Belowground and aboveground biomass in young postfire lodgepole pine forests of contrasting tree density

Creighton M. Litton, Michael G. Ryan, Daniel B. Tinker, and Dennis H. Knight

Abstract: As much as 40% of live biomass in coniferous forests is located belowground, yet the effect of tree density on biomass allocation is poorly understood. We developed allometric equations using traditional harvesting techniques to estimate coarse root biomass for ≈13-year-old postfire lodgepole pine trees (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.). We then used these equations, plus estimates of fine root and aboveground biomass, to estimate total tree biomass and belowground to aboveground biomass ratios in young postfire lodgepole pine stands with a wide range of tree densities. Belowground biomass allocation increased with tree density, but the increase was largely determined by inherent differences associated with tree size, not competition. Stand biomass in trees ranged from 46 to 5529 kg·ha^{-1} belowground, from 176 to 9400 kg·ha^{-1} aboveground, and from 222 to 13 685 kg·ha^{-1} for total biomass. For individual trees, the ratio of belowground to total biomass declined with tree size from 0.44 at a basal diameter of 0.5 cm to 0.11 at a basal diameter of 8 cm. This shift in individual tree allocation caused the proportion of total stand biomass in belowground tissues to increase from 19% in low-density stands with larger trees to 31% in high-density stands with small trees.

Résumé : Jusqu'à 40 % de la biomasse vivante dans les forêts de conifères se trouve sous terre mais nous connaissons mal l'effet de la densité du peuplement sur l'allocation de la biomasse. Nous avons développé des équations allométriques à l'aide des techniques traditionnelles de récolte pour estimer la biomasse des grosses racines de pins lodgepole (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) issus d'un feu survenu il y a environ 13 ans. Nous avons ensuite utilisé ces équations, en plus d'estimés de la biomasse épigée et de celle des racines fines, pour estimer la biomasse totale des arbres et le rapport de la biomasse hypogée sur la biomasse épigée dans de jeunes peuplements de pin lodgepole issus de feu avec un large éventail de densités. L'allocation de la biomasse hypogée augmente avec la densité des tiges mais l'augmentation est en grande partie déterminée par des différences inhérentes associées à la dimension des arbres et non à la compétition. La biomasse des peuplements qui se retrouve dans les arbres varie de 46 à 5529 kg·ha^{-1} dans le sol, de 176 à 9400 kg·ha^{-1} au-dessus du sol et de 222 à 13 685 kg·ha^{-1} pour la biomasse totale. Dans le cas des tiges individuelles, le rapport de la biomasse hypogée sur la biomasse totale diminue avec la dimension des tiges passant respectivement de 0,44 à 0,11 pour un diamètre basal de 0,5 à 8 cm. Ce changement dans l'allocation chez les arbres individuels entraîne une augmentation de la proportion de la biomasse totale du peuplement qui se retrouve dans les tissus souterrains. Cette augmentation va de 19 % dans les peuplements de faible densité formés d'arbres plus gros à 31 % dans les peuplements de forte densité formés de petits arbres.

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Introduction

Forests cover more than one third of the earth's land surface and are the most important carbon pool in terrestrial

C.M. Litton[1] and D.H. Knight. Department of Botany, University of Wyoming, P.O. Box 3165, Laramie, WY 82071, U.S.A.
M.G. Ryan. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, 240 West Prospect Road, Fort Collins, CO 80526, U.S.A., and Department of Forest Sciences and Graduate Degree Program in Ecology, Colorado State University, Fort Collins, CO 80523, U.S.A.
D.B. Tinker. Department of Geosciences and Natural Resources Management, Western Carolina University, Cullowhee, NC 28723, U.S.A.

[1]Corresponding author (e-mail: clitton@uwyo.edu).

ecosystems, containing some 80% of all global aboveground carbon (Waring and Running 1998) and accounting for as much as 75% of global net primary productivity (Melillo et al. 1993). Considerable progress has been made in describing terrestrial carbon cycling and storage on regional and global scales, with much of the emphasis placed on remote sensing techniques and modeling (e.g., Harvey 2000; Running et al. 2000). Fundamental to scaling and modeling efforts is the existence of a reliable body of information on processes and mechanisms that can be used to construct a theoretical framework. As a result of natural and anthropogenic disturbances, young developing stands occupy much of the forested landscape. Extrapolating the results of studies conducted in mature forests to young stands could lead to erroneous conclusions when scaling to the region or biosphere.

