FINDING NONDESTRUCTIVE PARAMETERS FOR ROOT-TO-SHOOT RATIOS IN DOUGLAS-FIR, GRAND FIR, AND REDWOOD SAPLINGS IN NORTHWEST CALIFORNIA FOR BIOMASS AND CARBON STORAGE ESTIMATES

By

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ABSTRACT

FINDING NONDESTRUCTIVE PARAMETERS FOR ROOT-TO-SHOOT RATIOS IN DOUGLAS-FIR, GRAND FIR, AND REDWOOD SAPLINGS IN NORTHWEST CALIFORNIA FOR BIOMASS AND CARBON STORAGE ESTIMATES

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There is a need for better understanding of how woody biomass is allocated above and belowground and how this allocation might differ among tree species. In this field of research, investigators face challenges such as the laborious task of removing trees from the soil with destructive sampling, and the cleaning, drying, and weighing of belowground biomass (BGB). Therefore, researchers and practitioners most often rely on existing models to predict BGB from easily-measurable aboveground variables such as stem diameter and height. Such models have been developed for many tree species, but commonly these models require inputs of diameter at breast height (dbh) and are not designed to make predictions for younger saplings (i.e., below 5 cm dbh). To fill knowledge gaps in young conifer BGB allocation, we studied three conifers native to the north coast of California: coast redwood (*Sequoia sempervirens)*, coast Douglas-fir (*Pseudotsuga menziesii* var *menziesii*), and grand fir (*Abies grandis)*. We sought to determine: (i) Does the root-to-shoot ratio differ between the three species Douglas-fir, grand fir, and coast redwood in afforestation plots? (ii) Does the root-to-shoot ratio of the three species differ according to age (i.e. sampling across a span of three years?) (iii) Does the competing flora alter the root-to-shoot ratio of any of the three species? (iv)

What are the best “easily-measurable” aboveground variables to be included in prediction equations for BGB in the three tree species?

Experimental plots were planted in 2008/09, and another in 2009/10 at the L. W. Schatz Demonstration Tree Farm located in Humboldt County, CA. Five species were planted: coast redwood, coast Douglas-fir, grand fir, red alder (*Alnus rubra*), and black cottonwood (*Populus balsamifera*). Redwood, Douglas-fir, and grand fir were destructively sampled for BGB measurement. A random sample of these three species were excavated by hand, and separated into three sections: stems, roots and branches. Each species had 24 trees sampled across the 3 years of data collection for a total of 72 trees. The sapling biomass components were weighed, dried in an oven, and re-weighed to determine bone dry weight and root-to-shoot biomass ratios.

Before final root-to-shoot ratios and BGB models were created, auxiliary models were developed to predict the weight of any roots that were broken off during the excavation of the saplings. Models for severed root weight were tested against sapling height, average crown width, lower crown base height, and stem diameter. Results showed high correlation between root weight and stem diameter at ground line (caliper, mm). Exponential models made the best predictions of weight of individual pieces of broken root for all three species: Douglas-fir (R^2= 0.86), grand fir (R^2= 0.91), and redwood (R^2= 0.79).

After missing root weights had been predicted for each broken root on the root system of each sample tree, summed, and added to the overall root mass, equations to predict BGB were developed and tested. Multivariable models were tested for all three species, but showed no statistical significance. Bivariate regressions of BGB as function of tree height (cm), average crown width (cm), lower crown base height (cm), stem diameter (mm), year, and percent cover of competing flora were tested. In species-specific bivariate regressions, tree height, average crown width, and stem diameter were all found to be statistically significant predictors of BGB for all three species. Douglas-fir BGB was best predicted with a linear model utilizing caliper as the explanatory variable (R^2= 0.77). Grand fir BGB was also predicted well by a linear model with caliper as the explanatory variable (R^2= 0.92). Redwood BGB exhibited an exponential relationship with caliper (R^2= 0.91).

Root-to-shoot ratios for the three species averaged between 0.27 and 0.46. All variables tested for BGB were also tested as predictor of root-to-shoot ratios, however for Douglas-fir and grand fir, no significant relationships between root-to-shoot ratio and the candidate predictor variables were found. For redwood, stem diameter, average crown width, and sapling height all were significant predictors of root-to-shoot ratio. Redwood sapling height was the best predictor of root-to-shoot ratio (R^2= 0.37). For all three species, ANOVA tested for differences in root-to-shoot ratios among sample ages. The youngest Douglas-fir saplings (three years old) had higher root-to-shoot ratio than the five and seven year old trees. Grand fir showed no differences in root-to-shoot ratios according to age. Redwood root-to-shoot ratios were significantly different between ages three and four, between ages four and five, and between ages four and six years old.

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1. INTRODUCTION

Trees sequester CO_2 from the atmosphere and store it as carbon in above and belowground biomass. Since CO_2 is a greenhouse gas, trees have the potential to offset CO_2 emissions causing climate change. We need better understanding of relationships between carbon, tree size, and forest growth to inform forest management and policy makers.

With growing concerns about greenhouse gas emissions and ways to mitigate for the harmful effects, we need to find solutions for rising atmospheric carbon that can be implemented quickly. In response to this need, in 1992 several countries agreed to the United Nations Framework Convention on Climate Change (UNFCCC). The UNFCCC had the goal of developing inventories of greenhouse gas emissions and sinks, or places carbon could be stored. They also wanted to find ways to increase sinks and lower the overall net greenhouse gas emissions (FAO, 2001). In 1997, the UNFCCC agreed on the Kyoto Protocol to reduce greenhouse gas emissions to $\leq$ 5% 1990 levels by 2012. This protocol allowed countries that emit more carbon than the agreed upon limit to purchase carbon offsets from countries or areas that have carbon sinks.

There are three ways that forest managers can help increase carbon sinks and produce carbon credits to sell. The first way carbon can be stored is carbon sequestration which includes afforestation, reforestation, restoration of damaged lands, and improved silvicultural techniques to increase tree growth rate. Carbon conservation is the second approach which includes conservation of biomass and carbon in soils, improved harvesting techniques to maximize wood processing efficiency, and better use of harvesting residuals from typical burning practices. The last way carbon can be handled is carbon substitution that is intended to convert forest biomass into durable wood products that will replace other energy dependent products, increased use of waste material for biofuels and bioenergy production, and carbon storage in live biomass plantations before use as biofuel (Montagnini & Nair, 2004). The carbon conservation has potential for fast mitigation; however there is a cap that will likely be reached in conservation. For more long term mitigation carbon sequestration would be the more favorable option. Afforestation and reforestation both promote carbon sequestering and storage in long-lived organisms (Trabucco et al., 2008).

