Tree density and stand age effects on allometric equation development and biomass partitioning in lodgepole pine forests near Yellowstone National Park, WY

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Abstract

Allometric equations that estimate biomass for various tree components are often sensitive to geographic location, as well as differences in tree age and stand density within a given area. We developed new allometric equations for predicting above- and belowground biomass of mature lodgepole pine (*Pinus contorta* var. *latifolia* (Engelm. ex Wats.) Critchfield) in the Greater Yellowstone Ecosystem (GYE) in three stands that differed in stand age and tree density using standard harvest techniques. We compared our new equations to lodgepole pine allometrics developed in other areas to evaluate their usefulness; we also tested the utility of equations developed previously in the GYE for young, postfire saplings for predicting biomass of mature trees. Finally, we evaluated the influence of stand age and tree density on biomass partitioning in the three stands. R-squared values for the nine equations developed in this study ranged from 0.92 - 0.98, and diameter at breast height (dbh) was the primary predictor for all nine models. The influence of stand age and tree density was variable for individual aboveground and belowground biomass components; however, equations that predict total tree and total aboveground biomass were not influenced by either age or density. Allometric equations developed for lodgepole pine elsewhere - in southeastern Wyoming and British Columbia – consistently produced poorer estimates of biomass for mature lodgepole pine in the GYE, supporting the idea that many allometric relationships in forested systems are site-specific. Similarly, equations developed for young saplings in the GYE did not accurately predict the biomass of mature trees, nor did our new equations adequately predict biomass of young, postfire saplings. Proportionately, all aboveground tree biomass components were significantly higher in the young, sparse stand than in the young, dense or old, sparse stands, suggesting an influence of both density and age. The young, dense stand showed significantly higher total aboveground biomass partitioning and significantly lower total root biomass than either of the sparse stands. Overall biomass partitioning patterns were more similar between the young, dense and old, sparse stand (bole > fine fuels > total coarse root > branches) than the young, sparse stand (bole > fine fuels > branches > total coarse root biomass). While some recent studies have suggested using a universal, functional approach for estimating total forest biomass, our study demonstrates measurable and significant differences among allometric equations developed in the Rocky Mountains for a single tree species, supporting the continued development of these kinds of predictive tools.

Keywords: allometric equations; lodgepole pine; Yellowstone; biomass

Introduction

The ability to relate easily measured tree characteristics, such as diameter and height, to total tree biomass and individual component biomass is an important statistical and management tool. For example, forest managers may use this information when investigating relationships between forest productivity and stand density, to measure woody fuel amounts (Agee 1983), or to estimate carbon accumulation and storage in forested systems (e.g., Giardina and Ryan 2002). It is often difficult, if not impossible, for managers or researchers to develop biomass equations for each project in which they are involved, and must often rely on existing equations to provide biomass estimates (Crow 1988). However, largely because of geographic and physiographic differences among study areas, biomass equations are not universally applicable and models developed in a particular area may not be appropriate across the range of an individual tree species, even if many may already exist.

Allometric equations for estimation of above- and belowground biomass of mature lodgepole pine (*Pinus contorta* var. *latifolia* (Engelm. ex Wats.) Critchfield) trees have been developed in Alberta, Canada by Johnstone (1971), in southeastern Wyoming by Pearson et al. (1984), in southeastern British Columbia by Comeau and Kimmins (1989), and in Washington and Oregon by Gholz et al. (1979). More recently, allometric equations for predicting biomass in young, post-fire forests have also been developed in Yellowstone National Park (YNP) for aboveground biomass by Turner et al. (2004) and for belowground biomass by Litton et al. (2003). Despite the robust nature of most allometric equations, these previous studies have suggested that they may not be universally applicable in stands of varying densities, ages, and site qualities. For example, Johnstone (1971) identified a need to consider stand density and age when he developed allometric models for 100-year-old lodgepole pine in Alberta, Canada.

Later, Pearson et al. (1984) suggested that differences in stand density, age, and site quality may have caused considerable variability in tree crown biomass, and both Pearson et al. (1984), and Comeau and Kimmins (1989) found that the foliage biomass: sapwood area ratio decreased with increasing stand density. Such variability among sites suggests that allometric relationships are also likely to differ among geographic locations due to differences in substrate, topography, and climate. Keyes and Grier (1981) found that Douglas-fir had proportionately more total root biomass on a low productivity site than on a high productivity site, and Comeau and Kimmins (1989) found that belowground production represented a greater proportion of total production in two xeric sites compared to two mesic sites.

