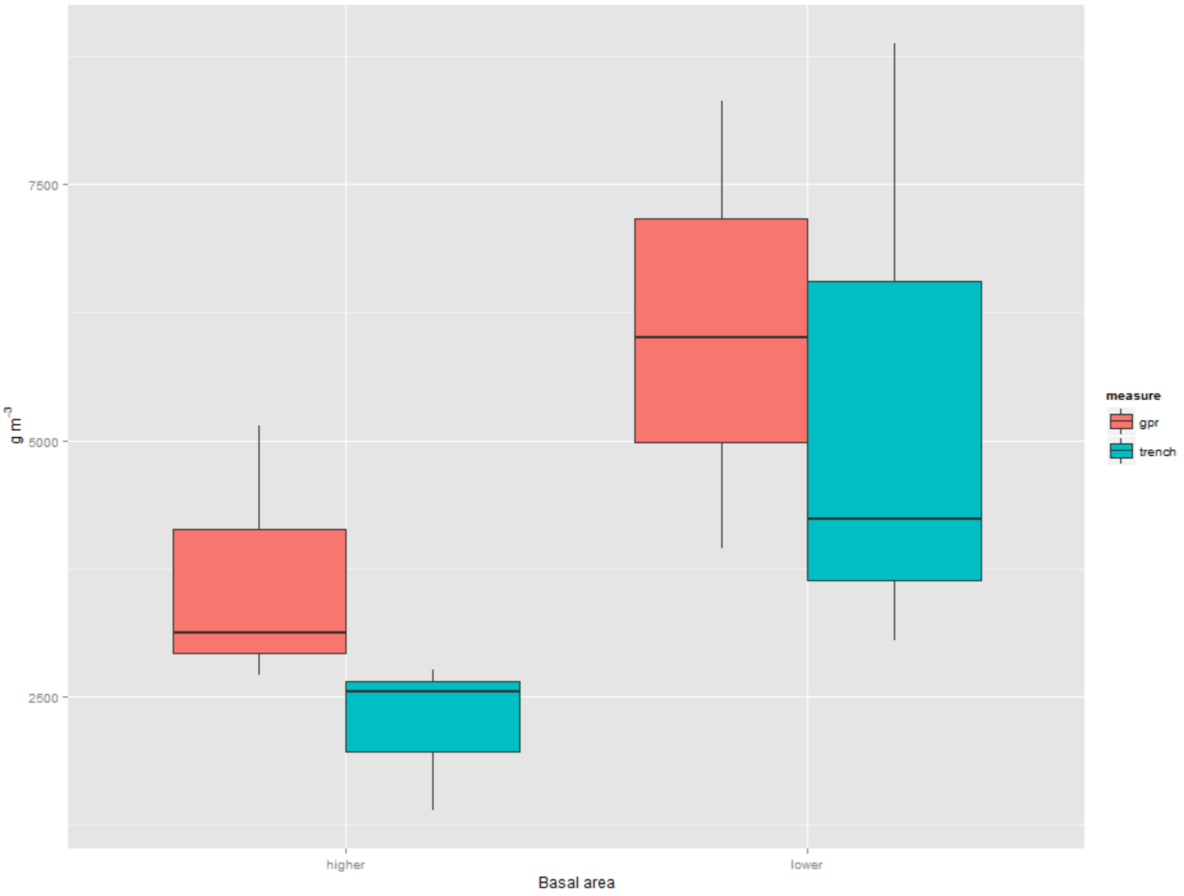


Figure 19: Comparison by forest type and relative biomass (plots above and below the mean for a given forest type) of root measurements taken by ground-penetrating radar and trench measurements.

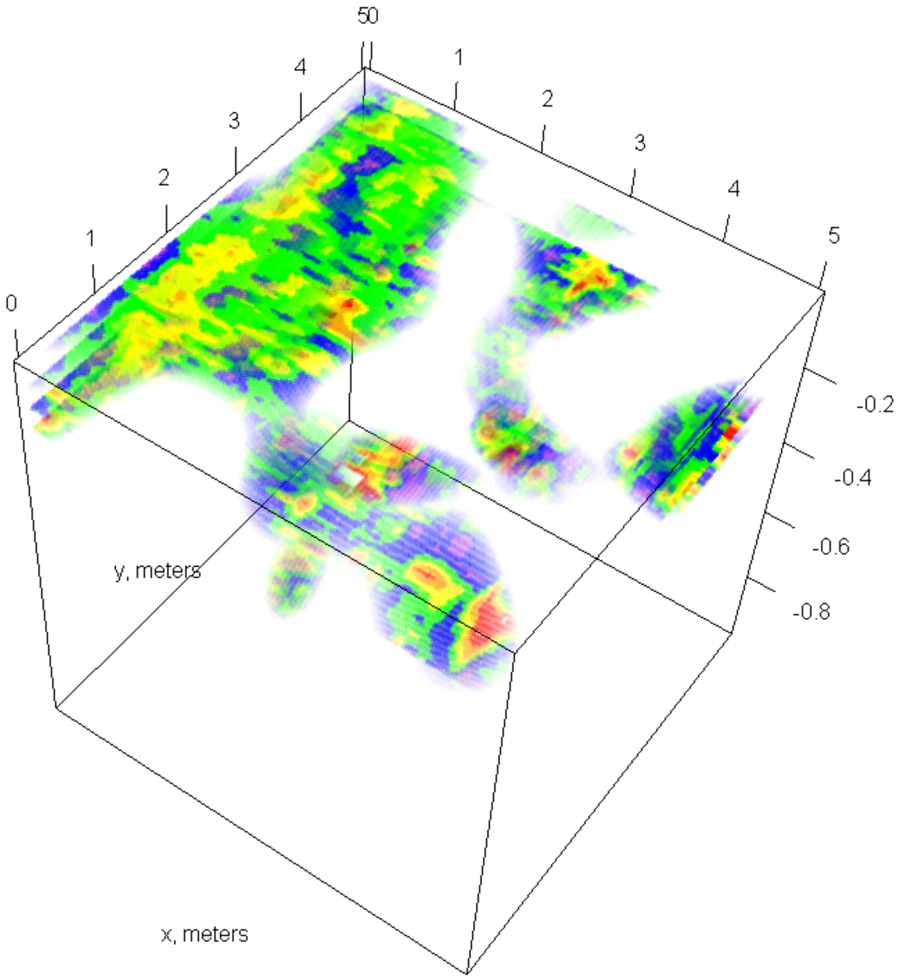


Figure 20: Smoothed GPR scans from a sampled plot .

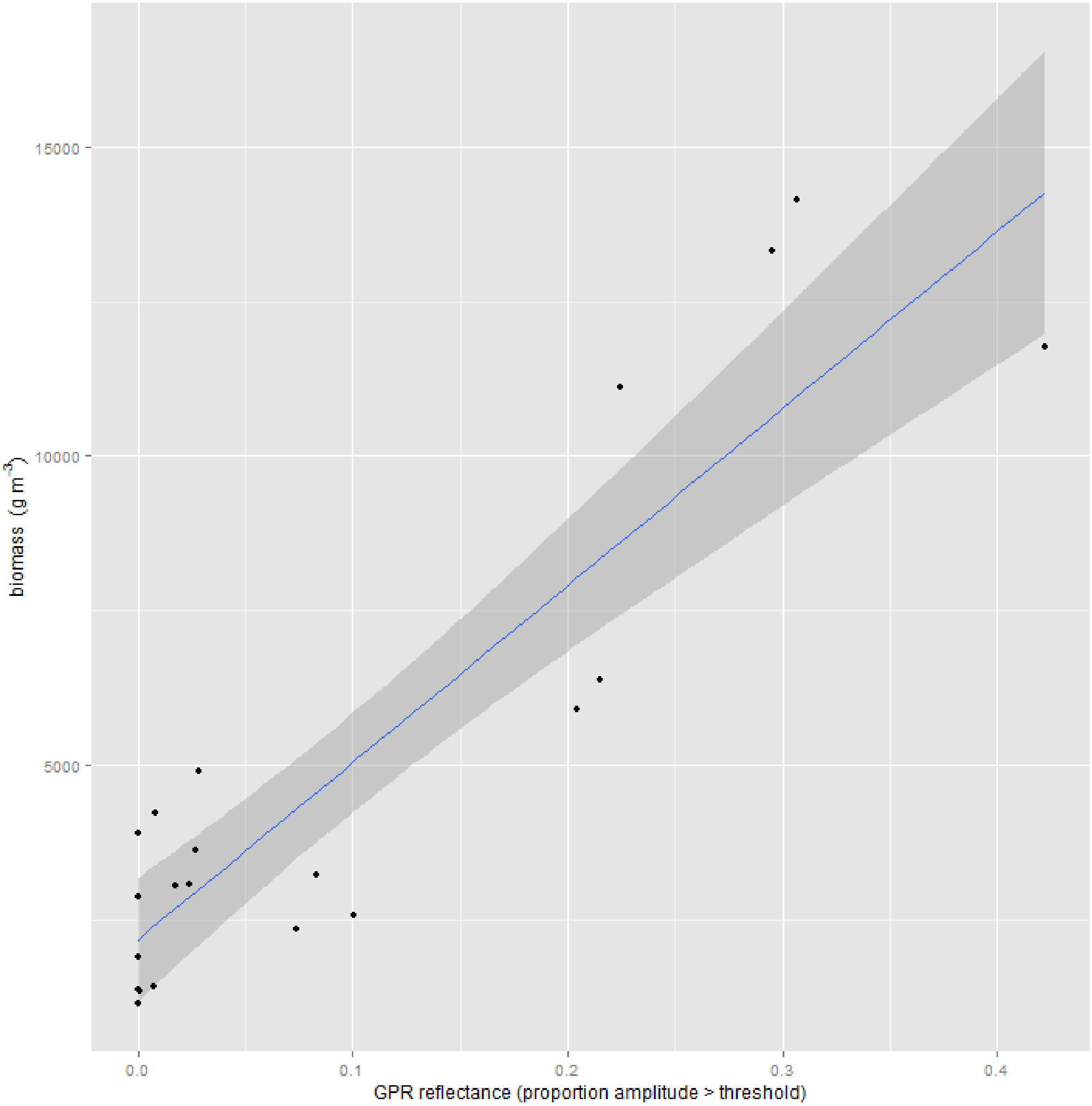


Figure 21: Linear regression of GPR reflectance on coarse root biomass using amplitude thresholds optimized by site. The shaded area is the confidence interval at the 95% level. DF=20, adj. R2=.80.