For carbon assessment in forests and the modeling and sale of carbon credits, we must accurately estimate the biomass in each tree. There are numerous equations and methods to estimate aboveground biomass (AGB) for hardwoods and conifers (Cairns et al., 1997). Unfortunately, there has been less research into estimating belowground biomass (BGB) in root systems of trees due to the difficulty of sampling. Estimating root biomass from aboveground measurements to circumvent destructive sampling will help economically and efficiently predict carbon storage in trees (Nielson & Hansen, 2006). A better understanding of belowground carbon sequestration and storage should give policy makers confidence to include tree roots in carbon calculations and the sale of carbon offsets.

Root biomass allocation has been studied in several tree species. It is variable among and within species. For example, Namm (2012) extracted 10 adult tanoaks (*Notholithocarpus densiflorus*) root systems to determine root-to-shoot ratios of single or multi-stemmed tanoak. He reported root-to-shoot biomass ratio between .11 and .65 showing the wide range of ratios that can occur in one species. Tanoak root-to-shoot ratio varied according to tree size and stand density. Root morphology models were developed to predict biomass of tanoak roots lost during excavation (Namm & Berrill, 2016). Van Hees & Clerkx (2003) found 37-46% of biomass for pedunculate oak *(Quercus robur)* and as high as 41-50% for beech (*Fagus sylvatica*) was found belowground.

Root biomass allocation patterns vary according to tree size and age. Monk (1966) examined root systems for adult loblolly pine (*Pinus taeda*) to determine dry root mass, and discovered that root-to-shoot ratios were lower in trees with larger DBH. Jenkins et al. (2003) showed that root biomass allocation decreases sharply as tree size increases to 10 cm DBH, then decreases slowly as tree size increases further. Unknown is how competing flora may help or hinder a species belowground carbon storage ability (Monk, 1966). More research into root biomass allocation in younger trees is needed to better understand how carbon storage might change throughout the life of the tree (Brown, 2002). This information will allow for better understanding of how much and where carbon is stored in young forests. Accurate total biomass measurements will inform studies of carbon dynamics in reforestation and afforestation projects. The difficulty and cost of destructive sampling for root biomass motivates us to develop regression equations that predict BGB and root-to-shoot ratios in younger trees at different ages.

According to the California State Air Resources Board (ARB), two methods are in use to account for BGB in forest carbon offset programs. All states besides California, Oregon, and Washington use the United States Forest Service's Component Ratio Method (CRM) (California Air Resource Board, 2013a). The CRM estimates volume in the non-bole components of the tree as ratios of total AGB. These volumes are summed to give total AGB and BGB converted to tons of carbon dioxide equivalents (CO_2e) on a per acre basis. For California, Oregon, and Washington, various equations are used to predict bole volume and total AGB (California Air Resource Board, 2013b). The estimates are then converted to CO_2e and summed for all trees to give AGB on a per acre basis. For BGB in these states, the Cairns equation's (Cairns et al., 1997) must be used to calculate CO_2e. Cairns et al. (1997) used an assemblage of data from the literature to develop regression equations to predict BGB. A problem with this method that Cairns et al. (1997) discuss is that this approach can lead to an overestimation of BGB as high as 20%. This lessens our confidence in predictions of BGB and suggests more destructive sampling and model building is needed.

This thesis describes a study of BGB in three commercially and ecologically important conifers native to north coastal California: coast redwood (*Sequoia sempervirens)*, coast Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*), and grand fir (*Abies grandis)*. The objective was to study factors hypothesized to affect BGB and root-to-shoot ratio, then develop predictive models allowing users to estimate BGB from easily-measurable aboveground variables. Variables hypothesized to affect BGB and root-to-shoot ratio were tree species, size, age, and weed competition in young trees excavated from two mixed plantations in different years.

2. METHODS

2.1 Site Description

The conifer saplings were excavated from two mixed plantations located at the L.W. Schatz Demonstration Tree Farm (LWSDTF) 40°46'06.7"N 123°52'12.6"W, approximately 40 km inland of Arcata in Humboldt County, California. The LWSDTF covers approximately 150 hectares and is owned and used by Humboldt State University as an experimental forest and teaching aid for students and faculty.

Coastal fog rarely reaches inland as far as the LWSDTF, so the Mediterranean climate of the LWSDTF has warmer dry summers reaching average highs of 25.8 °C in August. The average high and low temps for the coolest month are 0.3 and 12.2 °C for January. Annual rainfall in the region averages 1010 mm and typically falls in the winter months of November through March (Western Regional Climate Center, 2015).

The study site occurs within the Coastal Range Geomorphic Province and is comprised mostly of the Franciscan Complex. The Franciscan Complex contains "graywacke, shale, minor conglomerate, radiolarian chert and siliceous shale, minor limestone, volcanic rocks, mafic-ultramafic putonic rocks, and their zeolite-to-blueschist-facies metamorphic equivalents" (Berkland et al., 1972).

The old-growth Douglas-fir forests were cleared from the area in the 1950s and 1960s, and grazing was attempted. Unstable geology and other factors such as unwanted tree regeneration impacted pastoralism, prompting interest in restoring forest cover. Tanoak and other hardwoods regenerated naturally. Sporadic natural regeneration of Douglas-fir was supplemented by planting in an attempt to restore cover and productivity using this merchantable native species. A few grand fir and hemlock had also regenerated naturally and their advanced regeneration can now be found in the understory. Decades after the original harvest, some redwoods were planted under the shade and shelter of heavily thinned tanoak/fir stands and survive to this day. Unknown was whether redwood plantations could be established in full sun, outside of their natural range for this location, and how they would fare compared to the locally-adapted firs.