Although Litton et al. (2004) and Tinker and Knight (2000) have suggested that allometric models developed by Comeau and Kimmins (1989) or Pearson et al. (1984) could be appropriate for use in the GYE, this may not be true. During the study by Litton et al., the equations of Comeau and Kimmins and Pearson et al. were tested on only five mature trees in a single stand, and did not account for variability in stand density and age. In addition, allometric equations from these two studies for predicting belowground biomass in mature stands were not evaluated. In fact, in general, because of methodological inconsistencies, along with site-specific differences in tree density and stand age, using existing allometric equations outside the areas where they have been developed often produce inconsistent biomass estimates (Peichl and Arain 2007; Wang et al. 2000; Jenkins et al. 2003; Tateno et al. 2004). Therefore, new allometric models specific to mature forests of the Greater Yellowstone Ecosystem are needed that consider differences in lodgepole pine biomass, which may vary with tree density and stand age. In this study, we developed new allometric models for predicting above and belowground biomass in mature lodgepole pine forests of the GYE.

The specific objectives of this study were to: (1) develop allometric equations for predicting above and belowground biomass of mature lodgepole pine trees in the GYE, accounting for differences in stand density and age; (2) compare allometric equations developed in this study to allometric equations developed in other locations and equations developed for young trees in YNP to determine model variability and applicability across geographic locations and age classes, independent of forest structure; and (3) to determine how patterns of above and belowground biomass partitioning for trees in three mature lodgepole pine stands of the GYE vary with stand age and density.

Methods

Study Areas

The two study areas were located in the Caribou-Targhee National Forest (CTNF), one bordering the western boundary of YNP, near Island Park, ID, and the other near the southern boundary of YNP; both sites are dominated by lodgepole pine. Allometric equations were developed in three lodgepole pine stands (two near Island Park and one near YNP) on the CTNF that represented two age classes and two density classes. Elevations in the three stands ranged from 1,951 m to 2,249 m (Table 1). In the young (~65 years old) age class, two stands of different densities were examined; one young, dense (YD - 2,452 trees/ha) and the other young and sparse (YS - 725 trees ha^{-1}). A single sparse (674 trees ha^{-1}) stand was sampled in the older age class (OS) (~165 years old), because older stands typically have low tree densities, regardless of their initial tree density (Kashian et al. 2005).

All three sites were located on the Koffgo soil series, consisting of loamy-skeletal, mixed, superactive Vitrandic Cryochrepts. Parent material was local residuum, colluvium, or alluvium developed from volcanic ash, igneous rocks, and loess (Bowerman et al. 1999). Average annual precipitation was ~ 115 cm yr^{-1} in the oldest stand and ~ 75 cm yr^{-1} in the younger stands (Dirks and Martner 1982). All sites were located at least 50 m from the road to facilitate equipment hauling, yet avoiding road influences. Stand basal area was determined using six variable radius plots in each stand (Avery and Burkhart 1994). Stand basal area was similar between the OS (16.84 m^2 ha^{-1}) and YS stands (19.71 m2 ha^{-1}), but was quite different for the YD stand (28.32 m^2 ha^{-1}; Table 1).

Field and Lab Methods

All aboveground tree biomass was harvested from a total of 46 trees within the three stands, and 24 root systems were excavated to develop allometric equations between easily measurable tree characteristics (e.g., dbh, tree height) and above- and belowground tree biomass components. Fourteen and 15 trees were harvested in the YD stand and the YS stand, respectively, and 17 trees were harvested in the OS stand. Five root systems were excavated in each of the YS and OS stands and 14 root systems were harvested in the YD stand.

In each stand, trees were harvested along each of three 25-m transects. Trees were selected at 5m intervals along each transect to represent the range of tree sizes found for trees in their respective stands. Trees with unusually poor tree form, excessive mistletoe, or any defect that could alter the biomass of the tree, such as heart rot or insect damage, or any tree outside of the acceptable age range (≤15 years of the oldest tree in the stand) were avoided.