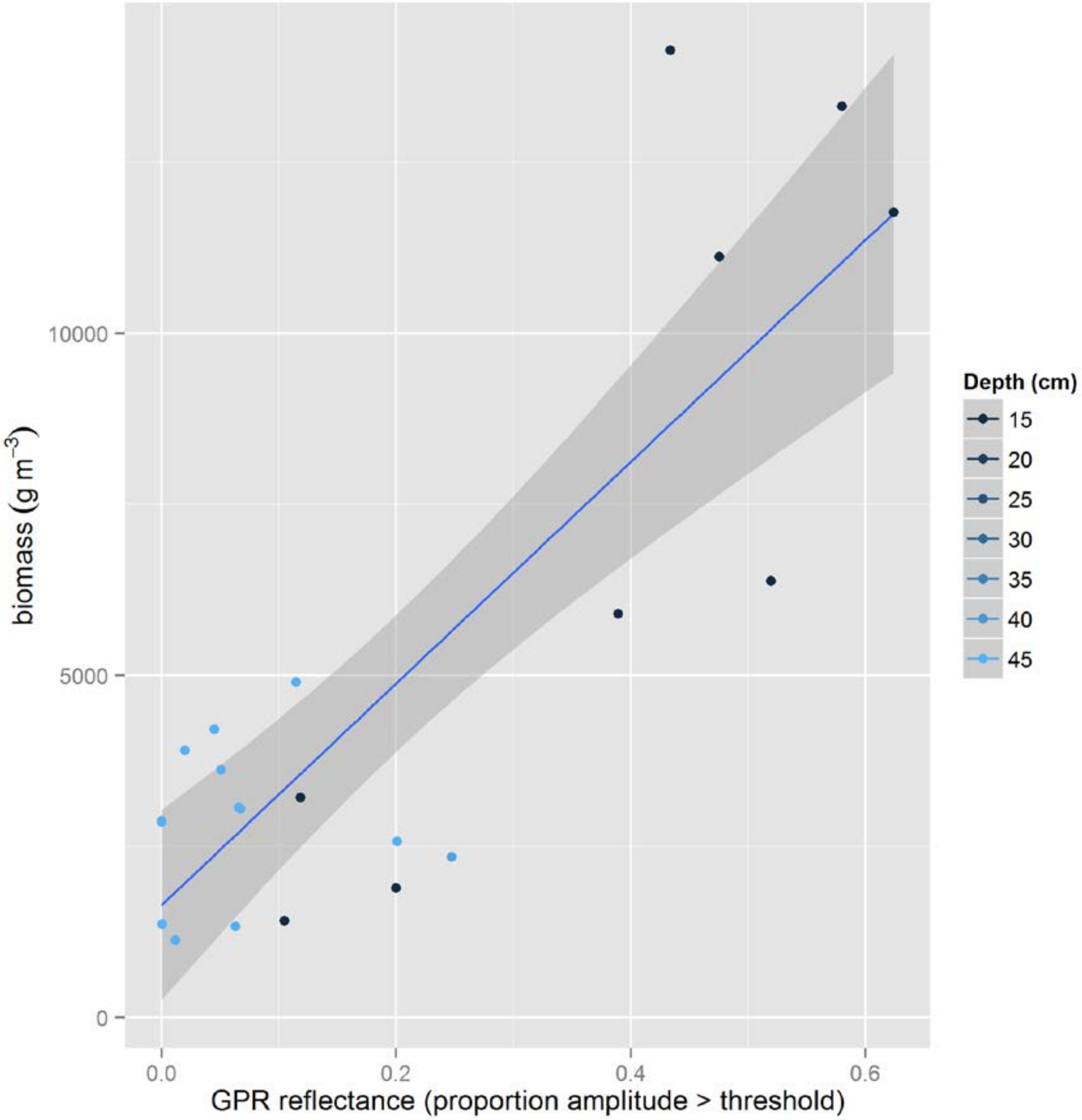


Figure 22: Linear model for of GPR reflectance on coarse root biomass using a single amplitude threshold for all sites. Mean depth for a given measurement is indicated by color on the left-hand plot. The shaded area is the confidence interval at the 95% level. DF=20, adj. R^2=.69.

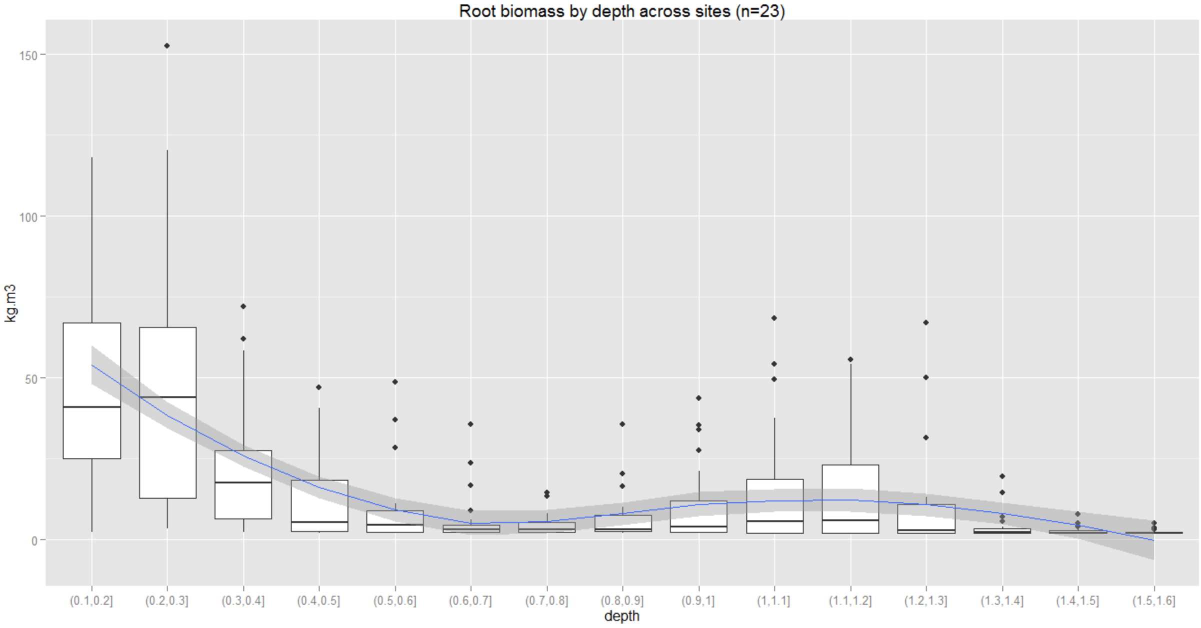


Figure 23: Root biomass by depth, as determined from GPR reflectance across plots. Biomass is estimated from the regression presented in Figure 9, and divided into 10 cm bins.

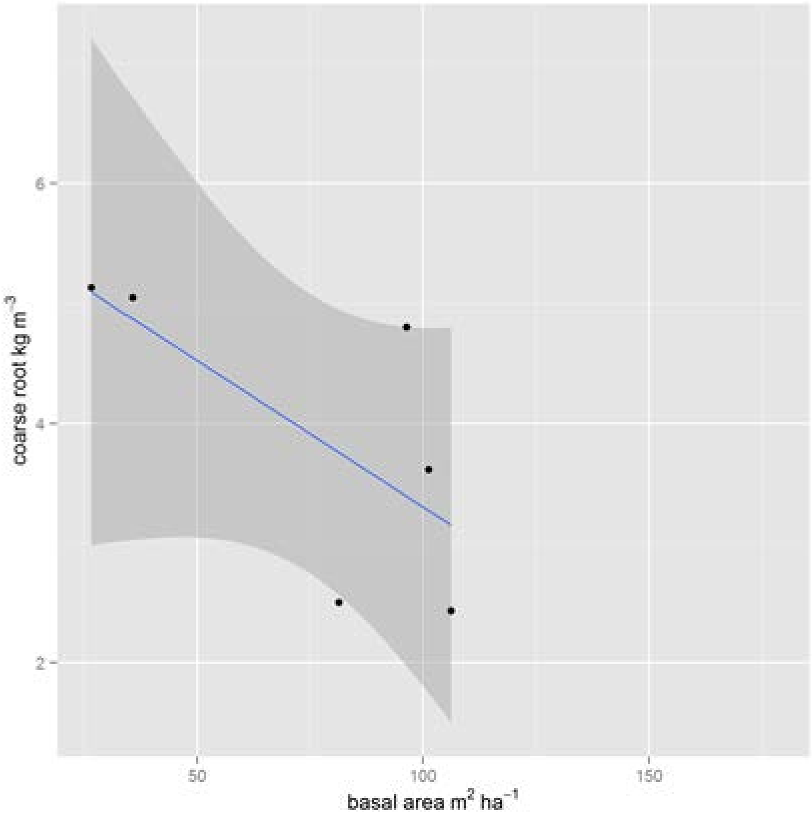


Figure 24: Coarse root to basal area model for coast redwood sites. Coarse root biomass decreases at the depths measured as basal area increases.

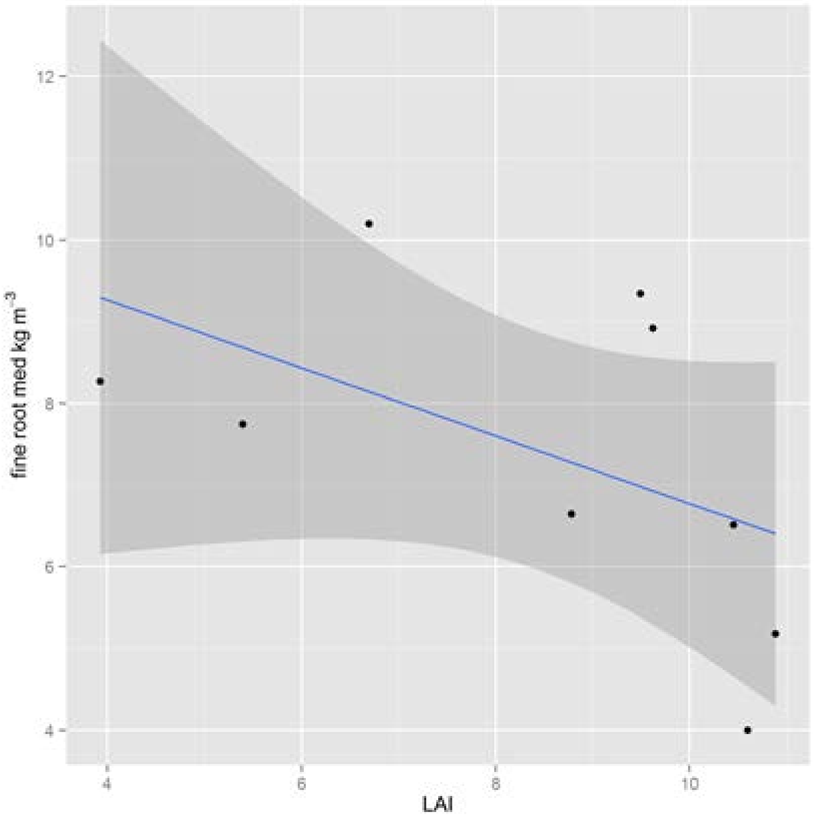


Figure 25: Leaf area to fine root model. Fine root biomass decreases in the depths measured as leaf area increases.

3 Estimation of root biomass in forested ecosystems: a gap analysis and way forward

Introduction

Roots in forested ecosystems are widely recognized as understudied, but vital to understanding terrestrial carbon dynamics (Cairns et al. 1997, Brown 2002). Functioning as organs of nutrient and water uptake, roots play a critical role in supporting photosynthesis. It is difficult, however, to obtain similar information on roots that we collect relatively easily for above-ground portions of trees, such as abundance, distribution, and biomass turnover (Vogt et al. 1996, Pregitzer 2002). Since root growth and turnover constitutes a significant fraction of net primary productivity (Nadelhoffer and Raich 1992, Vogt et al. 1996), data on belowground biomass represents a key gap in our understanding of whole-plant function. There are two major deficiencies in root biomass data collected to date. First, there is a general paucity of data on mature tree roots (Brown 2002, Mokany et al. 2006) which results in imprecise estimates of root biomass. Second, much of the available data has been gathered using inconsistent methods, or methods that result in biased estimates of root biomass (Mokany et al. 2006, Day et al. 2013, Taylor et al. 2013).

There are major implications of error in estimates of below-ground biomass for forested ecosystems. One which is globally relevant is the impact of this error on the estimates of terrestrial greenhouse gas stocks and fluxes used to model the effects of land use change on global climate (Aalde et al. 2006). Land-use change is a significant source of GHG emissions to the atmosphere and driver of global climate change (Barker T. et al. 2007, Pan et al. 2011, Harris et al. 2012). However, it is generally well-accepted that there is still great uncertainty in climate models. In the past ten years there has been a concerted and largely successful effort to improve the precision of the estimates of carbon stocks in above-ground biomass at landscape scales, with the impetus of improving inputs for climate models and carbon accounting efforts under the United Nations Framework Convention on Climate Change (UNFCC) (Asner 2009, Saatchi et al. 2011). Approaches to reduce uncertainty have used multiple methods, but have generally linked high-precision metrics that are slow or expensive with methods that can be extended to larger geographic scales using hierarchical models. For example, combinations that have been used with success include ground-based measurements with LIDAR, LIDAR with MODIS, and LANDSAT with MODIS. These efforts are converging on global and regional estimates of above-ground biomass (Saatchi et al. 2011, Baccini et al. 2012). While there is still considerable necessary refinement of GHG fluxes associated with land use change (Harris et al. 2012, Zarin 2012) and allometric equations used for ground-based estimates of biomass (Vieilledent et al. 2012), estimates and methods for above-ground stocks are mature enough that we should begin to focus on the other larger source of uncertainty in forest biomass estimates, the below-ground portion.