To compare survival and growth of planted redwood, Douglas-fir, grand fir, and other species in mixed even-aged plantations, two experimental test plots were planted within 2009; the first experimental test plot (site #1) was planted in February of 2009, while the second experimental test plot (site #2) was planted one growing season later in December of 2009. The first experimental test plot covered an area approximately 10 × 40 m (33 × 132 ft). It was planted with five species: Douglas-fir, grand fir, coast redwood, along with red alder (*Alnus rubra*), and black cottonwood (*Populus trichocarpa*) that were not sampled for BGB. Seedlings were acquired though Smith River Nursery, Hastings LLC. Ten replicates of each species (40 trees per species) were planted in four-tree row plots with 1 m spacing between trees, and 2 m spacing between each row resulting in 5,000 stems/ha (~2,000 tpa). The second experimental test plot also covered an area approximately 10 × 40 m. The same replication, spacing, guard row, and nursery stock was utilized; however, because of establishment failures in the first experimental plot, bigleaf maple (*Acer macrophyllum*) was planted instead of cottonwood (but it also fared poorly). Both sites were mowed prior to planting and in between data collections.

2.2 Sapling Excavation and Data Collection

Data collection was done in the summer of 2013 when seedlings were just over three years old (i.e. >3 years since planting on site #2) or just over four years old (site #1), then in the summer of 2014 when they were just over four or five years since planting. A final data collection was performed when the trees were just over six years (site #2) or seven years since planting (site #1), between March 2016 and August 2016. In each data collection period, three random replicates of Douglas-fir, grand fir, and coast redwood were collected in site #1, and six replicates of the same species in site #2. Measurements of percent cover were made for vegetation type in the immediate vicinity; these included Scotch broom (*Cytisus scoparius*), poison oak (*Toxicodendron diversilobum*), salal (*Gaultheria shallon*), coyote brush (*Baccharis pilularis*), grasses, forbs, and self-seeded conifers or hardwoods (Figure 1A). Sapling height (cm), live crown base height (cm), stem diameter at ground line (caliper; mm), crown width (cm), and presence/absence of browsing was recorded before excavation began. Each sapling was marked at the ground line for reference after the sapling was removed from the soil. Shovels were used to excavate as many of the roots as possible (Figure 1B). Maximum coarse root depth (mm) was recorded after the sapling was removed. The excavated sapling was separated into stem, branch, and root biomass components (Figure 1C). For each sapling, the stem was removed from the roots at the mark of the ground line, and the branches removed from the stem. All stems, branches and roots were placed into separate labeled weighed bags and re-weighed to record the green weight. The bags were then placed in an oven set to

60^0C and weighed each day until the weight became constant, giving dry weights for roots, stem, and crown biomass components.

Figure 1.) Excavation techniques and data collection of 3 to 7-year-old saplings planted at the L.W. Schatz Demonstration Tree Farm, Humboldt County, CA. A.) Visual description of competing flora in vicinity of each sapling on study site. B.) Manual excavation technique capturing as many coarse roots as possible. C.) Example of excavated sapling (grand fir), before being separated into stem, branch, and root components. D.) Measuring small end diameter of roots >2 mm that broke during excavation.

2.3 Missing Root Measurements

Coarse roots were defined as roots with diameter >2 mm. It was common to find that some coarse roots broke during excavation. Once the root ball was separated from the stem, terminal diameter of any broken roots >2 mm was recorded (Figure 1D). Pieces of broken root that were recovered during excavation were stored separately for each sapling. The entire root system for each sapling was weighed green, then dried and weighed repeatedly until it reached constant weight. Individual roots were removed that were complete and terminated at a diameter of 2 mm or smaller. The total dry weight of each sapling's entire root system (including the root ball and coarse roots) was recorded.

All available pieces of coarse roots for each species were placed back in the oven (60^0C) until a stable weight occurred. Each root's large-end diameter was measured to a hundredth of a millimeter, then it's weight was recorded. These data were used to develop a regression model predicting the mass of any piece of root based on its large-end diameter. Linear and exponential models were created to account for the missing root mass, beyond the end of severed root ends >2 mm diameter. These models allowed for a better representation of total BGB of the saplings by replacing coarse root biomass lost during the excavation process with a prediction of biomass lost for each root that broke at a diameter > 2 mm.

2.4 Analysis of Factors Influencing Belowground Biomass and Root-to-Shoot Ratio

The below ground biomass (g) and root-to-shoot biomass ratio for each sapling was regressed against the following candidate explanatory variables: percent cover of competing flora (grass or shrub cover (%)), tree size (caliper (mm)), height (cm), live crown base height (cm), crown width (cm), tree age, and a categorical species variable to test for significant differences among Douglas-fir, grand fir, and redwood. Data were transformed to reduce skewness in distributions. Linear, polynomial, exponential, and power models were fitted using R 3.2.2 (R Foundation for Statistical Computing, 2015). The models were compared in terms of goodness of fit by taking the square root of the absolute residuals to determine error, normality was assessed through Q-Q plots along with Anderson-Darling normality tests, and influential outliers were identified by plotting Cook's distance. After testing sapling age through a linear model as a continuous variable assessing if age was significant, ANOVA and a TukeyHSD test were used to test for differences between sample ages. To determine the best predicters of BGB and root-to-shoot ratio for each species, competing models were compared in terms of Akaike information criterion with correction for small sample size (AICc). Model comparison information was reported in terms of Bayesian information criterion (BIC), R^2, Adjusted R^2, standard error of residuals, and the number of influential outliers. An influential outlier was defined as an observation with a Cook's distance > 1.

3. RESULTS

3.1 Missing Root Models

Regressing the weight and large-end diameter measured on individual pieces of coarse root gave models designed to predict root mass lost during excavation. A total of 75 Douglas-fir roots, 68 grand fir roots, and 55 redwood roots were measured. The number of separate pieces differed by species because all available roots were measured and weighed, and the Douglas-fir and grand fir saplings had more roots. Pieces of coarse roots lost during excavation amounted to 1-22% of the total BGB. Exponential models fit the data for root weight versus large-end diameter (LED) best and were selected for all three species (Table 1, Figure 2). These exponential models can be used to predict weight of a missing root in grams as a function of root diameter (LED; mm) at the broken end, such that:

$$\text{Douglas-fir missing root weight} = 0.36e^{0.31LED.} \qquad \text{(Eq.1)}$$

$$\text{Grand fir missing root weight} = 0.92e^{0.21LED} \qquad \text{(Eq.2)}$$

$$\text{Redwood missing root weight} = 0.58e^{0.27LED} \qquad \text{(Eq.3)}$$

Missing root biomass accounted for 0.3 to 8 % of total BGB in redwood, 0.04 – 4.8% in Douglas-fir and 4.5-9.8 % in grand fir.