Prior to harvest, DBH (diameter at breast height, 1.37 m) was measured and crown width was estimated using a meter tape. After felling of the tree, total height and height to live crown base were measured. Crown base was defined as the point along the bole at the bottom of roughly 90% of the crown mass. Crown length was calculated as:

$$CL = H - HCB \tag{1}$$

where CL = crown length, H = total tree height, and HCB = height to crown base.

Aboveground Components

Tree Bole **–** After all branches were removed, each bole was cut into multiple smaller sections and weighed using a digital hanging scale (Salter-Brecknell). Several discs were collected from the bole to return to the laboratory for determining sample dry mass. Discs were also collected at DBH, and at crown base, and the following measurements were taken on the discs for determining sapwood area: phloem + bark thickness, total diameter, and heartwood diameter. Sapwood diameter was determined by subtracting the heartwood diameter from total diameter.

Branches - Branches were cut flush to the tree bole and small twigs and foliage that were < 6.4 mm in diameter were separated from the larger branches. This was done because most of these small branches and foliage are likely to be consumed by fire (Despain 1990), and were analyzed separately to allow for post-fire estimates of fine fuel consumption. A subsample of the branches was collected to determine moisture content for dry weight for each tree.

Fine Fuels and foliage - The fine fuels component that were removed from the larger branches were defined as all needles and associated twigs < 6.4 mm in diameter. Fine fuels were separated into lower, middle, and upper crown sections for each tree, as foliage moisture contents may vary with crown height (Brown 1978). Also, because many of the current year needles were not fully expanded, and because samples were collected at varying times throughout the summer of 2004, the current year's growth (2004) was removed and discarded. We have observed that lodgepole pine does not drop its oldest needles until autumn, so by discarding any expanding foliage and measuring the rest during summer, we estimate the mean annual foliage biomass. All fine fuels were weighed, and a random subsample was taken from each crown section to determine moisture content. We then removed all remaining needles from the twigs and weighed them separately to determine foliage biomass.

Belowground Components

The entire coarse root system (>10mm diameter) was excavated for 24 trees with a backhoe or portable winch. Prior to excavation, smaller roots (~ 10-20 mm) that could potentially be damaged by the backhoe or other excavation techniques were manually removed. After excavation, the root system was divided into four size classes and weighed using a digital hanging scale: root crown (i.e. the massive structure directly beneath the tree bole), lateral roots > 50mm in diameter, lateral roots 25-50 mm in diameter, and lateral roots 10-25 mm in diameter. Subsamples from each size class were taken and weighed to determine moisture content for dry weight of each size class.

Allometric Equation Development and Comparisons

We used multiple linear regression to identify relationships between measured tree characteristics and the various biomass compartments described above. Rather than develop equations from each stand sampled, we wanted to create equations for each tree biomass component that were developed for pooled data from all three sites, but which would include variables representing stand age and density. We tested a suite of tree- and stand-level measures, including dbh, tree height, sapwood area, stand density and stand age, as well as all interaction terms. An iterative approach was used that initially included all independent variables and their interaction terms, and subsequent iterations continued until only predictor variables that were significant ($p \leq 0.05$) in the model were remaining. Tree dbh was log-transformed, and we used binary dummy variables for both stand age (old = 1; young = 0) and stand density (sparse = 1;

dense = 0). Equations that retained variables or interaction terms related to stand age or stand density in the final model represent significant effects of age or density on a given biomass compartment. All equation development was done using Minitab 15 (2007).

Geographic Location Comparisons - Equations developed for mature lodgepole pine in this study were compared to equations developed by Pearson et al. (1984) for lodgepole pine in the Medicine Bow Mountains of southeastern Wyoming and by Comeau and Kimmins (1989) for lodgepole pine trees in British Columbia. Equations selected for comparison were developed in stands that were similar in stand density and age to those developed for this study. Paired, two-tailed t-tests were used to assess whether biomass estimates from this study differed statistically from biomass estimates produced from the other equations ($\alpha = 0.05$). Actual biomass values from this study were compared against values estimated using our allometric equations to determine whether our estimated biomass values were more similar to the actual values than estimated values calculated using equations developed by Pearson et al. (1984) and Comeau and Kimmins (1989).