To date, below-ground biomass estimates at regional and global levels, and the models used by the Intergovernmental Panel on Climate Change (IPCC), assume constant ratios between above-ground and below-ground biomass (Aalde et al. 2006). The ratios are available for all but one of the major forest ecosystems (tropical mountain systems) considered by the IPCC. The ratios themselves are based on four papers (Fittkau et al. 1973, Poupon 1980, Li and Kurz 2003, Mokany et al. 2006), but rely almost exclusively on estimates from a single synthetic examination of root/shoot ratios, from Mokany et al. (2006). Mokany and his co-authors produced their work after a literature review of studies which reported data on above and belowground biomass, and then selectively removed data based on criteria related to the adequacy of methods used. Of the other three studies used, Fittkau et al.'s (1973) results were reported from excavation of a single large plot in Pará state, Brazil, and Poupon's (1980) from his thesis work in Senegal. Although both Li and Kurz's (2003) paper and Mokany et. al is referenced by the IPCC in table 4.4 (the list of default ratios for below and above-ground biomass), the ratio reported is from Mokany et al. (2006).

The ratios used for land-use change associated GHG flux estimates in regional and national carbon accounting and estimates of GHG fluxes (see e.g. Asner 2009, Saatchi et al. 2011, Shoch et al. 2013) are Tier-I values (i.e. defaults for global estimates). The uncertainty of the estimated root biomass in practice, however, is not treated separately from that associated with the above-ground biomass. Moreover, some of the ratios may be biased or may have underestimated the range of error associated with the estimates. As estimates of above-ground biomass become increasingly precise, the relative error associated with the estimates of below-ground biomass will grow progressively larger without additional improvement; it is inappropriate to continue pairing Tier-I global defaults for root biomass to maps of above-ground biomass that give estimates at the sub-hectare level. While global models will probably use default relationships for the foreseeable future, more effort should be made to ensure that the estimated uncertainty is appropriately bounded and unbiased.

In this analysis, I first examine the reliability of the root/shoot ratios currently used as defaults in carbon accounting and climate models. I focus on forested lands and present a gap analysis of areas that are problematic in terms of possible bias, under-sampling, and inappropriately estimated uncertainty. Second, I use existing data on the size and variability of the biomass pool in each stratum from Mokany et al. (2006) and used by the IPCC, and the geographic location of the same studies to estimate root/shoot ratios and generate a sampling plan within the FAO global ecological zones (GEZ). Last, I review and update the literature on methods for root sampling and biomass estimation, in order to identify the most efficient and unbiased combination of methods to use when sampling.

Drawbacks of IPCC defaults for roots

Global ecological zones (GEZ) are divisions of the earth's terrestrial biomes based on precipitation, latitude, and vegetation developed by the FAO (FAO 2001). Root-shoot ratios specific to the GEZ are the default method for estimation of below-ground biomass for the IPCC. Root-shoot ratios are the estimated relationships between above and below-ground biomass for a given flora.

The four studies (Poupon 1980, Singh et al. 1994, Li and Kurz 2003, Mokany et al. 2006) used by the IPCC were used as the best available data on the relationship between above and belowground biomass. Because the GEZ were not used to define the sampling frame or the original ratios, ratios were applied to the zones of the GEZ based on qualitative similarities in the vegetation classes used by the original authors. The original data were not reanalyzed based on the sampling locations within the GEZ to estimate new ratios. Consequently there is a mismatch in the sampling frame and the sample. For example, the same estimated ratios from Mokany et al. (2006) were used for ecosystems that are clearly distinct (e.g.,tropical and subtropical zones). Since the sample is not representative of the ecosystems, it would seem impossible to accurately infer below-ground biomass values from above-ground biomass. In addition to sampling issues, there are serious problems associated with use of the root/shoot ratios as they are currently estimated.

Of the four papers cited by the IPCC as sources for root/shoot ratios, I reviewed each of them in detail for the location, methods, analysis, and conclusions reached. In the case of Mokany et al. (2006), the original dataset used in that analysis was requested and obtained from the primary author. These data were reanalyzed by ecosystem to assess the potential for bias in parameter estimates and the appropriateness of the reported variance of the data. The data were also broken out spatially by the location of each study within the GEZ, and the relationship between above- and below-ground biomass for each GEZ re-estimated using a hierarchical model.

Analysis of Mokany et al. 2006

Mokany et al.'s paper on root/shoot ratios was an important step forward for estimated global root/shoot defaults. The authors recognized that much of the synthetic works used to estimate root/shoot ratios up to that date (e.g., Vogt et al. 1995, Cairns et al. 1997) drew on data from studies that used a less developed methodology for vetting inputs. Mokany et al. 2006 introduced criteria to evaluate the adequacy of methods used to estimate below-ground biomass. They required that the data used include measurements of the root crown, above-ground biomass, fine root biomass, and depths. Mokany et al. also required that each study had replication, and that the data were not from sites which had undergone recent major disturbance.

There was a significant difference in the estimates presented in Mokany et al. (2006) compared to prior results, a clear indication that root/shoot data needs to be carefully vetted before use. Moreover, Mokany et al. make clear in their paper that data from certain biomes were too limited. The authors' caveat about the robustness of existing data was seemingly overlooked, as subsequent IPCC guidelines for greenhouse gas inventories adopted the biomass ratios from Mokany et al. for almost every ecosystem (Aalde et al. 2006).

There are some areas of Mokany et al.'s (2006) paper that deserve re-analysis. First, the work presents simple ratio data that would be more properly analyzed to account for the nested nature of the data using analysis tools now available in mixed effects models (Zuur et al. 2009). Second, Mokany et al. do not specifically address the number of unique studies or locations used to construct the ecosystem-level ratios. As a result, there are thus issues of incomplete coverage and unrepresentativeness in the data used.

Improvements Mokany et al.'s models could address several potential problems. First, current estimates in some cases have an artificially deflated model standard error due to data unrepresentative or without full coverage of the full range of random effects in a population. The data in this case often do not include the full range of ecotypes in an ecosystem. Second, samples that do not include the full range of values for the independent variable that exist in the population may give biased estimates; in this case, the data should include the range of above-ground biomass values we would expect in an ecosystem. Although with currently available data it may not be possible to ascertain if this is indeed an issue, it is certainly clear that the risk of such bias is high. Third, treatment of data such as this (belowground and aboveground biomass over a range of values) as a simple ratio implicitly assumes a relationship described by a first-order polynomial with intercept of zero. This approach can create biased estimates of that ratio. There is no theoretical basis for this relationship: the root/shoot data would better be modeled using a mixed-effects regression that allowed the slope to vary over the range of the independent variable (in this case above-ground biomass). Each of these key areas are examined below to determine how existing data could best be augmented in order to improve ecosystem-level root biomass estimates.

The range and source of data included in a given 'vegetation category'

If the difference in root/shoot relationships between sites in the same ecosystem is large compared to the error within sites, that between-site error will be masked if the data are skewed to a subset of the range of the variability present in that ecosystem. Moreover, if a modeled relationship is heavily influenced by what is essentially a random site effect, as can be the effect if data are not representative of the population, the potential for bias is introduced.

Mokany et al. (2006) present root/shoot relationships specific to 'vegetation categories' binned by a range of above-ground biomass in each ecosystem (Table 1, Figure 1). This reduces the standard error of the estimated root/shoot ratio for each of the vegetation categories. It also accounts for the fact that the ratio appears to be a function of the above-ground biomass for some vegetation categories (Figure 1).

Binning the data this way is problematic because it reduces the sample size in each category (although it does offer the chance to reduce bias in some cases). Another issue is the fact that in the vegetation categories for which there is a larger sample size, the sample is often dominated by data from one location (generally one study) (Table 3). Moreover, in vegetation categories dominated by a few or one sites, the extreme values (the most influential) in a given bin may be from the same study (Figure 1). Data from moist tropical forests provide a good example of a deflation of standard error due to a sample dominated by one study (Figure 5). Data from one study in the central Indian Himalayas (Singh et al. 1994) make up sixty percent of the sample and contain both the high and low values reported. If the data are modeled in a regression, or using ratios, the standard error reported is the lowest for any of the vegetation classes, but it is most likely an effect of one instance of that particular vegetation class dominating the relationship (i.e. the dominance of a single random effect in the dataset). In a more extreme example from the same dataset, tropical and subtropical dry vegetation classes contain only one site each and sample size of 2 and 4, respectively (Figure 6).

As Mokany et al. (2006) note, data from temperate regions is more readily available than that from tropical zones. It is interesting to note that temperate vegetation classes, with more sites represented in each, tend to have higher standard errors than tropical and subtropical vegetation classes.

Range of independent variable by ecosystem

A representative sample should include the range of values present in the population or the sampling frame, (i.e. have full coverage) (Quinn and Keough 2002). In the case of root biomass measurements and estimation, the greater effort required to measure the roots of larger, mature stems has meant that much of the data has come from smaller stems, or that a larger proportion of the biomass from larger stems is estimated rather than measured.

For the papers used by the IPCC GHG inventory guidance, data on the distribution of diameters sampled was not available or reported for the majority of the studies used. Above-ground biomass was included, however, so I was able to compare the range of biomass values in those studies to those which the IPCC uses as defaults for those vegetation types or ecosystems (Table 4). In many cases, the 'vegetation type' used by Mokany et al. was used for more than one 'ecological zone' by the IPCC (Aalde et al. 2006, table 4.4). For five of the fourteen ecological zones, the median IPCC default was outside the inner quartile range of the data from the corresponding vegetation type in Mokany et al. (2006). The median percent absolute difference between the Mokany vegetation type and the IPCC default was 61.72 %, with a range of 11.90 % to 1150.00%.

While the summary in Table 4 is not diagnostic of any systematic bias in the data, the data are indicative of certain possible mismatches between the vegetation types used to generate root biomass estimates and those used to estimate above-ground biomass.

Treatment of data in a mixed effects regression; incorporation of the nested nature of data in estimates of error

Mokany and his co-authors' (2006) analysis used simple root/shoot ratios as the median value for each ecosystem, perhaps to aid comparability to prior work and remain consistent with the approach used by the IPCC. However, the standard errors reported in this approach were potentially misleading because error due to random and fixed effects is not appropriately partitioned. Furthermore, at a foundational level this approach does not allow the user to determine the significance of the relationship reported. Although the cutoffs for significance, and p-values have been fairly criticized as arbitrary (Schervish 1996, Hubbard and Bayarri 2003), together with metrics of goodness of fit they do provide a useful barometer of the degree to which we should give credence to a given modeled relationship. Such models are thus more credible and give more information than the median and standard error of the root/shoot ratio.

Data with random effects are properly modeled and analyzed by explicitly accounting for the correlation between observations due to random effects (e.g. spatial colocation or observations from the same observation unit over time) (Hurlbert 1984, Zuur et al. 2009). The data presented in Mokany et al. (2006) are clearly nested, with each vegetation type (population) including observations from multiple studies, each of which took place on different sites using unique methods. I therefore used mixed-effects models (Pinheiro et al. 2013) to model below-ground biomass as a function of above-ground biomass. A first-order polynomial was used to model the relationship between slope and biomass to aid comparison between that approach and one using ratios (Table 1). Half of all the vegetation types used by Mokany et al. had a slope that was not significant at the .05 level. Since belowground biomass is almost certainly a function of the aboveground biomass, this is an indication that the sample size for these vegetation classes was too small. The standard error for the ratio reported by Mokany et al. was often lower than found in this reanalysis (Table 1). Last, the median reported by the authors was as much as 100%

different from the value from the regression, which indicates bias in implicitly modeling the data as a first-order polynomial with a slope of zero. It may be the case that the data would best be modeled using a form that would allow the slope to vary with above-ground biomass.

By representing these data as simple ratios bias, underestimates of variance, and reliance on relationships that may well be due to chance are introduced to the IPCC guidance. Using the dataset from (Ruesch and Gibbs 2013), estimates of the magnitude of the proportion difference in the tonnes of belowground biomass estimated by global ecological zone range from 0.73 to 1.73 (Figure 10).