3.2 Tree Components

On average, BGB represented up to 29% of the total tree biomass for the three conifer species. Results also showed that allocation of biomass to roots was comparable to stem biomass allocation in each of the species (Figure 3). Roots of individual Douglas-

Table 1.) Candidate broken root weight models – relationship between root weight (W; g), large-end diameter (D; mm), and model fit statistics for Douglas-fir (DF), grand fir (GF) and redwood (RW) sapling roots terminating at 2 mm small-end diameter. Best model shown in bold.

Species	*Equation*	*AIC*	*BIC*	*R^2*	*Adj. R^2*	*Residual SE*	*Outliers*
DF1	**$W= 0.36e^{0.31D}$**	**166.73**	**173.60**	**0.87**	**0.86**	**0.74**	**0**
DF2	$W=-1.67+1.35D-0.22D^2+0.02D^3$	170.50	181.95	0.87	0.86	0.75	5
DF3	$W=1.31-0.471D+0.106D^2$	174.98	184.14	0.85	0.85	0.78	7
DF4	$W=-1.86+0.802D$	200.65	207.52	0.79	0.78	0.93	4
GF1	**$W=0.92e^{0.21D}$**	**248.54**	**255.16**	**0.91**	**0.91**	**1.50**	**0**
GF2	$W =-1.79 +1.61D-0.21D^2+0.01D^3$	249.70	260.73	0.92	0.91	1.50	4
GF3	$W=4.13-1.89D+0.16D^2$	262.25	271.10	0.90	0.89	1.65	5
GF4	$W=-4.1+1.44D$	329.48	336.10	0.71	0.70	2.75	4
RW1	**$W= 0.58e^{0.27D}$**	**143.18**	**148.97**	**0.80**	**0.79**	**0.95**	**0**
RW2	$W=1.19-0.33D+0.10D^2$	141.77	149.50	0.81	0.80	0.93	3
RW3	$W=2.46-1.13D+0.25D^2-0.01D^3$	143.24	152.90	0.81	0.80	0.93	2
RW4	$W= -1.63+0.85D$	156.43	162.23	0.74	0.73	1.08	3

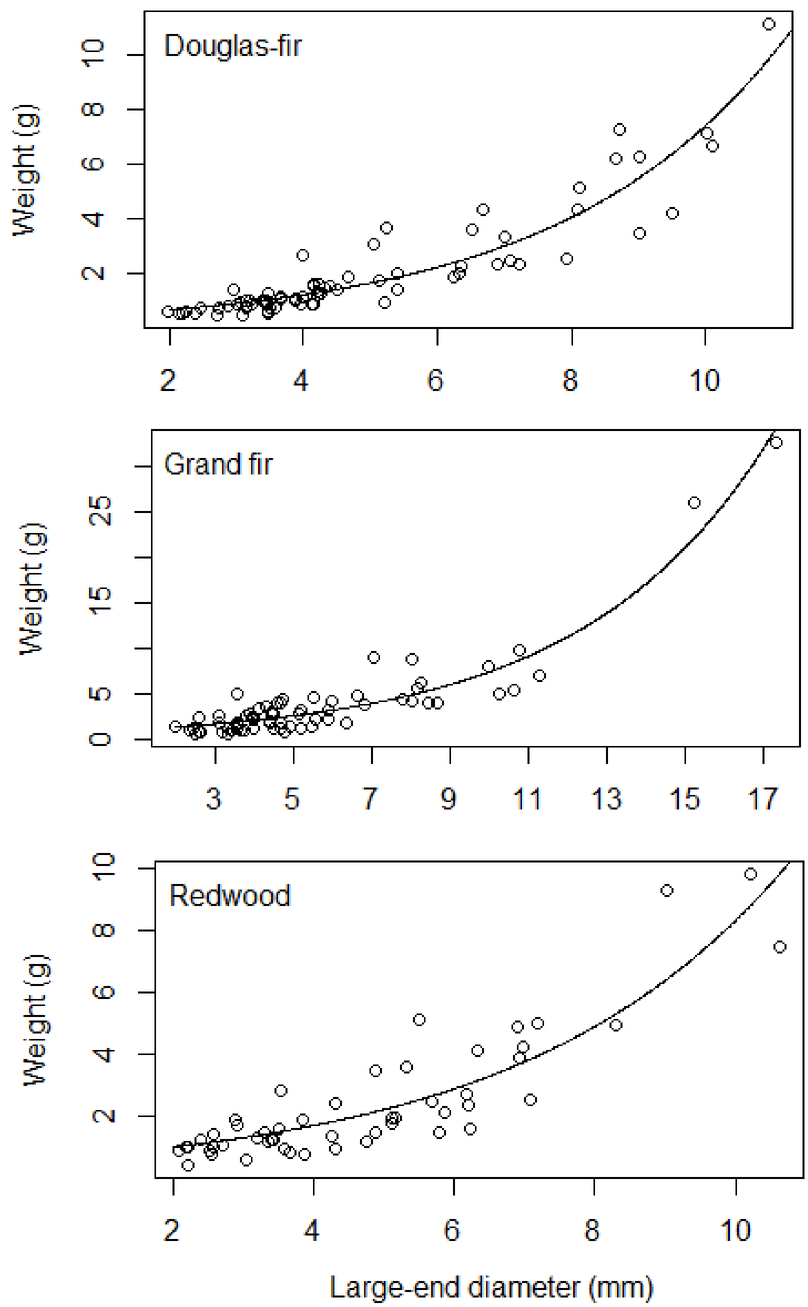

Figure 2.) Exponential relationship between broken root weight (g), and measured large-end diameter (mm) for Douglas-fir, grand fir, and redwood collected at the L.W. Schatz Demonstration Tree Farm, Humboldt County, CA. Note: different axis scales for each species depict different ranges of sample data.