Reciprocal comparisons with equations developed for saplings in YNP – Estimates of biomass using allometric equations developed in this study for mature trees were compared to biomass measurements and estimates developed in YNP for small, young saplings for both aboveground (Turner et al. 2004) and belowground (Litton et al. 2003) biomass compartments. We used total biomass measures from 36 randomly selected saplings that were harvested by Turner et al. (2004) during 1999 in YNP. Similarly, the equations developed by Turner et al. (2004) and Litton et al. (2003) were used to estimate the respective biomass compartments for mature trees harvested in this study. Paired t-tests were used to test for significant differences between measured and predicted values for all comparisons. Both of these sets of comparisons were done to determine the usefulness of allometric equations developed for mature trees in predicting biomass of young saplings, and vice versa.

Tree Level Biomass Estimations

The dry weight biomass values for the 24 trees that were completely harvested in this study (both above- and belowground components) were used to calculate biomass partitioning patterns for above and belowground components of lodgepole pine trees in the three study sites.

Statistical Analyses

All other statistical analyses were done using SPSS 14.0 (SPSS Inc. 2005). To determine whether partitioning patterns at the tree level differed as a function of density and/or age, one-way ANOVAs were conducted, followed by Tukey's HSD post-hoc analyses. The following variables were used for comparisons: biomass, and percent of total biomass for bole, branches, foliage, needles, total coarse root, root crown, and lateral roots; the total coarse root biomass: total aboveground biomass ratio was also calculated for the three stands. For these analyses, tree within stand was the sample unit.

Results

Allometric Equation Development

Equation summaries

The nine linear allometric models developed for all measured tree components are shown in Table 2; R^2 values ranged from 0.92 to 0.98. Plots of residuals versus dbh do not show evidence of bias or excessive heteroscedasticity for any of the nine models (Figures 1 and 2). All nine equations used a log-transformation of diameter at breast height (dbh) as the primary predictor variable, although other predictors were used in some models. Two of the nine equations – total aboveground biomass and total tree biomass - included dbh as the only independent variable, and neither stand age nor density influenced these equations. Tree bole biomass and fine fuels were the only two equations that were influenced by the interaction of both stand age and stand density with dbh, and the fine fuels equation also included an effect of stand density (Table 2). Foliage, total coarse root biomass and root crown biomass equations included stand age, or its interaction with dbh, in the best models for these components, yet lateral root biomass was influenced by stand density and its interaction with dbh, but not by stand age (Table 2). The equation for branch biomass was the only model that included height as an important predictor, and was not influenced by either stand age or stand density.

Comparisons among Geographic Locations

Predicted biomass values from equations developed in this study were closer to actual biomass of lodgepole pine in the Greater Yellowstone Ecosystem than predicted values from equations developed by Comeau and Kimmins (1989) and Pearson et al. (1984) (paired t-test, $p<0.05$; Figures 3 and 4). Predicted values applying our study's equations produced biomass values that were not significantly different (paired t-test, $p > 0.05$) from actual biomass values. However, estimates of branch biomass applying Pearson et al.'s equations were slightly more similar to actual values (paired t-test, $p = 0.005$) than were estimated values applying our equations (paired t-test, $p = 0.003$). The greatest difference in observed versus predicted biomass between studies was for larger diameter trees (Figures 3 and 4), supporting the observation of increased variation in allometric models with increasing tree size. Biomass estimates produced by models from studies northwest (Comeau and Kimmins 1989) and southeast (Pearson et al. 1984) of the GYE produced significantly higher estimates of root biomass, lower estimates of needle and branch biomass, and relatively comparable estimates of bole biomass (Figures 3 and

4). The root biomass estimates generated from models developed in the Medicine Bow Mountains produced slightly higher biomass estimates than from this study (Figure 4).

Reciprocal comparisons with equations developed for saplings in YNP

Allometric equations developed from this study for mature trees did not perform well when predicting above- or belowground biomass for young, postfire saplings in YNP. Our equations significantly overestimated total aboveground biomass ($p < 0.0001$), compared to measured values, and the range of predicted biomass values (41 – 35, 068 g) was over three times higher than the measured values (3 – 10,565 g; Figure 5a). Our equations also significantly overestimated total coarse root biomass ($p < 0.0001$), when compared to measured values, and the range of predicted values (4 – 2,566 g) was again over threefold larger than the measured values (0.7 – 801 g; Figure 5b).