The other datasets and studies used to derive root-shoot ratios also should be augmented to increase the size and representativeness of the sample. Data in Fittkau and Klinge (1973), the study by the IPCC used to derive the default value for tropical rain forests, is based on a single study in Pará state, Brazil, on a single large plot near Manaus. As the study has a sample size of one, the data is properly presented without a standard error. Using such an estimate for all tropical rain forests of the world presents clear drawbacks, of course, both in terms of error constraint and bias. Additional data is needed for this ecosystem, which is one of the most charismatic and biodiverse globally, contains about 42 percent of global above-ground biomass, and is the object of intense study (Broadbent et al. 2008, Asner et al. 2010). For global tropical shrub lands, data are also presented without an estimate of error, and comes from a single study in Senegal (Poupon 1980). Lastly, while Singh et al. (1994) are cited for tropical mountain systems, those same data make up sixty percent of the dataset used to estimate the root/shoot ratio for moist tropical forests (Table 3, Figure 9). Together, in terms of biomass, about 54% of the global root biomass estimates are based on a sample size of one for each ecological zone - that is, we do not know the error of our estimate for 54% of global root biomass, and the rest is improperly estimated.

A strategy for improvement: sampling and measurement methodology

Principle gaps - sampling design

It is apparent that there are serious deficiencies in the approach used to estimate below-ground biomass stocks in the IPCC default guidance. These are important not solely for global climate models, but also because the root/shoot ratios used by the IPCC are widely used as the defaults in national and subnational greenhouse gas accounting for global climate mitigation efforts (Shoch et al. 2013). Given the costs of monitoring and measurement, and the global extent of the sampling frame, efficiency will be critical to solve the problem with a reasonable amount of time and money. The primary needs for improved estimates of forested root biomass at global or regional scales – and to provide reasonable defaults for greenhouse gas inventories of land-use change – are improvements in fundamental sampling design.

To improve root biomass sampling there first needs to be a clear definition of the population of interest: at present this has been defined in the terrestrial biosphere, and stratified as the Global Ecological Zones (FAO 2001, Aalde et al. 2006). However, there has not been any effort to formally use those zones in estimation of root biomass. Instead, current procedures use an ad-hoc merge of ratios found in the literature, or in the case of Mokany et al. (2006), ratios calculated for other vegetation categories, within the zones of the GEZ. This is both confusing and misleading, as data from locations other than the zone of interest are used to estimate root biomass ratios. It would be an obvious and relatively inexpensive first step to recompile the data in the studies listed in the IPCC, and add sampling locations. The listed studies could then be overlaid on FAO's spatially explicit ecological zones. Sampling intensity per area or by the relative carbon stocks in each biomass or zone could then be appropriately parameterized.

Second, at present, sample data are neither proportional to area (Mokany et al. 2006) nor to total biomass; instead it is a convenience (a.k.a. opportunity or non-probability) sample (Lohr 2010). The GEZ can be used as strata and the data already compiled will then be useful as pilot data to determine the sampling intensity necessary to reach the desired precision. As a starting point, it is clear that tropical ecosystems are under-sampled in comparison to temperate ecosystems in current datasets (Figure 8, Table 3). As important reservoirs of biomass and biodiversity, and foci of a great deal of money for research to estimate above-ground biomass and land-use change, it is inefficient to ignore the paucity of data on below-ground biomass in these ecosystems.

Re-analysis using the global ecological zones as the sampling frame

Accordingly, I re-analyzed the existing data on root-shoot ratios using the strata defined by the GEZ. The dataset from Mokany et al. (2006) contains enough information to determine an approximate set of spatial coordinates for each sample. This information was overlapped with the GEZ to determine the number of studies in each GEZ.

Next, I used data available on estimated above-ground global biomass, again intersected with the global ecological zones, to determine the biomass and variability of that biomass within each GEZ (Table 2, Figure 8) (Ruesch and Gibbs 2013). By far the largest biomass pool is that in the tropical rainforest, which also had one of the lowest sample sizes.

Finally, by defining the sampling frame as the GEZ, it is possible to directly estimate a relationship, and the standard error of the mean for that relationship for each ecological zone (Table 2, Figure 9). The form of the model used was a first-order polynomial with the intercept constrained to zero, to provide the most comparability to the root-shoot ratio. The results of the model for many ecological zones are reasonable, with fairly small standard error of the estimated mean slope. For several ecological zones, however, (boreal mountain systems, polar, and temperate deserts) the slope is unrealistic and the model quite poor (Table 2). It should also be noted that constraint of the model intercept increases the potential for potentially large error in the estimated below-ground biomass of high-biomass locations, biasing the estimate to the lower end of the range of biomass (Figure 9).

Using basic methods in statistics and the information on pool size and variance, it is possible to determine the optimal sampling effort for each GEZ (Van Laar and Akca 2007). This was done and compared to existing data on each GEZ to determine the degree to which each zone had been over- or under-sampled to date (Figure 7). For the current sample size, tropical rain forests and tropical moist deciduous forest have been under-sampled to date, relative to other ecological zones. Other considerations (such as cost) aside, therefore, further studies of global root/shoot ratios should focus on these two zones.

It should be emphasized, however, that this analysis can only provide information on the relative effort that should be expended on sampling each ecological zone it is not possible to determine the absolute sample size required in each without some indication of the precision of the estimate desired or the available resources for sampling. These are questions of policy and resource availability.

As with any sampling, there is a tradeoff between the desired precision of the estimate and the cost required to achieve that precision. Since cost is partially a function of the cost of the measurements taken, I conclude with current methods available to reduce the cost of these measurements and reduce the bias of the sample data.

Options for improvement in root measurement

Root biomass measurement is complicated by the fact that most roots are buried in soil, an opaque, heavy, and heterogeneous medium (Bréda 2003). Methods to attempt measurement have not converged on a single approach for root measurement or clear agreement on measurement protocols. For example, there is no universally accepted diameter distinction between coarse and fine roots, nor is there a single measurement method that is clearly superior for all conditions (Pregitzer 2002, Bréda 2003). There are, however, some procedures for root measurement which should be avoided.   In the following discussion, these are used as a point of departure for a review of a combination of techniques and approaches that provide the most efficient and unbiased approach for root measurement and estimation.

To give some idea of the complexities inherent in root biomass estimation, it is important to understand the physiological basis for root extent and root distribution. Just as the above-ground organs of trees are plastic, capable of elongating and changing phenology based on light availability and water stress, root distribution is also affected by the environment (Hodge 2006, Brassard et al. 2009). The primary function of fine roots is nutrient and water uptake. Nutrients and moisture are correlated to the highly variable medium in which they are found: the soil. Root distribution, particularly fine root distribution, thus balances the competing goals of exploration of the larger volume of soil with the cost of maintaining that root network: root distribution is also influenced by genetics and ontogeny (Ryan et al. 1996, Gedroc et al. 1996, Hall et al. 1999, Shipley and Meziane 2002). It is thus difficult to predict the extent and concentration of fine roots in a given local.

Coarse roots are more likely to be found near the stems from which they originate. There are important controls on coarse roots, including genetics (e.g. the presence of a taproot) and environment (e.g. the presence of hardpan) (Raz-Yaseef et al. 2013). For both coarse and fine roots, in a location with multiple trees nearby, it is difficult to determine which roots originate from which stem. Indeed, roots from different stems may be grafted, connected by clonal linkages, or exchange nutrients via mycorrhiza: root measurements on a tree level may not be meaningful (Byle 1964, Hobbie 2006). Accordingly, a volume of soil must be explored, and inferences made about that volume. This sampling comes at considerable expense, and there is evidence that roots have been consistently under sampled, giving biased underestimates of root biomass (Day et al. 2013, Taylor et al. 2013).

Root distribution is fractal, with large roots giving rise to successively smaller, more widely distributed root networks (Taylor et al. 2013). The largest-diameter roots in mature forests are unlikely to be encountered without the examination of larger soil volumes. Taylor et al. (2013) were able to show that volumes of 5878 cm^2, on average, were required to encounter the majority of root diameter classes in a study in an unmanaged loblolly pine forest. It is therefore important to measure enough soil to obtain a representative sample. There are a number of methods which if used to minimize bias and reduce cost in sampling. Measurement methods are best divided into those used for coarse root and fine root biomass estimation. I will highlight here the potential of ground penetrating radar (GPR) to improve root measurement in both categories.

Within each GEZ, controls on the range of variation for root to shoot ratios have yet to be appropriately defined. If modeled variability for each zone is to be unbiased, it should include the range of covariates, such as genetic or edaphic characteristics, that exert a significant influence on the model (Brown 2002). Data collected to date indicate that some of the most important covariates to a modeled relationship between root and above-ground biomass are genetics, edaphic characteristics, water availability, and climate (Cairns et al. 1997, Brown 2002, Mokany et al. 2006).

Measurement of root biomass

Coarse roots

Coarse roots of mature stems found in the soil are typically divided into the lateral root system, which extends to the sides of the tree, predominantly horizontally, and the taproot system, which primarily extends vertically from the tree's base down into the soil profile (Dupuy et al. 2005).

Excavation is the default method for measuring coarse roots, with a long precedent in the literature. While in theory excavation is a straightforward approach to root measurement, in practice it is difficult to avoid under- sampling using excavation alone. Excavation was accomplished in the past by digging out the base of the tree stem, and, for larger trees, winching or another form of mechanical extraction to bring up the root crown. The disturbance necessary to excavate these roots makes it quite difficult to reconstruct all the root biomass associated with a stem, and unacceptable for permanent plots (Nadezhdina et al. 2003). Excavation will also damage trees adjacent to the subject tree, leading to undesirable effects on areas larger than a single tree. Due to the destruction and expense these measurement plots are typically small in extent.

While still reliant on excavation, with the attendant problems of site disturbance and stem death, excavation using compressed air or hydraulic extraction overcomes some of the concerns with the loss of root material with mechanical excavation (Nadezhdina et al. 2003). Typically this type of excavation removes all the soil around the roots, while leaving the coarse roots themselves intact. Hydraulic excavation is limited to areas with a ready supply of water and a slope for the run-off. Compressed air excavation requires specialized equipment, such as an air spade. In all forms of excavation, measuring the whole volume of root biomass is a logistical challenge, and another source of sampling error. Some recent approaches include excavation using compressed air followed by scanning with a ground-based LIDAR system to determine the volume of the root system.

Using any of the methods above, it is often impractical to excavate an entire root system, particularly when the tree is large and the root system is extensive. In this case, taper equations are developed for the major roots and used to estimate the root biomass not actually measured in the field (Danjon and Reubens 2007). To construct these equations, major roots are partially excavated and models fit to the taper of the root. Volume can be estimated from these models. Volume is then multiplied by density to estimate biomass.

Ground penetrating radar (GPR), a technology with a long history of use in the geophysical sciences, has recently been applied for root measurements in several forest sites in North America (Butnor et al. 2003, Raz-Yaseef et al. 2013, Day et al. 2013). This technology has the potential to complement methods used both for the measurement of fine and coarse roots. GPR is advantageous because it is non-destructive, and because it allows for the imaging and exploration of large volumes of soil and repeated measurements of roots on the same site.

GPR functions by measuring detected differences in reflected electromagnetic radiation, usually in the 50 to 1500 MHz range, actively emitted into the soil (Daniels 1996). Using different frequencies, a user can potentially resolve roots at 5 mm diameter (Day et al. 2013), or larger coarse roots at greater depths (Chapters 1 & 2, Raz-Yaseef et al. 2013). With very limited excavation, a GPR can be calibrated to the site conditions and used to estimate a root density for a given volume (Figure 3). Ground penetrating radar can also be used for root mapping and imaging, allowing the user to identify potential root grafts or assign root biomass to a given stem (Figure 4).

GPR has its own limitations and disadvantages. First, GPR has not yet been successfully used to measure vertically oriented roots in an unbiased manner, although efforts are ongoing (Butnor et al. 2006). Taproots will continue to be measured using some type of excavation, probably linked to taper equations (Kozak and Munro 1969, Coutts 1983). Second, there is an inherent depth/resolution tradeoff for the technology: there will always be an effective volume that ground penetrating radar can explore (Daniels 1996). Although its use has limitations, GPR is an extremely valuable method for root biomass measurement because it has the potential to reduce or eliminate downward bias in root biomass measurements, and because it allows repeated measures of the same site. GPR is thus a complement rather than a substitute for traditional measurement methods.