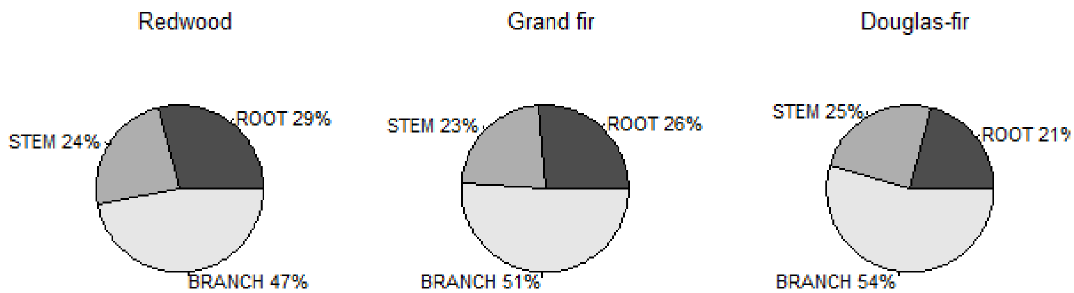

Figure 3.) Percent representation of average above- and belowground biomass components from 3 to 7-year-old conifer saplings planted at L.W. Schatz Demonstration Tree Farm, Humboldt County, California.

fir saplings comprised 14-32% of whole tree biomass. Grand fir roots represented a high of 37% and a low of 17% of BGB, respectively. Redwood roots comprised the highest proportion of total tree weight, with BGB ranging from 26-44% of totals. Branches and foliage were the heaviest of the three tree biomass components for all three species. Douglas-fir branches and foliage represented a high of 69% and a low of 36% of total tree weight. Grand fir branches and foliage represented between 39% and 63% of total tree biomass. The weight of redwood branches and foliage was least variable, ranging from 37% to 52% of total tree biomass in saplings aged 3 to 7 years old.

3.3 Belowground Biomass (BGB) Models

A total of 24 saplings of each species were sampled for BGB of coarse roots (Figure 4). Generalized linear models with ‘Species’ as a categorical variable were tested for all three species, and showed that all species had significantly different BGB. A comparison of model AICc among models with one or more explanatory variables indicated that bivariate models were best. For all three species, bivariate models indicated that BGB was positively correlated with stem diameter (mm), sapling height (cm), age (years), or average crown width (cm) ($P>0.0001$). Results from the TukeyHSD test showed BGB differed significantly only between years four and six for Douglas-fir and redwood. Grand fir BGB was significantly different across all years, except year four was not significantly different from any other year.

Douglas-fir BGB had strong correlation with sapling height and average crown width. Each model had very similar AIC values that only differed by 0.22, as well as residual standard error that differed by only 0.45 (Table 2). Each had almost the

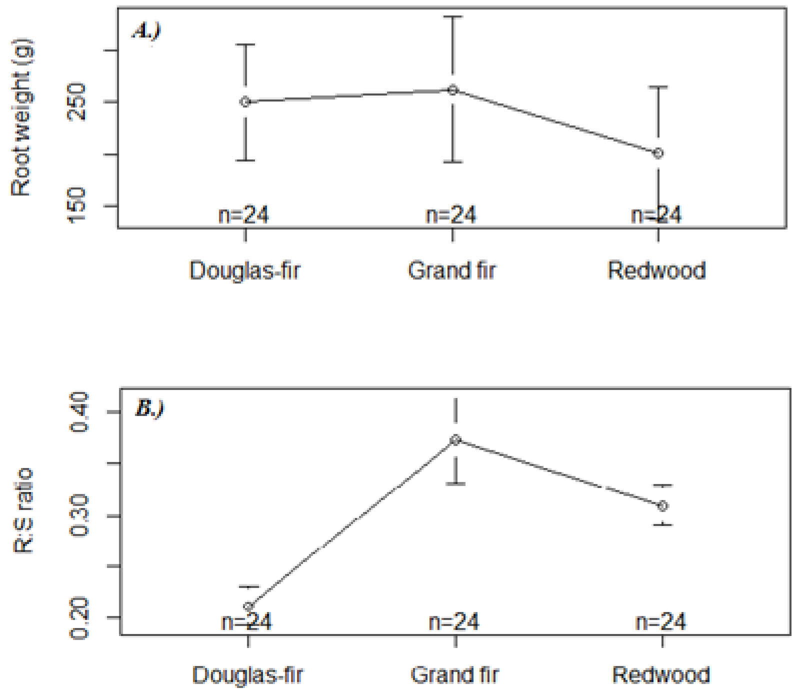

Figure 4.) (**A.**) Mean root weight of Douglas-fir, grand fir, and redwood, with 95% confidence intervals. (**B.**) Mean root-to-shoot ratio for Douglas-fir, grand fir, and redwood with 95% confidence intervals. Data collected at L.W. Schatz Demonstration Tree Farm, Humboldt County, CA.

same R^2 (0.49 for average crown width and 0.48 for sapling height) showing that less than 50% of the variation in root mass was explained by sapling height or average crown width. The best predictor of BGB was stem diameter (caliper). Two separate models, one linear model and one exponential model, used caliper as a predictor variable (Table 2). Again, the difference between these models was minimal with both AICs for the linear and exponential model equaling 270.78. The residual standard errors were within 0.01, but when fitting and evaluating the linear model, an outlier was detected. The exponential model did not result in identification of influential outliers and appeared to fit the data well (Figure 5), so it was determined to be the best model.

Grand fir BGB also had high correlations with stem diameter at ground line (caliper), sapling height, and average crown width. Models of grand fir BGB as a function of either height or average crown width had similar R^2, with adjusted R^2 that were within 0.1 of each other, and similar residual standard errors (Table 2). Unlike Douglas-fir BGB, a linear model of grand fir sapling caliper worked better than the exponential model (Table 2, Figure 5), and was identified as the best BGB model.

Belowground biomass for redwood was best predicted by sapling stem diameter (caliper). An exponential model fit the redwood BGB-caliper data best (Table 2, Figure 5).