Similarly, allometric equations developed by Turner et al. (2004) and Litton et al. (2003) for young, postfire saplings significantly underestimated both above- and belowground biomass for mature trees ($p < 0.001$; Figure 3).

Age and Density Effects on Biomass Partitioning Patterns

Mean total tree biomass was greatest in the OS stand, as expected, but not significantly greater than in the YS stand (Table 3). However, the mean total tree biomass of both sparse stands, regardless of age, was significantly higher than the young, dense stand ($p < 0.001$; Table 3). This allocation pattern was similar for three of the four aboveground biomass components; branches, fine fuels, and needles in both the OS and YS stands were significantly higher than the YD stand, but were not significantly different from each other. Mean bole biomass, on the other hand was significantly higher in the old stand than the two younger stands ($p < 0.001$; Table 3).

Mean total root biomass and lateral root biomass per tree were both significantly lower in the YD stand than either the OS or YS stands ($p < 0.001$; Table 3).

When expressed as a proportion of total tree biomass, mean total aboveground biomass per tree was similar among the three sites, but was significantly higher in the YD stand (90.5%) than in the OS or YS stands (84.5% and 87.7%, respectively; Table 3). Tree boles were the largest individual biomass component for all three stands, but these values were highly variable among the three sites. Proportionately, all aboveground tree biomass components were significantly higher in the YS stand than in the YD and OS stands (Table 3). Both sparse stands showed proportionately higher total root biomass than the YD stand, but all stands showed higher root crown biomass than lateral root biomass.

The hierarchy of biomass partitioning for the OS and YD stands was bole > fine fuels > total coarse root biomass > branches; for the YS stand it was bole > fine fuels > branches > total coarse root biomass (Table 3). The total root: total aboveground biomass ratio was highly variable among the three sites, and ranged from a mean value of 0.11 in the YD stand to 0.19 in the OS stand. The OS and YS stands were not significantly different from each other, but only the OS stand ratio was significantly higher than the YD stand ($p < 0.05$; Table 3).

Discussion

Allometric Equation Development

The absence of bias for our equations suggests that they work well for lodgepole pine across the range of tree diameters measured in this study (Figures 1 and 2). Diameter at breast height (dbh; log transformed) was the primary morphological predictor of all biomass components for this study, although stand age and density influenced some relationships. Interestingly, tree height only proved to be a secondary, significant predictor of branch biomass, which was surprising (Table 2). Typically, a tree's ability to produce stemwood biomass, a major component of tree bole and total aboveground biomass, is often influenced by site productivity (Barnes et al. 1998). Therefore, a model that includes tree height, a variable relating more strongly to site productivity than any other measured parameter (Barnes et al. 1998), can often explain a large amount of the variability in bole and total aboveground biomass, although that was not the case in this study. Our three sites were similar with respect to site productivity, perhaps explaining the lack of importance of height in our equations.

Notably, our equations that predict both total aboveground biomass and total tree biomass were predicted by dbh alone, and were not influenced by either stand age or tree density (Table 2). One plausible explanation for this pattern is that stand densities may not have been different enough for some of the models to differ according to stand density or to be less different than for models pooled by age. Although 2,452 trees ha^{-1} was considered in this study to be a dense stand, "dog-hair" stands of mature lodgepole pine that are of comparable age can sometimes reach densities higher than 10,000 trees ha^{-1} (Koch 1996). Kashian et al. (2005), in their study of stand structural development in YNP, identified two such stands that were less than 100 years old, however, such stands are rare in the GYE. It is unclear whether our equations would prove to be as robust in predicting various biomass compartments in very dense stands such as these. On the other hand, Peichl and Arain (2007) also found that a single allometric equation was effective in predicting total aboveground, belowground, and total tree biomass for eastern white pine (*Pinus strobus* L.) across a range of stand ages in Ontario, suggesting that allometric equations that include some form of tree diameter (dbh, basal diameter) are very useful and robust.

Total coarse root biomass (>10 mm) and root crown biomass were best predicted by dbh and either age, or the interaction with age and dbh (Table 2), whereas lateral roots were influenced by tree density and its interaction with dbh. Similarly, Litton et al. (2003) also found no significant influence of tree density on equations predicting total coarse root biomass in ~13-yr old stands of lodgepole in YNP, and a diameter metric (basal diameter) was also the most effective predictor of this component.