Fine roots

Fine root biomass is generally measured using a variation of either minirhizotrons or cores. Although used to estimate root biomass, minirhizotrons are probably inappropriate for root biomass estimation as they explore a volume of soil too small to give unbiased estimates of biomass (Taylor et al. 2013). They may continue to have utility in root growth monitoring and measurement, however.

Root cores are a straightforward approach to the measurement of fine roots. Cores of a known volume are removed from the soil, and all roots extracted and measured from each core. Sampling involves collecting enough cores to arrive at an acceptable level of pooled error. The primary difficultly is of under-sampling. Fine roots are highly spatially and temporally variable, so many cores must be taken. Moreover, it is time-consuming to extract all the root material from a given core. Taking enough cores to arrive at an acceptable level of precision without obtaining a downwards-biased estimate due incomplete root extraction can therefore be very expensive (Metcalfe et al. 2007).

Metcalf and co-authors (2007) showed that root extraction time per core could be substantially reduced in an unbiased manner by modeling the diminishing returns on roots extracted over time from a given core. Using this approach, root biomass is extracted from a sample of the root cores collected at set time intervals. Models are then fit to the cumulative extracted root biomass, and the median time interval at which modeled root biomass is acceptably close on average to the measured root biomass is used going forward. This approach is much more efficient, and allows the researcher to more efficiently optimize sampling effort without risking bias from under-extraction of cores. Time spent in core extraction in the lab can be reduced by up to 60% in some cases (Chapter 1).

There is some indication that with a high-frequency antenna a GPR can read returns from fine roots (< 2 mm diameter), or clumps of fine roots (Day et al. 2013). Further studies should be undertaken to confirm this result.

In another promising approach to non-destructive methods for root biomass measurement, several groups have pioneered the use of electrical capacitance to measure the functional absorbing surface are of roots (Cermák et al. 2006, Phillips 2013). These new methods are promising as they make possible not only the estimation of biomass and functional surface area, but may also allow the detection of interconnected networks of roots between organisms that are separate above-ground (Ellis et al. 2013).

An integrated strategy for root stock estimation

A measurement approach that leverages the methods mentioned without downward bias is to use root cores for the measurement of fine root biomass, with the methods developed by Metcalfe et al. (2007) used to estimate root biomass for a given core. A limited number of pits could be used to both estimate taproot biomass and calibrate a GPR to the site. The GPR could then be used to measure root biomass extensively, potentially for the entire site. Some excavation will always be necessary, however, particularly in situations where GPR will not operate well or read accurately.

A Californian example

Comparing estimates from ground-based measurements and estimates to those from Mokany et al. (2006), it is possible to arrive at a sense of the difference in the estimate from global and site-specific plot measurements. Comparing data on above- and below-ground biomass from plots in the Sierra Nevada and coastal Californian taken in 2013 (Chapters 1 and 2) using a GPR to the same values that would have been estimated from the ratio used by the IPCC, the difference is quite pronounced.Directly measured data estimated total below-ground biomass of approximately 41% of above-ground biomass, while the ratios from Mokany et. al. (2006) would have predicted 23% for the same plots. Although the ratios from Mokany et. al. were never meant to be used at a regional level, it could be argued it is inappropriate to compare Tier-I and Tier-III values in this way. The reality is that regional estimates of biomass are being made with Tier-I models for root/shoot biomass. The above example thus serves to illustrate the problems inherent in such an approach.

Summary and next steps

The ecophysiological controls on root biomass and distribution are sufficiently well-studied to describe and, to some extent, make predictions over large landscapes or gross ecological transitions. Roots function as organs for nutrient and water uptake, as structural elements to keep trees upright, and, in some cases, to regenerate a stem after disturbance (Pregitzer and Friend

1996, Nadezhdina et al. 2003). At smaller spatial scales, it has not been possible to model root biomass based on ecophysiological controls, since the measurement of all the necessary inputs for a working model are impractical. A statistical model based on the measurement of above-ground biomass is recommended.

The current data used by the IPCC should be improved to for inference of below-ground biomass from above-ground biomass. The current sample is biased and the associated estimates of precision flawed. The sample should be augmented using basic sampling principles, beginning with amplification of largely temperate data with data from tropical forests. Data could be collected as part of the growing number of countries involved in greenhouse gas inventories via the United Nations Framework Convention on Climate Change (UNFCC), or another comparable mechanism. Data should be collected using a system of cores, GPR measurements, and some limited excavation to estimate taproot biomass and calibrate GPR to the site.

Once measured with sufficient coverage and in an unbiased way, estimates of root biomass should be relatively straightforward to tie to existing estimates of above-ground biomass. Numerous studies have demonstrated a strong predictive relationship between root biomass and above-ground biomass (Cairns et al. 1997, Mokany et al. 2006). In addition to refining these estimates of coarse root biomass using model covariates, there is both theoretical and empirical support for the use of leaf area as a predictor of fine root biomass (Shinozaki et al. 1964, Chapter 1). Both leaf area and biomass can be estimated, at least at a 30m resolution from LANDSAT. It is feasible then to use these data for regional estimates of above-ground biomass, tied to a network of plots in which below-ground biomass has been measured. This effort, coordinated globally, would then provide a sound basis for the estimation and modeling of global terrestrial biomass.

Figures and Tables

Vegetation category	slope	DF	SE (95%)	p	Data points	Mokany median	Mokany SE
Tropical/Subtropical/Temperate Dry Woodland	0.10	2	0.37	0.82	6	0.32	0.09
Tropical/Subtropical Moist Woodland	0.39	2	0.12	0.08	6	0.42	0.03
Tropical/Subtropical Dry Forest (>20t/ha)	NA	NA	NA	NA	2	0.28	0.00
Tropical/Subtropical Dry Forest (<20t/ha)	0.41	2	0.41	0.43	4	0.56	0.09
Tropical / Subtropical Moist Forest (>125t/ha)	0.29	4	0.01	**0.00**	10	0.24	0.01
Tropical / Subtropical Moist Forest (<125t/ha)	0.23	2	0.01	**0.00**	4	0.21	0.04
Temperate Oak Forest (>70t/ha)	0.12	9	0.04	**0.01**	14	0.30	0.07
Temperate Eucalypt Forest/Plantation (50-150t/ha)	0.25	6	0.09	**0.04**	11	0.28	0.06
Temperate Eucalypt Forest/Plantation (>150t/ha)	0.49	1	0.14	0.18	6	0.20	0.03
Temperate Eucalypt Forest/Plantation (<50t/ha)	0.36	6	0.04	**0.00**	10	0.44	0.05
Temperate Conifer Forest/Plantation (50-150t/ha)	0.20	12	0.11	0.08	19	0.29	0.02
Temperate Conifer Forest/Plantation (>150t/ha)	0.27	1	0.12	0.27	10	0.20	0.03
Temperate Conifer Forest/Plantation (<50t/ha)	0.40	26	0.02	**0.00**	33	0.40	0.04
Other Temperate Broadleaf Forest/Plantation (75-150t/ha)	0.18	4	0.11	0.17	12	0.23	0.02
Other Temperate Broadleaf Forest/Plantation (>150t/ha)	0.42	0	0.08	NA	10	0.24	0.03
Other Temperate Broadleaf Forest/Plantation (<75t/ha)	0.31	7	0.12	**0.03**	14	0.46	0.06
Boreal Forest (>75t/ha)	0.14	11	0.03	**0.00**	18	0.24	0.02
Boreal Forest (<75t/ha)	0.21	6	0.04	**0.00**	13	0.39	0.06

Table 9: Comparison of ratios presented by Mokany et al. between below-ground and above-ground biomass to the relationship between above ground and below-ground biomass modeled using a linear mixed effects model with a Gaussian error distribution. Significant relationships are in bold.

Vegetation category	slope	DF	SE (95%)	p
Boreal coniferous forest	0.18	15	0.03	0
Boreal mountain system	12.31	3	2.18	0.01
Boreal tundra woodland	NA	NA	NA	NA
Polar	-0.24	8	0.19	0.24
Subtropical desert	0.25	5	0.01	0
Subtropical dry forest	0.14	10	0.06	0.04
Subtropical humid forest	0.18	7	0.01	0
Subtropical mountain system	0.26	19	0.01	0
Subtropical steppe	0.35	20	0.03	0
Temperate continental forest	0.21	15	0.03	0
Temperate desert	3.43	1	2.43	0.39
Temperate mountain system	0.27	25	0.04	0
Temperate oceanic forest	0.25	1	0.03	0.08
Temperate steppe	0.26	12	0.05	0
Tropical desert	0.26	5	0.03	0
Tropical dry forest	0.56	11	0.06	0
Tropical moist deciduous forest	0.15	7	0.04	0.01
Tropical mountain system	0.24	2	0.05	0.04
Tropical rainforest	0.28	3	0.02	0
Tropical shrubland	0.11	5	0.02	0.01

Table 10: Fitted models for a model of below-ground biomass based on above-ground biomass for the GEZ. The model used is based on a hierarchical linear model with slope constrained to zero. Data is that from which the ratios used by IPCC as defaults are estimated.

Vegetation classification	n	Unique locations	Maximum proportion of data represented by any one location
Temperate conifer plantation	2	1	1.00
Tropical/Subtropical Dry Forest (<20t/ha)	4	1	1.00
Tropical/Subtropical Dry Forest (>20t/ha)	2	1	1.00
Boreal Forest (>75t/ha)	18	6	0.67
Tropical/Subtropical Moist Woodland	6	3	0.67
Tropical/Subtropical/Temperate Dry Woodland	6	3	0.67
Temperate Eucalypt Forest/Plantation (<50t/ha)	10	3	0.60
Tropical / Subtropical Moist Forest (>125t/ha)	10	5	0.60
Temperate Oak Forest (>70t/ha)	14	4	0.57
Temperate Eucalypt Forest/Plantation (>150t/ha)	6	4	0.50
Temperate Eucalypt Forest/Plantation (50-150t/ha)	11	4	0.45
Temperate Conifer Forest/Plantation (<50t/ha)	33	6	0.36
Other Temperate Broadleaf Forest/Plantation (<75t/ha)	14	6	0.36
Temperate Conifer Forest/Plantation (50-150t/ha)	19	6	0.32
Other Temperate Broadleaf Forest/Plantation (75-150t/ha)	12	7	0.25
Tropical / Subtropical Moist Forest (<125t/ha)	4	4	0.25
Boreal Forest (<75t/ha)	13	6	0.23
Other Temperate Broadleaf Forest/Plantation (>150t/ha)	10	9	0.20
Temperate Conifer Forest/Plantation (>150t/ha)	10	8	0.20

Table 11: Sample size, number of unique locations, and maximum proportion of sample size from one location by ecosystem, using the Mokany et al. (2006) dataset.

Ecological zone/Domain	Percent Absolute difference of median, IPCC and Mokany	1st Quartile, Mokany et al.	3rd Quartile Mokany et al.	Median IPCC ABG Default
Boreal Forest	79.75%	43.46	128.7	**17.5**
Subtropical Coniferous Forest	64.29%	7.99	134.8	75
Subtropical Eucalyptus Forest	6.40%	23.52	138.6	75
Subtropical Broadleaf Forest	27.18%	42.65	153	75
Subtropical Oak Forest	73.69%	239.2	379.5	75
Subtropical Dry Forest	1150.00%	10.2	56.51	**150**
Subtropical Moist Forest	11.90%	109.8	232.8	220
Temperate Coniferous Forest	173.82%	7.99	134.8	125
Temperate Eucalypt Forest	77.33%	23.52	138.6	125
Temperate Broadleaf Forest	21.36%	42.65	153	125
Temperate Oak Forest	56.16%	239.2	379.5	**125**
Tropical Dry Forest	1108.33%	10.2	56.51	**145**
Tropical Moist Forest	22.08%	109.8	232.8	**240**
Tropical	59.15%	NA	NA	140

Table 12: Comparison between the above-ground biomass defaults by ecosystem used in IPCC GHG inventory guidance (Aalde et al. 2006) and AGB values in data used to derive root shoot ratios (Fittkau et al. 1973, Mokany et al. 2006). Units are tonnes dry biomass ha^{-1}. Bolded values for the median IPCC ABG defaults are those outside the inner quartile range for the corresponding vegetation type used in Mokany et al (2006).