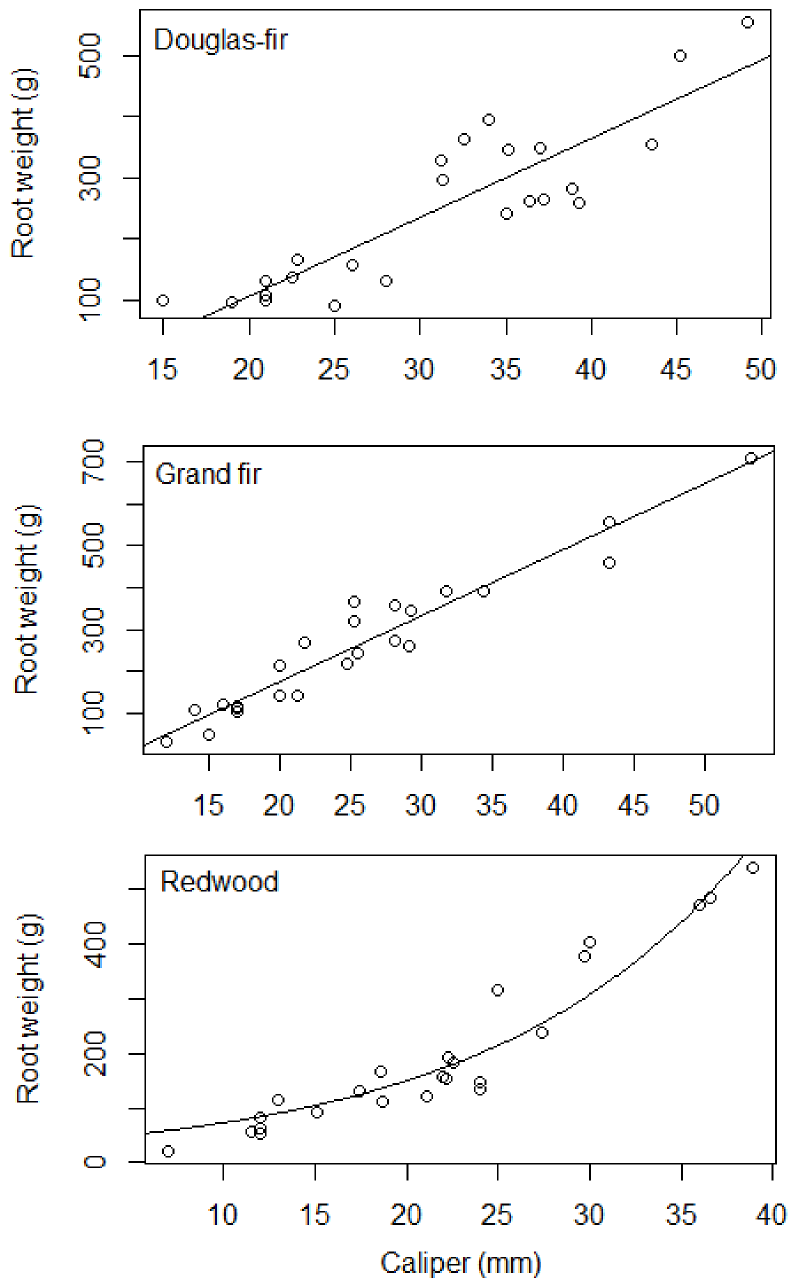

Figure 5.) Relationship between belowground biomass (root weight; g), and tree size (caliper; mm) for age 3 to 7-year-old Douglas-fir, grand fir, and redwood saplings planted at L.W. Schatz Demonstration Tree Farm, Humboldt County, CA. Note: different axis scales for each species depict different ranges of sample data.

3.4 Root-to-Shoot Ratio Models

A GLM of root-to-shoot ratio as a function of species (categorical variable) and age (continuous variable) indicated that the ratio differed significantly among species (Figure 4), and according to age. The highest root-to-shoot ratios were recorded for the youngest (age 3) redwood, Douglas-fir, and grand fir (Table 3). Using the same model, interactions were tested revealing that there were no significant differences in slope between the three species (Figure 6). Counter to our expectations, competing flora did not have a detectable influence on the root-to-shoot ratio or BGB of conifer saplings planted at LWSDTF.

The average root-to-shoot ratio for all 24 Douglas-fir saplings was 0.27, with a high of 0.47, and a low of 0.16. Ratios for Douglas-fir tended to fall with an increase in aboveground biomass. Root-to-shoot ratios were tested against age with an ANOVA to determine if there was a difference between them. When the saplings were four years old, the root-to-shoot ratio was significantly higher than in the five and seven-year-old trees. There were no other statistically significant differences between the other sample ages. All variables used in BGB equations were tested as predictors of root-to-shoot ratios, however only the model with age was statistically significant ($P<0.05$) (Table 3).

Grand fir had a 10% higher average root-to-shoot ratio than Douglas-fir at 0.37, with a high of 0.58, and a low of 0.20 for all 24 trees. However, after testing with ANOVA for sapling age and root-to-shoot ratios, there were no statistically significant differences found. Again, just like Douglas-fir, age was the only variable that was significant in predicting root-to-shoot ratios (Table 3).

Redwood had the highest root-to-shoot ratios for all 24 trees with an average of .46, a high of .78, and a low of just .36. Redwood root-to-shoot ratio was also most variable across all sample ages. Using ANOVA, redwood root-to-shoot ratios were significantly different between ages 4-5, 5-6, and 5-7, but not 3-4 or 6-7 years old. Unlike the other two species however, redwood stem diameter, sapling height, average crown width, and age were all statistically significant predictors of root-to-shoot ratio. Sapling height was the best predictor of root-to-shoot ratio in redwood saplings, indicating that root-to-shoot ratios was lower among taller redwood saplings (Table 3).

Table 2.) Candidate belowground biomass models – relationship between belowground biomass (B; g) and stem caliper (C; mm) or stem height (H; cm) or average crown width (CW; cm) or sapling age (A; years) and model fit statistics for Douglas-fir (DF), grand fir (GF) and redwood (RW) sapling roots terminating at 2 mm small-end diameter, including biomass predicted for missing roots.