Differences between Geographic Locations

Differences in allometric equations among geographic locations are likely attributed to differences in soil, topography, and climate. The soils on which Pearson et al. (1984) developed allometrics in the Medicine Bow Mountains were generally less infertile and were derived primarily from glacial till and fluvial conglomerates, while soils in British Columbia were Orthic Eutric Brunisols for xeric sites and Brunisolic Gray Luvisols for mesic sites (Comeau and Kimmins 1989). In contrast, soils of this study were more infertile and were developed on volcanic substrates (Bowerman et al. 1999).

Predicted bole biomass was the tree component that differed the least between the GYE and the Medicine Bow Mountains (Pearson et al. 1984), and was also the component most similar between the GYE and British Columbia (Comeau and Kimmins 1989), suggesting that relationships between bole biomass and its predictor(s) (tree diameter and/or total height) may be relatively constant across gradients of elevation, topography, climate, and site productivity.

Needle biomass estimates derived from equations developed in southeastern Wyoming (Pearson et al. 1984) and British Columbia (Comeau and Kimmins 1989) were lower than actual and predicted biomass from sites in this study (Figures 3 and 4), although less so for southeastern Wyoming. Conversely, root biomass in the GYE was over-predicted by equations developed in

British Columbia and southeastern Wyoming. This suggests that coarse root biomass has little impact on the trees ability to uptake water and nutrients, because less coarse root biomass should have been needed to uptake water and nutrients in British Columbia and southeastern Wyoming, which are more productive sites than the GYE. However, a portion of this difference could also be attributed to differences in the definition of a root crown between studies. For this study, a root crown was the portion of the coarse root system that is directly below the basal swell of the tree bole and within the lateral extent of the diameter of the tree at ground level. In contrast, Pearson et al. (1984) defined the root crown as the structure directly below the basal swell of the tree bole extending laterally to a distance of 1.5 x DBH.

The greatest differences in the biomass of tree components among geographic locations occurred for larger trees (Figures 3 and 4), suggesting that differences in site conditions may become increasingly important as forests become older and trees become taller. This is attributed to an increase in nutrient limitation (Berger et al. 2004; Ryan et al. 1997; Smith and Resh 1999; Smith and Long 2001), hydraulic limitation (Ryan and Yoder 1997), and potential changes in carbon balance (Ryan et al. 1995) with increases in stand age and tree height.

Biomass Partitioning Patterns

Aboveground Biomass

Allocation to tree boles was lowest in the YS stand at the individual tree level, while bole allocation to the OS and YD stands were surprisingly comparable to each other. The low proportion of total tree biomass for boles in the YS stand is likely attributed to a high proportion of branch and foliage biomass due to its young age and open-grown stand structure. The similarity in allocation to tree boles between the OS and YD stands may be related to their competitive similarity. Although not quantified, our observations suggested both of these stands exhibited crown closure, yet the YS stand seemed to show lower crown density. The observed increased biomass found in boles in the dense and older stands with greater crown competition was consistent with the results of Nilsson and Albrekston (1993) and Kaufmann and Ryan (1986). They found that tree bole biomass was greater than foliage biomass for competitively suppressed trees. Future studies should include more direct measurements of competition among trees, such as nearest neighbor analyses. Ryan et al. (1997) suggested that young trees allocate more resources to foliage rather than to woody components, and this trend becomes less pronounced with crown closure. This is supported by the results of this study, as the open-grown YS stand had 22.3% of total aboveground biomass allocated to foliage, while the OS stand with greater observed crown closure had 10.9% of total biomass allocated to foliage (Table 3). In fact, on average, trees in the YS stand had higher branch, fine fuels, and foliage biomass than the OS stand, as well as higher proportions of these components.

Below: Aboveground Biomass Ratio

For this study, below: aboveground biomass was found to vary as a function of both stand age and tree density (Table 3). Our two sparse stand (old and young) did not differ significantly from each other, nor did the two young stands (sparse and dense), but the ratio in the old, sparse stand was significantly higher than the young, dense stand (Tale 3), indicating that both stand density and age had an important effect on allocation to coarse root biomass. Although there are some similarities in the ratio of below: aboveground biomass among sites, especially at the stand level, biomass partitioning within above and belowground components was found to be highly variable with stand density and age. This is similar to findings by Litton et al. (2004), who found that carbon pools in young and old lodgepole pine stands in YNP were indeed influenced by tree age and stand density over time following disturbance.