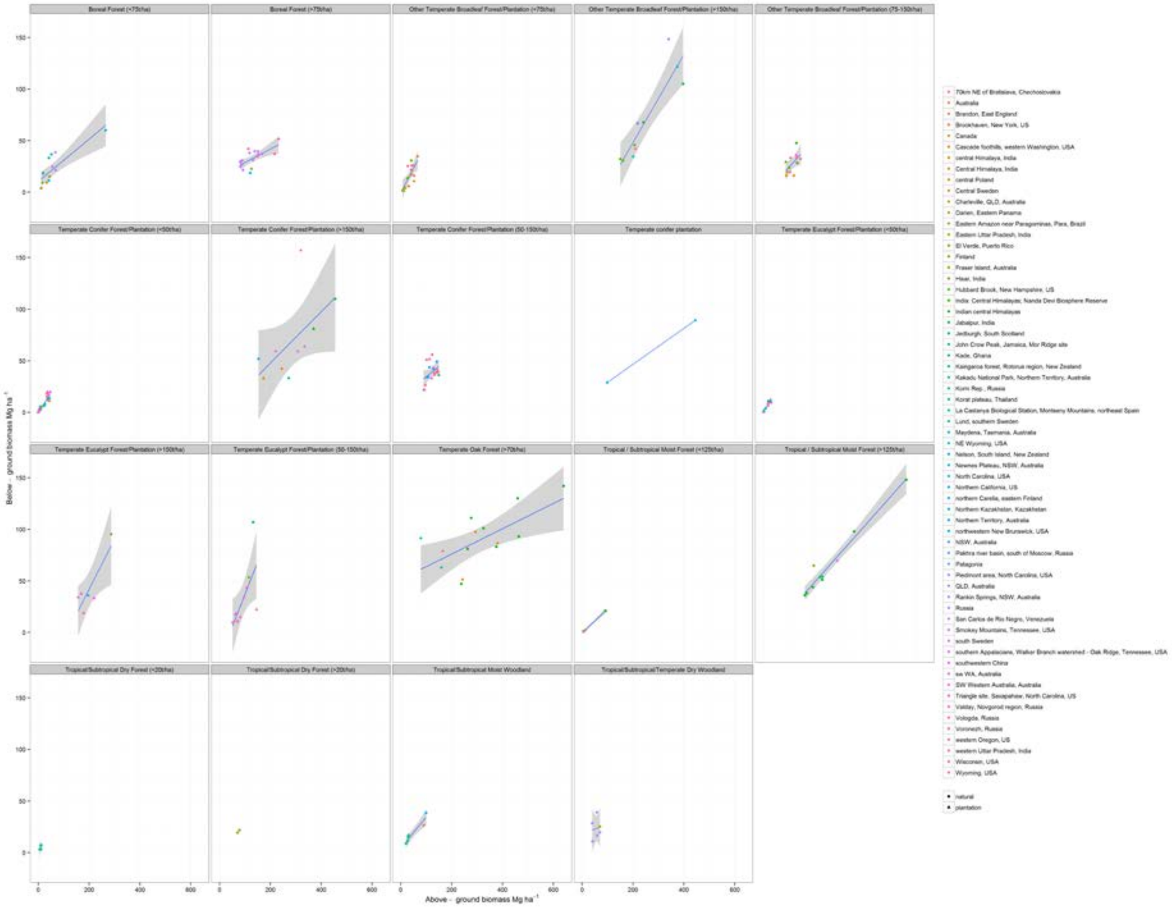


Figure 26: Relationship between above and below-ground biomass modeled using a first-order polynomial by vegetation type. Confidence intervals are the SE of the slope at the 95% level. Data and vegetation types from Mokany et al.

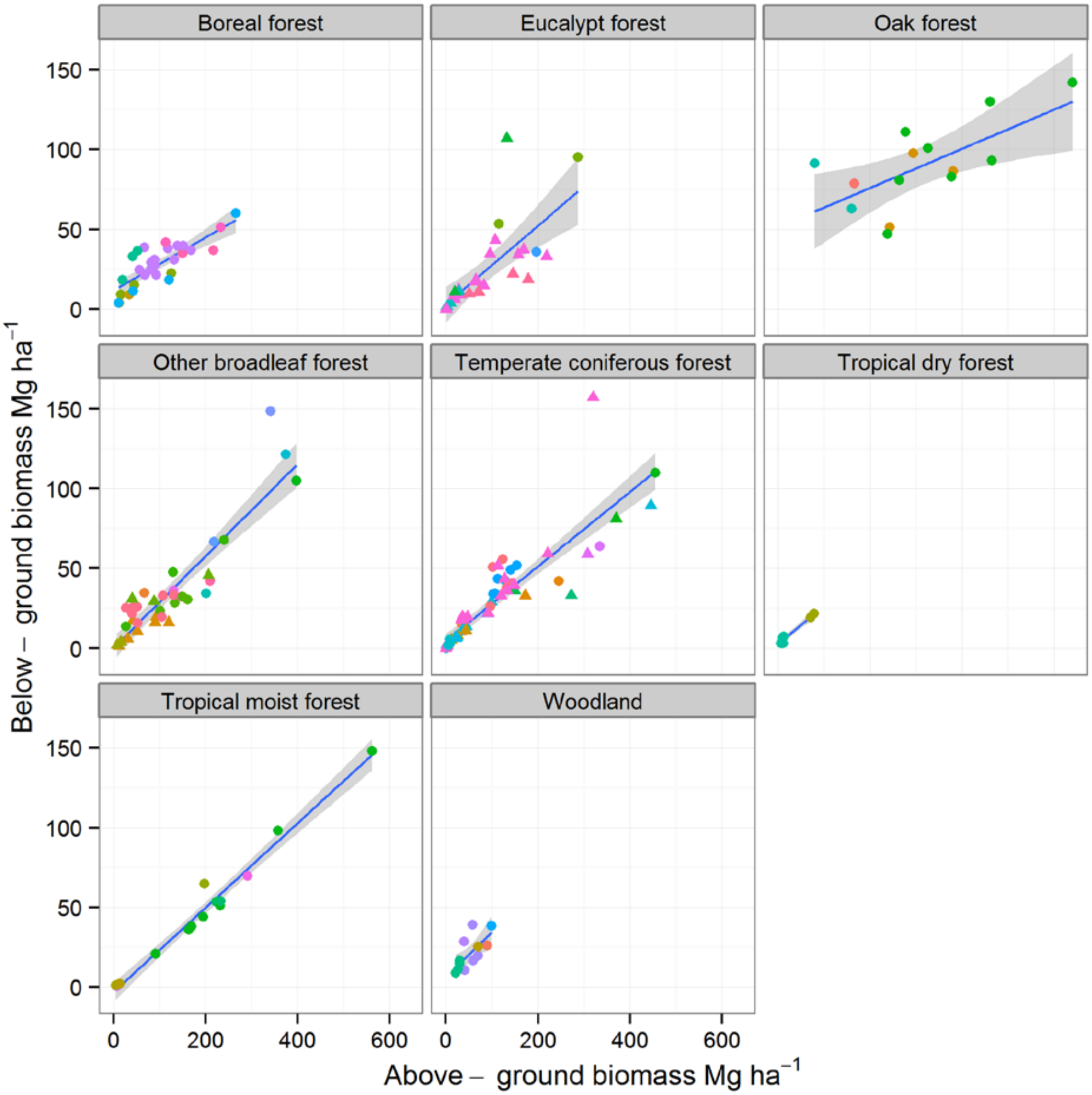


Figure 27: Vegetation categories used by Mokany et al., pooled without regard to biomass. Error bars shown are se of the slope at the 95% confidence level.

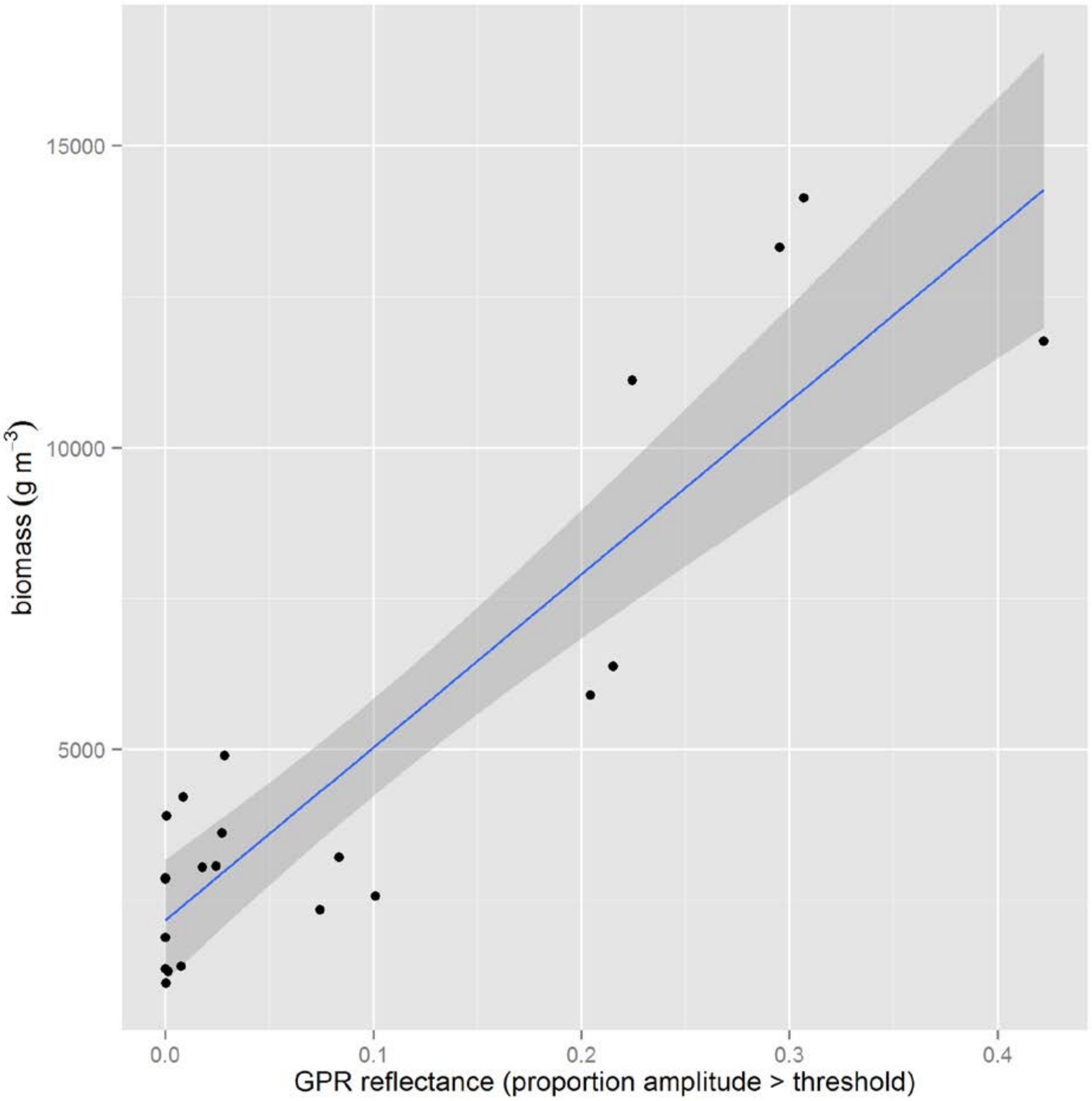


Figure 28: Example of sample data for estimation of root biomass using data from a GPR. Data from Chapters 1 and 2. Adj. R^2=.8.