Model	*Equation*	*AICc*	*BIC*	*R^2*	*Adj. R^2*	*Residual SE*	*Outliers*
DF.C1	**B=-152.310+12.935C**	**271.98**	**274.31**	**0.78**	**0.77**	**62.85**	**0**
DF.C2	$B=11.369e^{0.0058C}$	271.98	274.31	0.78	0.76	62.84	1
DF.CW	B=33.782+2.469CW	292.54	294.88	0.49	0.47	96.46	2
DF.H	B= -0.898+1.398H	292.76	295.10	0.48	0.46	96.91	1
DF.A	B=2.37+52.24A	302.23	304.56	0.24	0.20	118.00	2
GF.C1	**B=-137.49 +15.682C**	**256.35**	**259.88**	**0.93**	**0.92**	**46.53**	**1**
GF.C2	$B=83.814e^{0.042C}$	273.78	277.31	0.84	0.83	66.91	1
GF.CW	B=-72.547+3.939CW	275.56	278.97	0.73	0.72	88.82	1
GF.H	B=-292.032+3.245H	285.06	288.59	0.75	0.74	84.63	2
GF.A	B=-245.35+106.91A	296.45	298.78	0.62	0.60	104.60	1
RW.C2	**$B= 35.764e^{0.0718C}$**	**254.04**	**257.58**	**0.92**	**0.91**	**44.35**	**2**
RW.C1	B= -156.500+16.535C	262.40	265.93	0.88	0.88	52.78	1
RW.H	B= -275.564+2.932H	270.90	274.44	0.83	0.82	63.01	1
RW.CW	B = -58.036+3.215CW	273.02	276.55	0.82	0.81	65.85	2
RW.A	B=-129.38+69.56A	305.46	307.80	0.32	0.29	126.30	1

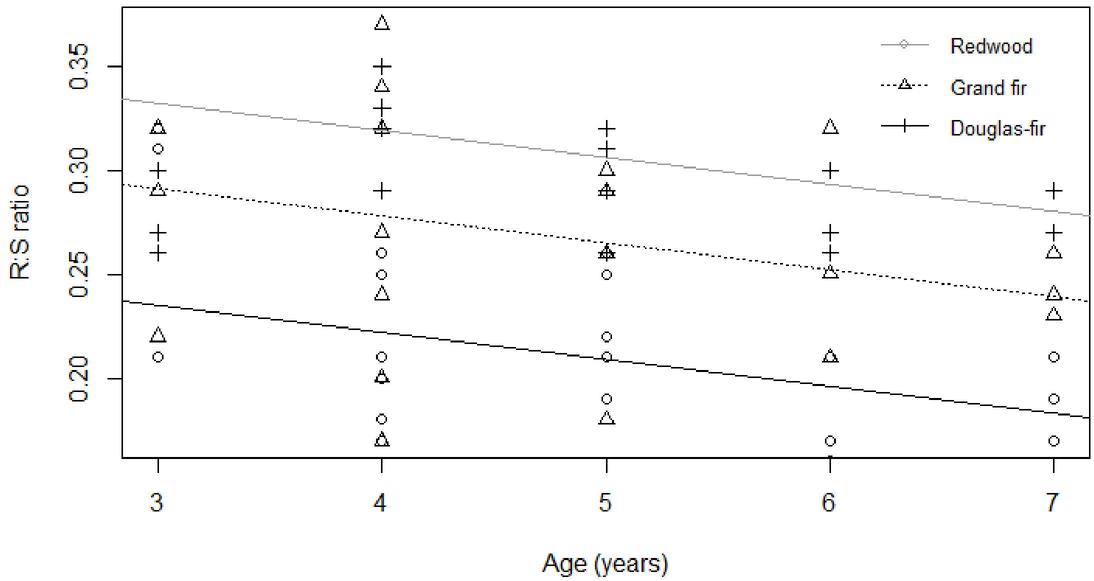

Figure 6.) Age effect on root-to-shoot ratio; includes models for redwood, grand fir, and Douglas-fir. Interaction variable tested showed no significant difference in slope among species.

Table 3.) Candidate root-to-shoot models – relationship between root-to-shoot biomass ratio (R:S) and stem caliper (D; mm) or stem height (H; cm) or average crown width (CW; cm) or sapling age (A, years) and model fit statistics for Douglas-fir (DF), grand fir (GF) and redwood (RW), and interaction between age and species (A&S1, A&S2).

Model	***Equation***	***AICc***	***BIC***	R^2	***Adj.*** R^2	***Residual SE***	***Outliers***
DF.R:S.A	R:S=0.376+-0.014A	-75.51	-73.81	0.13	0.09	0.05	1
GF.R:S.A	R:S=0.314-0.010A	-68.74	-66.40	0.93	0.05	0.01	1
RW.R:S.H	R:S=0.417-0.000H	-85.37	-83.03	0.42	0.39	0.04	1
RW.R:S.C	R:S=0.386-.004C	-84.68	-82.34	0.41	0.38	0.04	1
RW.R:S.CW	R:S=0.362-0.0007CW	-82.13	-79.80	0.34	0.31	0.04	1
RW.R:S.A	R:S=0.376+-0.014A	-75.51	-73.81	0.13	0.09	0.05	1
A&S1	R:S=0.33-0.06DF+0.04RW-0.01A	-233.30	-222.80	-	-	0.05	3
A&S2	R:S=0.31-0.03DF+0.06RW-0.01GFA-0.01DFA-0.004RWA	-228.80	-214.60	-	-	0.05	3

4. DISCUSSION

4.1 Belowground Biomass (BGB)

We discovered for Douglas-fir, grand fir, and redwood there were easily measured aboveground components that correlated strongly with BGB. For all three species, we hypothesized that stem diameter, tree height, average crown width, live crown base height, and competing flora would explain variations in root biomass. Each species had the same variables correlating with sapling BGB. Predictive models performed best when utilizing the stem diameter at ground line (caliper) of each sapling to predict BGB. Out of the hypothesized variables only sapling age, stem diameter, average crown width, and height were statistically significant predictor variables. At our site in northern California, height was highly correlated with crown size (Pearson's correlation coefficient = 0.89, P-value < 0.0005) explaining why it also predicted BGB well. This may not hold over a wider range of tree species. Vogt et al. (1983) found that root biomass tended to increase with an increase in tree size until crown closure, suggesting that this was due to a tree's tendency to extend their roots to reach the edge of crown "drip line".

We did not test for effects of stand level variables on BGB. Other variations in BGB can be explained by stand level variables. The study site from which the saplings were excavated was a warm south facing slope receiving full sun. We did not sample saplings from different sites with different aspects, or saplings in the understory of multi-aged stands. Danjon et al. (2005) showed how root morphology can be altered by stand level variables such as wind, soil, water table, and site class. This suggests further research is needed to determine if other planted or naturally regenerated even-aged and multi-aged stands follow the same trends as found in this paper reporting results for conifers planted in a mixed plantation.

The expectation was that conifer saplings would have greater BGB with advancing age. For Douglas-fir and redwood, no significant differences were found according to tree age. For grand fir, BGB increased significantly each year except for between year four and year five. High variation in tree size within each age sampled likely prevented detection of differences according to tree age.