Conclusions

While some recent studies (e.g., Pilli et al. 2006; Zianis and Mencuccini 2004; West et al. 1999) have suggested a move towards a universal, functional approach to estimating total forest biomass, rather than an empirical approach used by this study, others believe that equations for predicting biomass at the tree level provide more accurate estimates than models that integrate biomass components using a common scalar (e.g., Bokma 2004; Kozlowski and Konarzewski 2004). Our research demonstrates measurable and significant differences among allometric equations developed in the Rocky Mountains for a single tree species, supporting the continued development of these kinds of predictive tools. Indeed, Litton et al. (2003), along with this study, identified a need for independent allometric models for young, developing saplings, rather than using equations developed for mature trees, even within the same study area. However, additional work is needed to determine when it is appropriate to use each set of equations and to determine when the relationships between biomass and tree morphological characteristics change.

Acknowledgements

This research was supported by grants from the Plummer Scholarships for Environment and Natural Resources Conservation and Management, University of Wyoming-National Park Service Research Center, and the USDA Joint Fire Sciences Program (Agreement No. 04-JV-11221610-039). We thank the resource managers of the Caribou-Targhee National Forest, the University of Wyoming-National Park Service Research Station in Grand Teton National Park, the Department of Forest, Rangeland, and Watershed Stewardship at Colorado State University, and the Botany Department at the University of Wyoming for financial and logistical support. We are grateful to Ken Gerow at the University of Wyoming for help with statistical analyses.

We also thank Lance East, Lance Farnam, Kellen Nelson, and Therese Tepe for their hard work during tree harvesting and all other aspects of field work, and we are grateful to Gail Stakes for her help with sample processing and data entry and organization in the forest ecology laboratory at the University of Wyoming.

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Figure Captions

Figure 1. Residual values (observed minus predicted values) of log-transformed linear equations for aboveground biomass components in three lodgepole pine stands from this study as a function of tree diameter at breast height.

Figure 2. Residual values (observed minus predicted values) of log-transformed linear equations for belowground biomass components in three lodgepole pine stands from this study as a function of tree diameter at breast height.

Figure 3. Comparison of biomass values among those directly measured by this study, those predicted by this study's allometric models, and those predicted by Comeau and Kimmins' allometric models.

Figure 4. Comparison of biomass values among those directly measured by this study, those predicted by this study's allometric models, and those predicted by Pearson et al.'s allometric models.

Figure 5. Comparisons of measured versus predicted values using allometric equations from this study to predict (a) young, postfire sapling total aboveground biomass, and (b) sapling root biomass; (c) the application of equations developed by Turner et al. (2004) for predicting lodgepole sapling aboveground biomass in YNP, but shown here predicting total aboveground

biomass of mature trees, and (d) equations developed by Litton et al. (2003) for predicting lodgepole sapling root biomass in YNP, but shown here estimating mature tree root biomass.

Table 1. Sites for the development of allometric equations in the Greater Yellowstone Ecosystem.

		NAD 83, UTM Zone 12				
Site Name	Elevation (m)	Northing (m)	Easting (m)	Stand Age (years)	Stand Density (trees > 5cm DBH per hectare)	Stand basal area (m^2 per hectare)
Grassy Lake	2249	4886015	511735	165	674	16.84
Coffee Pot	1951	4926541	472232	64	725	19.71
US 20	1951	4925932	472657	64	2452	28.32

Table 2. Allometric equations for predicting biomass (Kg) of nine different above and belowground components of *P. contorta* in the Greater Yellowstone Ecosystem. Each equation produces natural log-transformed biomass estimates that must be back-transformed. "Age" and "density" variables are binary (0,1); for "age", stands ≤ 65 years are considered young (0) and stands > 65 years are considered old (1). Similarly, for "density", stands that are ≥ 1500 trees per hectare are considered dense (0), and stands < 1500 trees per hectare are considered sparse (1).