In light of the paucity of data on belowground biomass storage, attempts have been made to generalize biomass allocation patterns for coniferous forests worldwide, with reported root to shoot biomass ratios ranging from 0.18

(Jackson et al. 1996) to 0.26 (Cannell 1982; Cairns et al. 1997). Patterns of allocation to belowground and aboveground biomass pools across nutrient and (or) moisture regimes are relatively well established for mature coniferous forests, although there are no rules for quantitative predictions of allocation. Various investigators have found that more biomass is allocated belowground as moisture and (or) nutrients become limiting (Keyes and Grier 1981; Comeau and Kimmins 1989; Kurz 1989; Gower et al. 1992, 1994). However, very little work has been done on the effect of stand density on allocation patterns. Increased stand density appears to result in increased allocation of biomass belowground (Pearson et al. 1984), which has important implications for accurately estimating patterns of carbon cycling and storage across the landscape. Validating the different components of the carbon budget, especially belowground where data are often missing or incomplete, is important for defining allocation rules that will allow accurate predictions across the landscape (Gower et al. 2001).

We developed allometric equations for predicting coarse root biomass (≥ 2 mm) in ≈ 13-year-old lodgepole pine trees (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) in Yellowstone National Park (YNP), Wyoming. We used these allometric equations, along with existing site-specific allometric equations for aboveground biomass (Tinker et al., submitted[2]) and fine root biomass estimates from coring, to estimate tree biomass (belowground, aboveground, and total) and various belowground to aboveground biomass ratios for young stands in YNP that cover a wide range of tree densities (<500 to >500 000 trees·ha^{-1}). Specific objectives of this study were to (*i*) develop allometric equations for estimating individual tree coarse root biomass (≥ 2 mm) in young trees from easily measured aboveground variables, (*ii*) determine if coarse root biomass allometry varies with stand density, (*iii*) investigate the effect of stand density on biomass allocation patterns in young, developing coniferous forests, and (*iv*) determine if the biomass allocation patterns that we measured in young lodgepole pine forests are comparable with those reported for mature coniferous forests.

Material and methods

We located 12 stands throughout YNP that have regenerated since the 1988 fires and span a wide range of tree densities. Live coarse roots were harvested for 45 trees, and allometric equations were developed to estimate coarse root biomass from basal diameter. We then applied our allometric equations to tree measurements from each stand to estimate coarse root biomass and used existing site-specific allometric equations to estimate aboveground biomass (Tinker et al., submitted[2]). The belowground and aboveground biomass estimates were used, together with fine root biomass estimates from coring, to estimate stand-level tree biomass (belowground, aboveground, and total) and various belowground to aboveground biomass ratios. We then grouped stands into density classes and evaluated biomass and biomass ratios to examine how biomass allocation patterns are affected by stand density.

Study area

YNP provides an ideal laboratory for forest ecosystem studies, as anthropogenic effects from management activities are minimal. The park is located in northwest Wyoming and covers a land area of some 9000 km^2, the majority of which is situated on several high-elevation, forested plateaus characterized by gently rolling topography (Turner et al. 1994, 1997). The predominant habitat types on the plateaus are in the subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) series where subalpine fir dominates the climax communities and lodgepole pine is the dominant seral species. Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and whitebark pine (*Pinus albicaulis* Engelm.) can also be abundant in some areas (Despain 1990). As a result of recurring fire and insect epidemics, lodgepole pine forests currently cover some 80% of the park (Despain 1990; Whitlock 1993). Site index at 100 years for lodgepole pine stands in YNP ranges from 9 to 20 (mean of 13, *n* = 30) (D.M. Kashian, unpublished data). The lodgepole forests of YNP occur over a large portion of the Rocky Mountain region and are similar to other pine forests in the Intermountain West (Knight et al. 1994).

Our stands were located on sites similar in environmental and topographic characteristics on the subalpine plateaus of YNP at elevations between 2000 and 2500 m (Table 1). All had regenerated since the 1988 Yellowstone fires (Fig. 1) and were located on soils derived from rhyolite. Rhyolite is the dominant parent material of the subalpine plateaus and is the result of major volcanic activity in the Quaternary Era (Despain 1990; Whitlock 1993). Soils derived from rhyolite are relatively infertile (e.g., mean values of 1.11% organic carbon and 0.048 mequiv. total nitrogen·100 g^{-1}) and are classified in the Cryochrept or Cryumbrept families (Trettin 1986).