4.2 Root-to-shoot Ratios

Root-to-shoot ratios can vary widely within and between species and forest types (Table 4). George et al. (1997) reported root-to-shoot ratios as high as 1, equal distribution of biomass above and belowground, in three-year-old potted Scots pine and Douglas-fir saplings grown in a temperature controlled green house (Table 4). Some species have a wide range of root-to-shoot ratios when a broad range of tree sizes are studied. For example, tanoak sampled across one 150 ha property had root-to-shoot ratios of 0.11 through 0.65 (Namm, 2012). Others species were shown to have small variations, such as balsam fir, which had ratios between 0.32 and 0.40 (Lavigne & Krasowski, 2007). In my study at the LWSDTF, the root-to-shoot ratios for Douglas-fir, grand fir, and redwood planted 3 to 7 years before excavation were highly variable (Figure 6). Root-to-shoot ratios decreased with advancing tree age, showing how coarse root growth

Table 4.) Range of root-to-shoot ratios (R:S) for individual tree species, and average R:S for common forest types found in the United States and Canada. Adapted from Namm (2012).

Species/Forest Type	**R:S**	**Tree ages**	**Author/Sample Country**
Abies balsamea	0.32-0.40	10-80 years	Lavigne & Krasowski, 2007
Abies grandis	0.20-0.58	3-7 years	Research results
Acer saccharum	0.18-0.47	12-39 years	Whittaker et al. 1974
Acer spicatum	0.29-0.31	19-260 years	Whittaker et al. 1974
Betula lutea	0.15-0.37	19-260 years	Whittaker et al. 1974
Betula pendula	0.34-0.48	2 years	Van Hees & Clerkx, 2003
Fagus grandifolia	0.15-0.47	19-260 years	Whittaker et al. 1974
Fagus sylvatica	0.04-0.13	44-114 years	Bolte et al. 2004
Fagus sylvatica	0.66-1.00	3 years	Van Hees & Clerkx, 2003
Notholithocarpus densiflorus	0.11-0.65	N/A	Namm, 2012
Picea abies	0.15-0.30	44-114 years	Bolte et al. 2004
Picea abies	0.68-0.72	3 years	George et al. 1999
Picea rubens	0.41-0.54	19-260 years	Whittaker et al. 1974
Pinus sylvestris	0.89-0.99	3 years	George et al. 1999
Pinus taeda	0.20-0.83	10+ years	Monk, 1966
Pseudotsuga menziesii	0.79-1.00	3 years	George et al. 1999
Pseudotsuga menziesii	0.14-0.32	3-7 years	Research results
Quercus robur	0.62-0.84	2 years	Van Hees & Clerkx, 2003
Sequoia sempervirens	0.23-0.59	1-4 years	Phillips et al. 2013
Sequoia sempervirens	0.26-0.44	3-7 years	Research results
Douglas-fir	0.21*	36-200 years	United States
Mesic deciduous hardwood	0.25*	43 years	United States
Mixed evergreen	0.53*	32 years	United States
Red alder	0.20*	Mature forest	United States
Spruce	0.23*	84-212 years	Canada
Subalpine coniferous	0.27*	70-78 years	United States

* Stand R:S (stand-level belowground biomass over the aboveground biomass) of forest types calculated from values summarized by Cairns et al. (1997) in their review of above- and belowground biomass from various biomes.

is a higher priority for young trees that eventually transition to allocating more growth to aboveground components. Grand fir had a high of 0.58 and a low of 0.20, among the 24 saplings sampled. Douglas-fir ranged from 0.16 to 0.47, which was lower than the range of values reported by George et al. (1997) for young Douglas-fir. Redwood had the highest root-to-shoot ratio recorded of 0.78, a low of 0.36, which was higher than the ratios reported by Phillips et al. (2013) for redwood ages 1-4 years old.

Douglas-fir ratios found at the study site were just slightly above that found by Cairns et al. (1997). The grand fir and redwood sampled at LWSDTF both had much higher root-to-shoot ratios than the average presented by Cairns et al. (1997) for the mixed evergreen forest type.

Some differences in root-to-shoot ratio between trees of the same species can be attributed to tree age. Monk (1966) found that root-to-shoot ratios tended to decline with advancing tree age. This was consistent with the data collected at the LWSDTF for all three species (Figure 6). The highest root-to-shoot ratios were observed in the first year of data collection when the saplings were three or four years old. Douglas-fir did not show a statistically significant difference in root-to-shoot ratios between ages four and seven, but regression analysis revealed a decrease in the root-to-shoot ratio with advancing age for all three species. George et al. (1997) and Monk (1966) showed that root-to-shoot ratios changed most rapidly in the first few years of the tree’s life. Root-to-shoot ratios in grand fir had yet to be reported, but by comparing the data for the LWSDTF to root-to-shoot from the same genus (*Abies balsamea)*, averages found at the

LWSDTF fell within the same range of values (Table 4). Average root-to-shoot ratios reported by Phillips et al. (2013) for redwood also were within the same range found at the LWSDTF, however this does not prove that location does not affect root-to-shoot ratio. Large sample sizes would be needed to detect differences due to the inherent variability in root-to-shoot ratios at a single site such as the LWSDTF. More data covering a wide range of ages are needed to reliably model the effect of tree age on root-to-shoot ratios. Due to the greater difficulty of sampling larger older tree root systems, any new research on root-to-shoot ratios for any species will be valuable and the raw data should be shared to allow for meta-analysis across broader ranges of ages and geographic areas and development of more robust predictive models for BGB and coarse root carbon.

4.3 Conclusions

Results of this research show that roots can represent almost as much as biomass as the visible portion of young trees. Douglas-fir, grand fir, and redwood data for the five sapling ages studied at the LWSDTF showed that root-to-shoot ratios declined with advancing tree age; as conifers get older, their above ground components amass biomass more rapidly than their root system.

Destructive sampling by excavation was laborious, and pieces of coarse roots lost during excavation amounted to 1-22% of the total BGB. Predictive equations created from destructive sampling data revealed high correlations between BGB and aboveground variables. Stem diameter for all three species explained the most variations in belowground root mass. Using these equations, forest landowners and managers can obtain predictions of the amount of carbon stored belowground in young conifer plantations, and how it increases as trees grow.

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