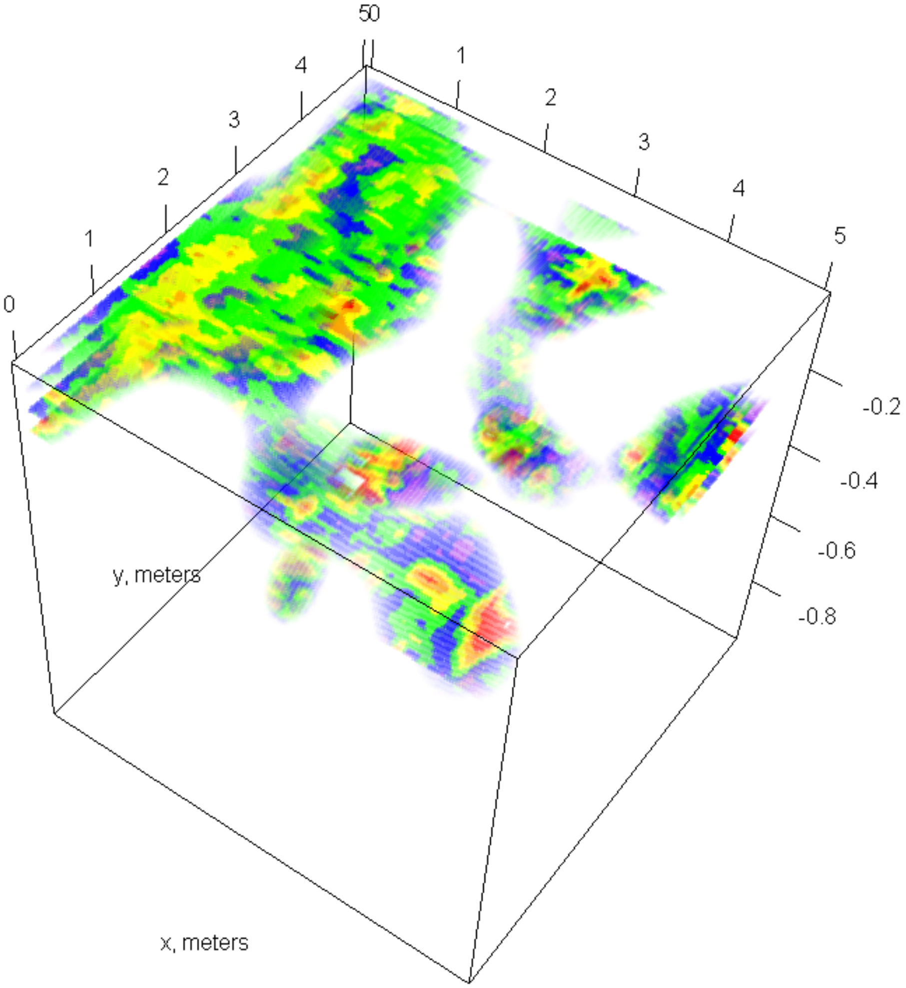


Figure 29: Root image generated using data from a GPR scan in a coast redwood (*Sequoia sempervirens*) forest.

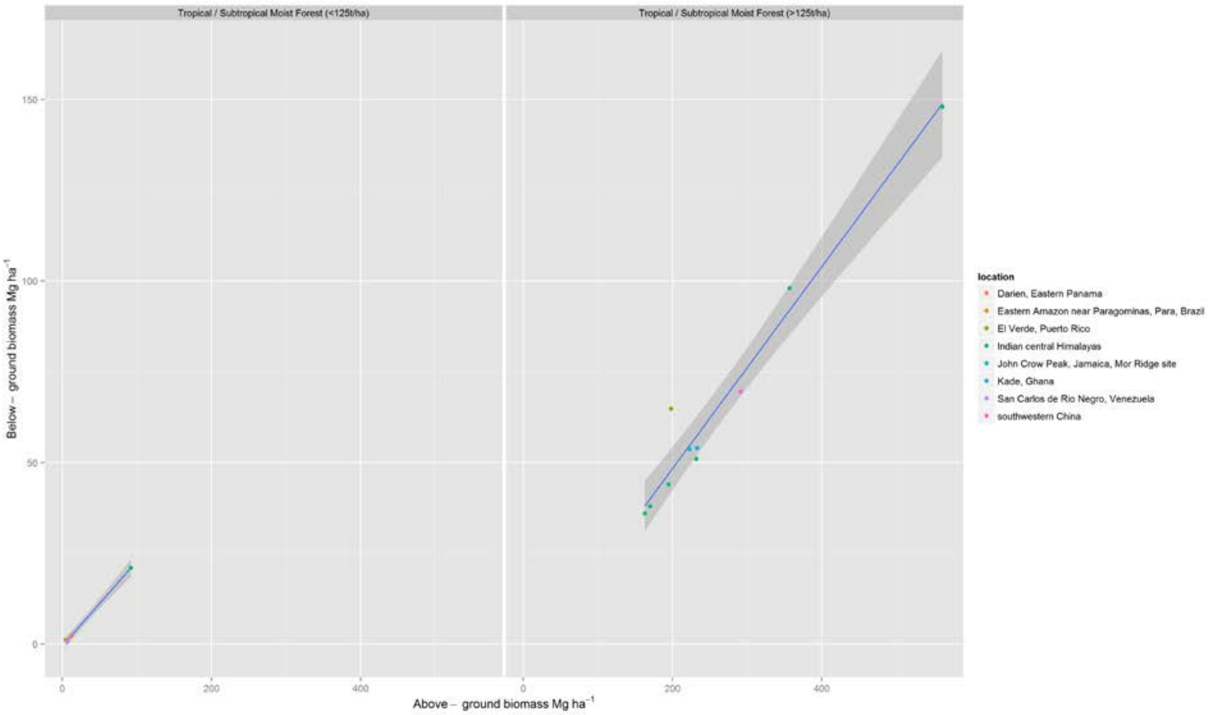


Figure 30: Relationship between above and below-ground biomass for moist tropical forests, Mokany et al. (2006) data.

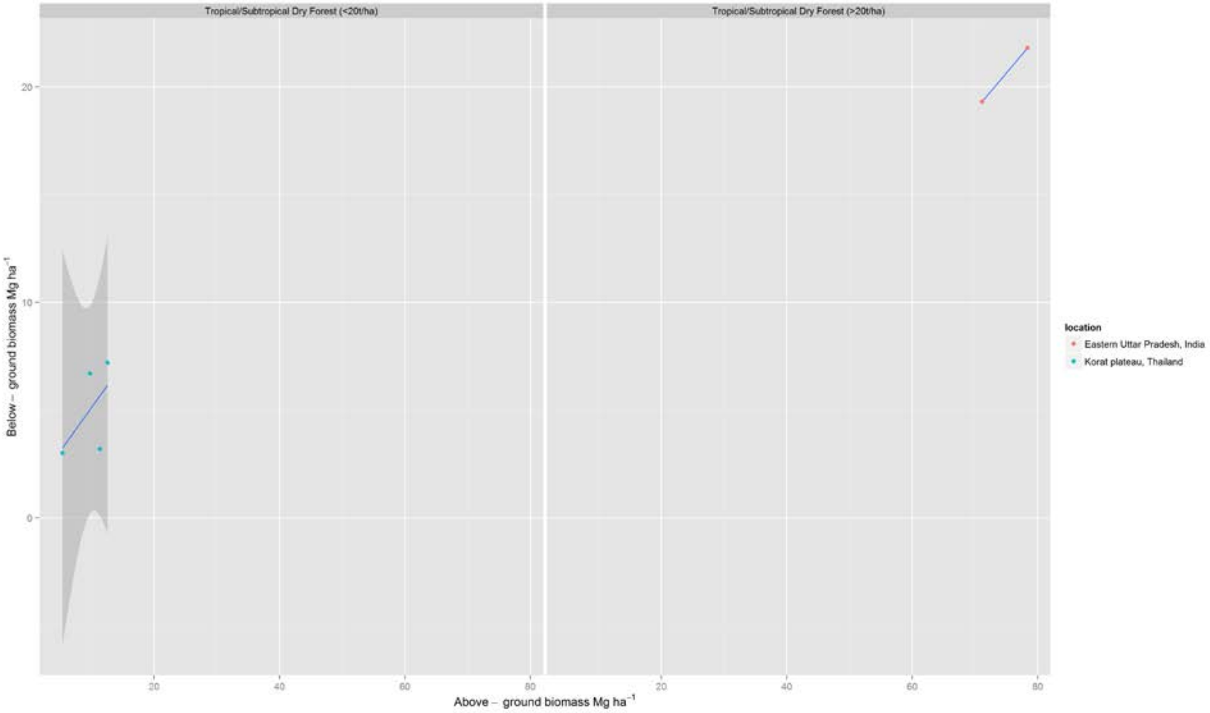


Figure 31: Relationship between above and below ground biomass, Tropical and subtropical dry forest, Mokany et al. data.

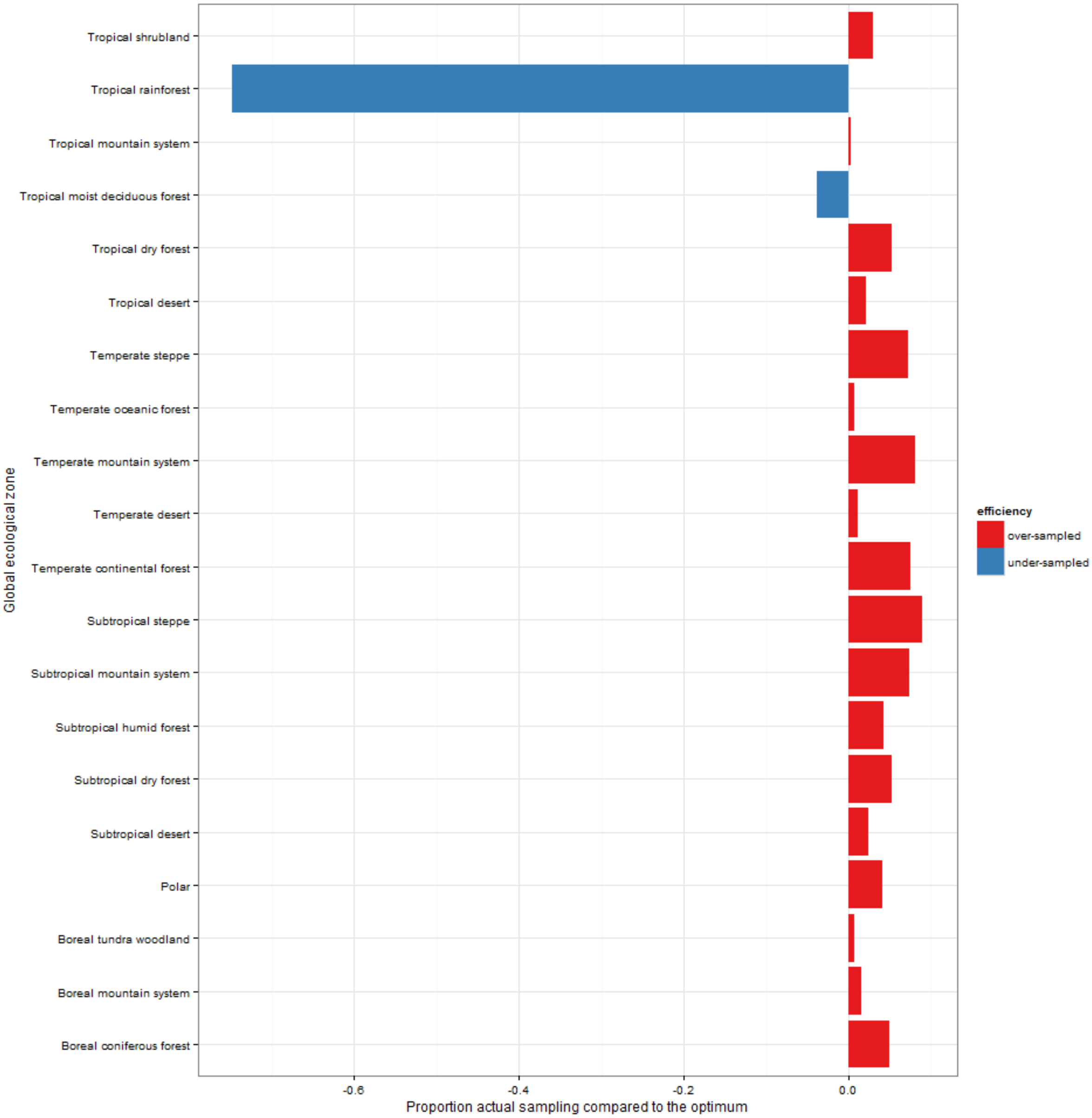


Figure 32: A comparison of the optimal vs the actual sampling effort for estimation of R/S ratios by GEZ, as a proportion.