The climate of YNP is characterized by cool temperatures throughout the year and dry growing seasons. At Yellowstone Lake, the mean January temperature is –11.8°C and the mean July temperature is 12.9°C; mean annual precipitation is 465 mm (Dirks and Martner 1982). Approximately 65–85% of the annual precipitation comes as snow, and snow cover usually exists from mid-October through late May (Despain 1990).

Root biomass harvesting

Three stands covering the natural range of variability in postfire tree density were chosen for sampling live coarse root biomass in early June of 2001 (Fig. 1; Table 1). We define coarse roots as ≥ 2 mm in diameter and fine roots as <2 mm in diameter. In each stand, 15 trees spanning the range of tree sizes present were randomly chosen for the destructive harvesting of root biomass. While most trees chosen for sampling were 13 years old, the inclusion of trees from the smallest size classes meant that a few younger trees were used. Before harvesting root systems, the trees were cut at ground level and the following measurements were taken: outside and inside bark basal diameter, basal ring widths for the years 1998–2000, total height, and the annual height increment during the period 1998–2000. Harvesting

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Table 1. Description of stands in Yellowstone National Park, Wyoming.

Stand[a]	Density class[c]	Density (trees·ha^{-1})	Mean (±1 SE) basal diameter (cm)	Mean (±1 SE) tree height (cm)	Elevation (m)	Soil textural class[d]
Cascade Meadows (1)	Low	425	2.4 (0.2)	61.6 (6.3)	2486	Sandy loam
Lewis Canyon North (2)[b]	Low	533	2.7 (0.3)	66.5 (6.8)	2372	Sandy loam
Cygnet Lakes (3)	Low	742	3.1 (0.2)	79.4 (6.0)	2508	Sandy loam
Pitchstone Plateau (4)	Low	758	3.2 (0.2)	82.2 (5.6)	2368	Sandy loam
Riddle Lake TH (5)[b]	Moderate	7 000	2.8 (0.1)	100.4 (3.7)	2429	Sandy loam
Lewis Canyon South (6)	Moderate	8 700	3.0 (0.2)	113.3 (5.0)	2363	Sandy loam
Biscuit Basin (7)	Moderate	25 250	2.6 (0.1)	121.2 (4.1)	2223	Sandy loam
Howard Eaton (8)	Moderate	39 167	1.9 (0.1)	94.3 (2.6)	2370	Loamy sand
Riddle High (9)	High	50 167	2.1 (0.04)	96.4 (1.8)	2417	Sandy loam
Firehole Loop (10)[b]	High	73 455	1.4 (0.06)	75.5 (2.9)	2166	Sandy loam
Gibbon Falls (11)	High	75 500	1.7 (0.05)	85.2 (2.0)	2131	Sandy loam
7-Mile Bridge (12)	High	598 462	0.9 (0.02)	60.4 (1.0)	2076	Sandy loam

Note: All stands were 13 years old in 2001.

[a]Numbers in parentheses refer to stand locations in Fig. 1.

[b]Stands used for harvesting coarse root biomass.

[c]Low density, <1000 trees·ha^{-1}; moderate density, 7000 – 40 000 trees·ha^{-1}; high density, >50 000 trees·ha^{-1}.

[d]Based on USDA classification scheme.

of coarse roots was accomplished with hand trowels and shovels by carefully following individual live roots from the root crown out and (or) down to the point that the roots became <2 mm in diameter. Working with small trees in the relatively sandy soils of YNP (≈60–70% sand in our stands) facilitated this work.

The extracted root systems were transported to the laboratory where they were divided into four root diameter categories (2–5, 5–10, >10 mm, and root crown) and washed thoroughly to remove any remaining dirt. The cleaned and sorted roots were placed in a forced-air oven and dried at 75°C to a constant mass (48–72 h). A small subset of samples (n = 10) was burned in a muffle furnace to determine percent ash to assess how thoroughly the roots had been washed. Values of percent ash ranged from 0.3 to 3.1% (mean = 1.6%, SE = 0.50). As these values did not differ significantly from percent ash values of foliage from our study area (p = 0.34), they were not used to correct the root biomass estimates.

Stand sampling

Twelve stands spanning a wide range of tree densities (<500 to >500 000 trees·ha^{-1}) were located across the subalpine plateaus of YNP to estimate stand-level biomass and investigate the effect of stand density on biomass allocation patterns (Fig. 1; Table 1). All stands were located close to the internal park road network but were at least 250 m from the road itself. Stands were divided into three classes based on tree density: low-density stands containing <1000 trees·ha^{-1}, moderate-density stands with 7000 – 40 000 trees·ha^{-1}, and high-density stands with >50 000 trees·ha^{-1} (Table 1). Scattered individuals of whitebark pine, subalpine fir, and Engelmann spruce can be found in young postfire stands, but of the 2569 trees that we measured in our stands, only 27 were not lodgepole pine (≈1%).