Biomass Component	**Equation**	***n***	**Mean, (range)**	**R^2 (adj.)**
Total Aboveground	$-2.10 + (2.35 * \ln(dbh))$	46		0.98
Bole	$-1.80 + (2.13 * (\ln(dbh)) + (0.187 * (age*\ln(dbh))) – (0.127 * (density*(\ln(dbh)))$	46		0.97
Branches	$-6.67 + (3.78 * \ln(dbh)) – (0.140 * HT)$	46		0.92
Fine Fuels	$-6.87 + (3.54 * \ln(dbh)) + (2.35 * density) – (0.228 * (age*(\ln(dbh))) – (0.807 * (density*(\ln(dbh)))$	46		0.95
Foliage	$-6.69 + (3.30 * \ln(dbh)) – (0.0229 * (age*(\ln(dbh)))$	46		0.93
Total Coarse Root	$-4.91 + (2.60 * \ln(dbh)) + (2.70 * age) – (0.809 * (age*\ln(dbh)))$	24		0.98
Root Crown	$-4.45 + (2.22 * \ln(dbh)) + (0.450 * age)$	24		0.94
Lateral Roots	$-8.30 + (3.58 * \ln(dbh)) + (4.51 * density) – (1.62 * (density*\ln(dbh)))$	24		0.97
Total Tree	$-1.92 + (2.32 * \ln(dbh))$	24		0.98

Table 3. Mean tree biomass (Kg) and percent of total biomass for above- and belowground components of individual trees harvested from the three stands in this study. Values are based on dry weight measurements from a total of 24 trees, representing only those trees where the entire tree was harvested. Mean percent values for bole, branches, fine fuels, and needles are proportions of total aboveground biomass; mean percent values for root crown and lateral roots are proportions of total root biomass (> 10mm diameter). Different letters for each component denote significant differences ($\alpha = 0.05$).

	Old, Sparse			**Young, Sparse**			**Young, Dense**		
	Biomass (Kg)		**Mean % of Total**	**Biomass (Kg)**		**Mean % of Total**	**Biomass (Kg)**		**Mean % of Total**
Component Biomass	**Mean**	**Range**		**Mean**	**Range**		**Mean**	**Range**	
Total Aboveground Biomass	**187.9** ^{a}	30.7 -336.4	**84.5** ^{a}	**128.8** ^{a}	41.7 -207.4	**87.7** ^{a}	**41.0** ^{b}	12.1 – 104.5	**90.5** ^{b}
Bole	141.2 ^{a}	26.5 – 245.2	76.9 ^{a}	59.7 ^{b}	26.0 – 93.9	49.1 ^{b}	31.2 ^{b}	10.2 – 81.1	79.1 ^{a}
Branches	14.9 ^{a}	1.7 – 40.1	6.9 ^{a}	24.3 ^{a}	3.9 – 54.7	16.5 ^{b}	2.7 ^{b}	0.3 – 5.9	5.9 ^{a}
Fine Fuels	31.8 ^{a}	2.5 – 51.1	16.2 ^{a}	44.9 ^{a}	11.8 – 70.2	34.4 ^{b}	7.1 ^{b}	0.5 – 17.5	15.1 ^{a}
Needles	22.0 ^{a}	1.6 – 38.4	10.9 ^{a}	27.5 ^{a}	8.5 – 39.1	22.3 ^{b}	4.6 ^{b}	0.2 – 11.5	9.8 ^{a}
Total Roots (>10mm)	**30.0** ^{a}	10.1 – 49.6	**15.4** ^{a}	**18.2** ^{a}	6.3 – 33.8	**12.3** ^{ab}	**4.5** ^{b}	0.7 – 10.5	**9.5** ^{b}
Root Crown	19.0 ^{a}	6.6 – 35.9	61.9 ^{a}	10.4 ^{b}	3.1 – 17.1	57.2 ^{a}	2.6 ^{c}	0.6 – 5.5	63.5 ^{a}
Lateral Roots (>10mm)	11.0 ^{a}	3.4 – 23.4	38.1 ^{a}	7.8 ^{a}	3.2 – 16.6	42.8 $_{a}$	1.8 ^{b}	0.1 – 5.1	36.6 ^{a}
Total Tree Biomass	**217.9** ^{a}	40.8 - 386	**100**	**147.1** ^{a}	48 – 241.1	**100**	**45.5** ^{b}	13.4 - 115	**100**
Total Root: Total Aboveground Biomass	**0.19** (0.13 – 0.33) ^{a}			**0.14** (0.10 – 0.16) ^{ab}			**0.11** (0.03 – 0.15) ^{b}		