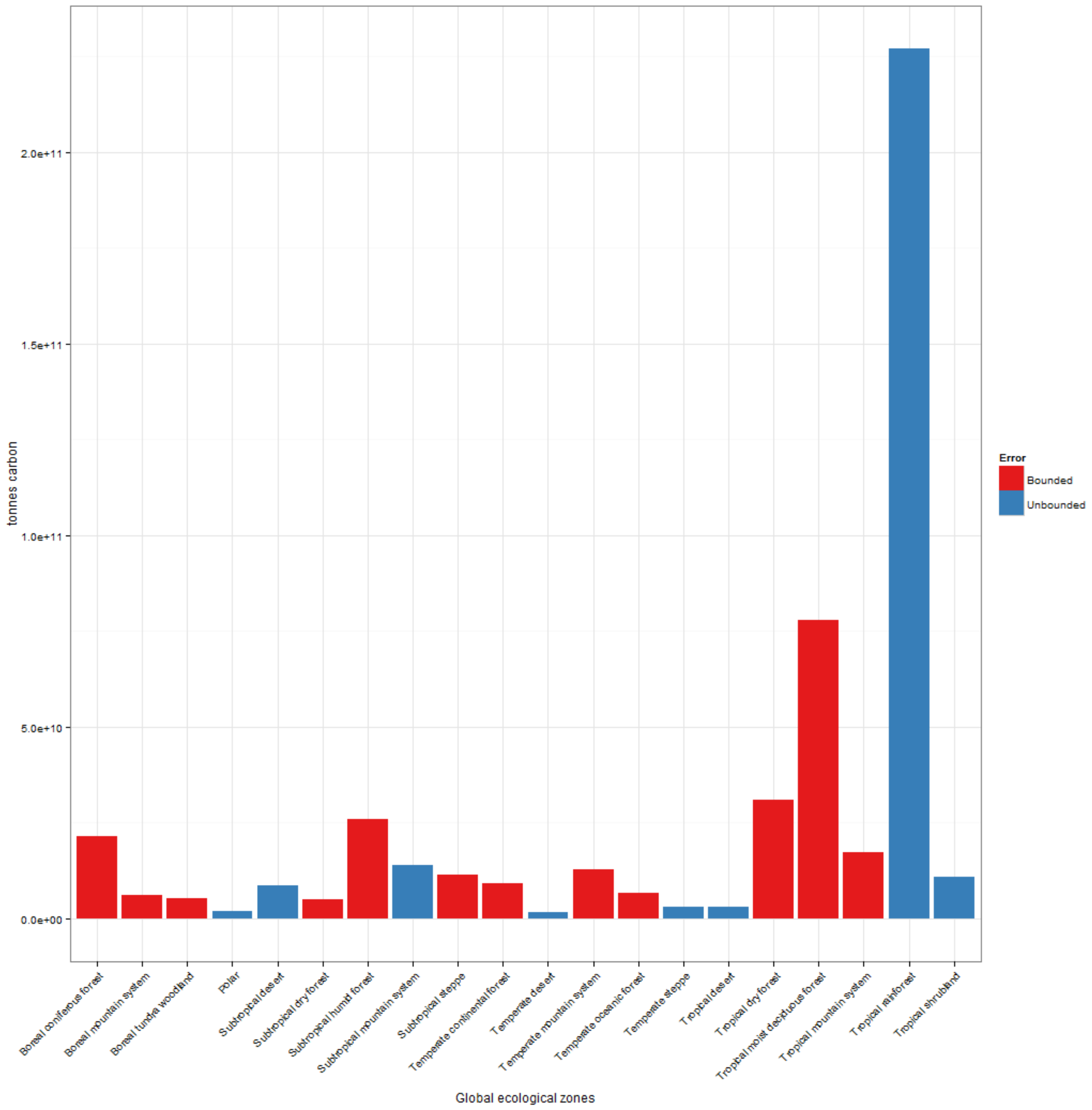


Figure 33: Size of the carbon pool by GEZ. Unbounded error indicates a sample size of one.

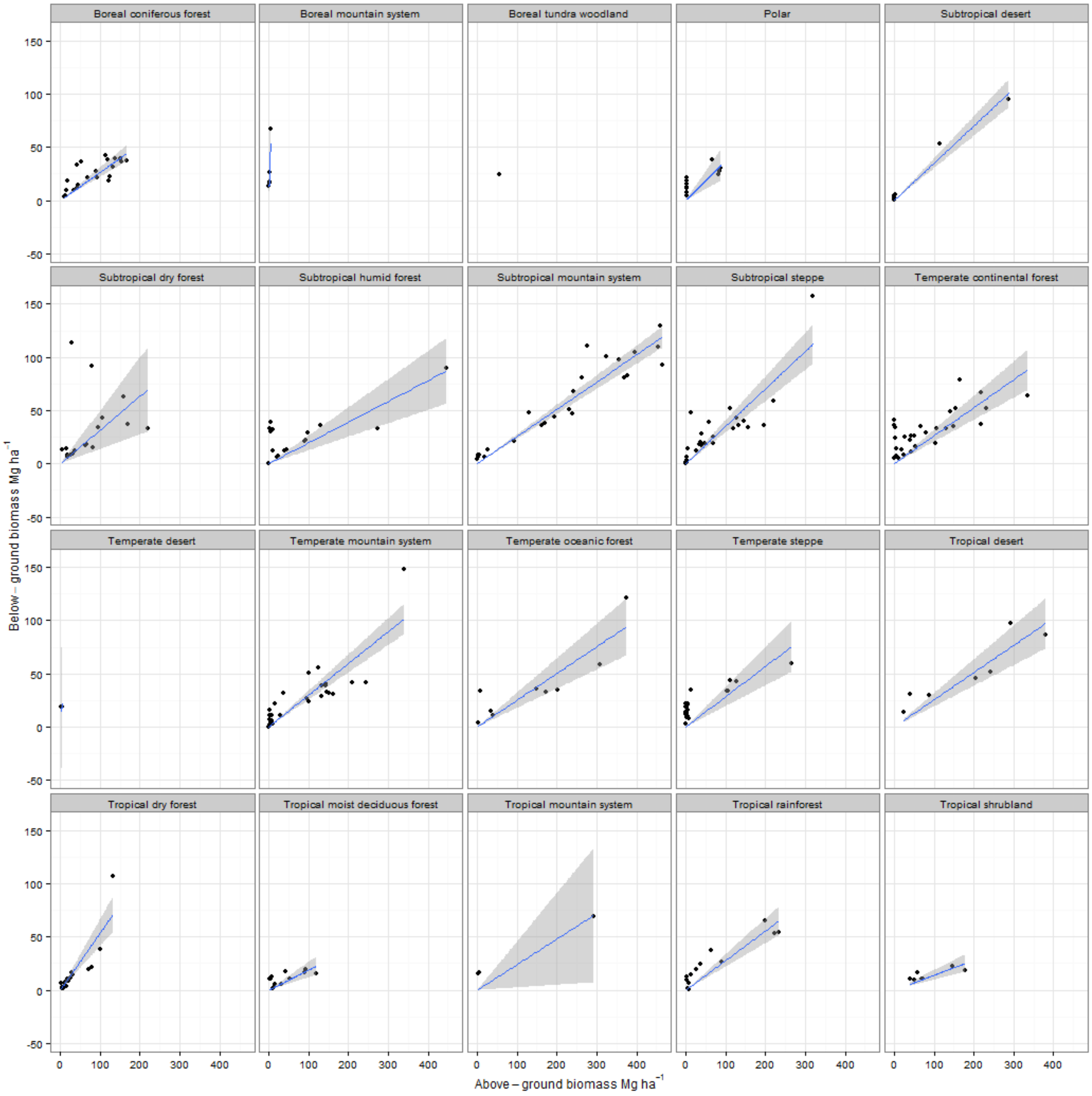


Figure 34: Modeled relationships between above-ground and below-ground biomas for the Global ecological zones based on the data used by the IPCC. Intercept constrained to zero. Error bars are the standard error of the estimated slope at the 95% confidence level.

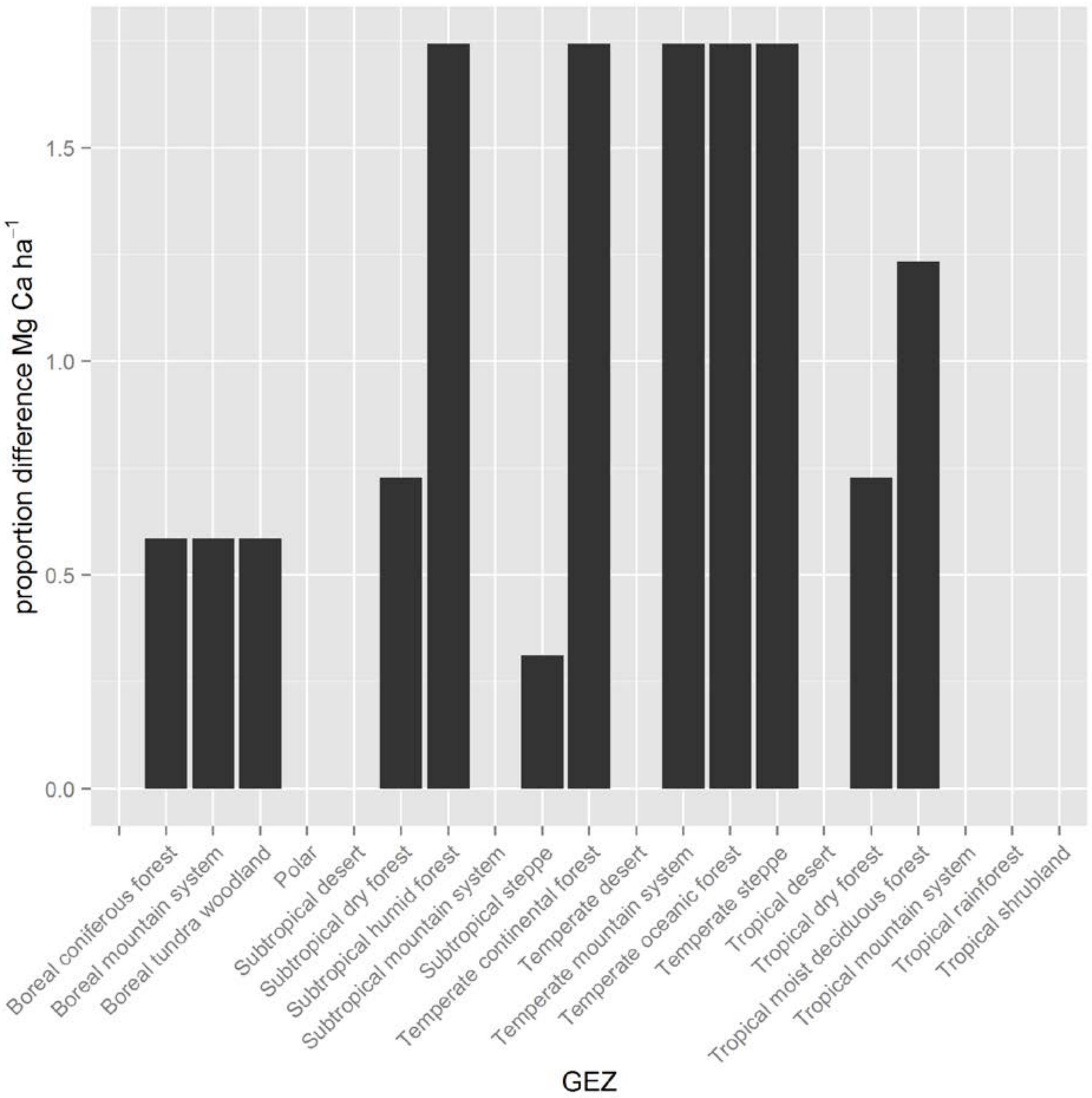


Figure 35: Effect size of using ratio instead of regression estimates for estimating belowground biomass. Units are Mg of belowground biomass.

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