Live fine root biomass was estimated in each of the 12 stands in late July – early August of 2000. Fifteen soil cores (6.35 cm in diameter) were taken to a depth of 30 cm in

each stand. Within 24 h of sampling, the 15 cores for each stand were composited and all roots were visually inspected. Live lodgepole pine roots were removed manually, separated into <2 and ≥2 mm root diameter categories, washed vigorously to remove any dirt and soil contaminants, and dried in a forced-air oven at 75°C to a constant mass (48–72 h).

At each of the 12 stands, density and individual tree dimensions were determined in three belt transects. The size of the belt transects varied with density, ranging from 20 × 20 m in the low-density stands to 1 × 5 m in the highest density stand. All trees within the belt transects were measured for the following variables: outside bark basal diameter, total height, and annual height increment during the period 1998–2000. Allometric equations for belowground and aboveground biomass were applied to individual tree measurements and used together with fine root biomass estimates from coring to estimate stand belowground, aboveground, and total tree biomass. Belowground to aboveground biomass ratios (root to shoot, fine root to foliage, and coarse root to aboveground woody) were estimated from stand biomass values. Aboveground woody biomass is defined as all aboveground tree biomass excluding foliage (stem plus branch plus bark).

For comparison with other studies, we use the terms root to shoot ratio (total belowground to total aboveground tree biomass) and biomass allocation, as they are commonly used in forest biomass studies. The term root to shoot ratio may be more appropriate for herbaceous species. The accumulation of large amounts of biomass in trees as wood may result in root to shoot ratios that no longer provide information on current year patterns in allocation. For trees, the ratio of fine root to foliage biomass (which we also report) is comparable with the root to shoot ratio in herbaceous species. The term allocation may be more appropriate for describing the flux of carbon to a particular organ per unit time. Biomass allocation, as used here, is the end result of carbon fixation, allocation, and loss via respiration over the life of the individual plant or stand.

Fig. 1. Map of Yellowstone National Park, Wyoming, showing stands that were sampled within areas burned in 1988. All stands were located close to the internal park road network but were situated at least 250 m from the road itself. Numbers refer to stand descriptions in Table 1.
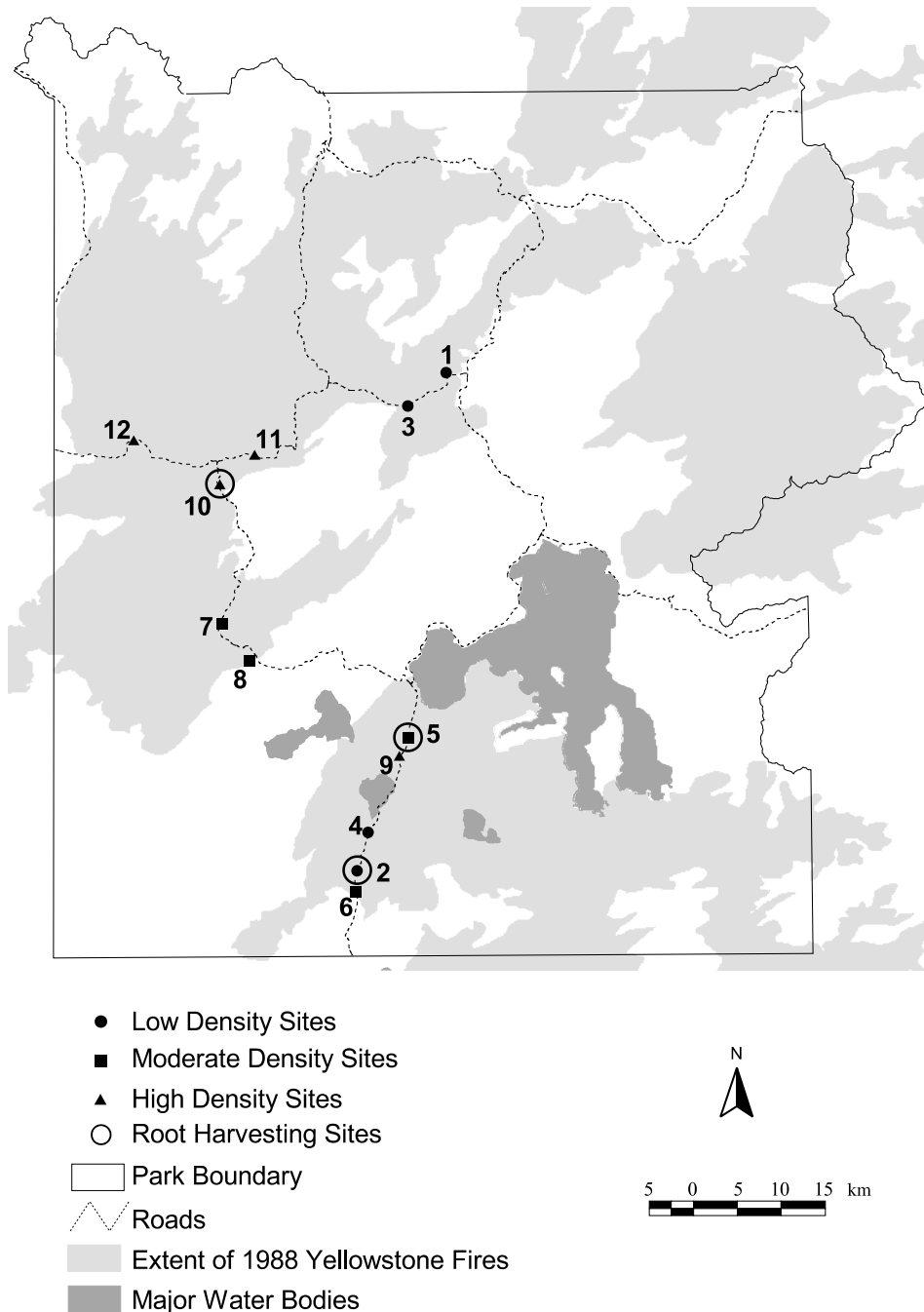
Statistical analysis

Nonlinear regressions were computed in SPSS 10.0 for Windows (SPSS Inc. 1999) using untransformed data and a power function of the form

[1] $Y = aX^b$

where Y is the dependent variable (e.g., total coarse root biomass, g dry mass), X is the independent variable (e.g., basal diameter, cm), and a and b are constants. The nonlinear model in eq. 1 is often referred to as Huxley's allometric equation (Günther and Morgado 1996). We used the sequen-

tial quadratic programming algorithm for an iteration method (SPSS Inc. 1999).

All measured independent variables (outside and inside bark basal diameter, basal ring widths for the period 1998–2000, total height, and annual height increment during the period 1998–2000) were examined for their utility as predictors of live coarse root biomass in five size categories: total coarse root biomass (≥ 2 mm), 2–5 mm root biomass, 5–10 mm root biomass, >10 mm root biomass, and root crown biomass. Nonlinear equations were also used to characterize the relationship between tree size and total belowground to

total aboveground biomass. Nonlinear models of this form are commonly used because they strike a good balance between accurate predictions and low data requirements (Ter-Mikaelian and Korzukhin 1997). Linear regression models that use log-transformed data are also common in allometry studies, and we investigated their applicability here. Ultimately, we used nonlinear regression techniques because (*i*) all of the relationships that we examined were nonlinear, (*ii*) linear regression techniques that use log-transformed data require methods to eliminate bias in retransformed values (Duan 1983), and (*iii*) nonlinear models proved superior to linear models in all cases.

The need for separate models based on tree density class was assessed for each root diameter category using an extra sum of squares analysis for nested models (Bates and Watts 1988). Goodness of fit for all models, nonlinear and linear, was determined by examining *p* values, the sum of squares of the residuals, the mean square of the error, the coefficient of determination, and by plotting the residuals (observed minus predicted values). Coefficients of determination (R^2) for each model were calculated as

[2] $R^2 = 1 - (SSR/corrected\ SST)$

where SSR is the sum of squares of the residuals and corrected SST is the total sum of squares of deviations from the overall mean.

Tests for density effects on mean values of biomass (total, aboveground, total belowground, belowground by root diameter category, and belowground to aboveground ratios) were performed using one-way analysis of variance with density class as a grouping variable. Post hoc tests for differences between density groups were performed with Tukey's honestly significant difference method. All statistical tests were performed at $\alpha = 0.05$.

Results

Belowground biomass allometry

Basal diameter was the most effective predictor of live coarse root biomass. The relationship between basal diameter (outside and inside bark) and individual tree coarse root biomass was nonlinear (Fig. 2) and highly significant for all root diameter categories (R^2 values ranging from 0.77 to 0.96; Table 2). In all cases, a nonlinear approach produced a superior fit compared with log-transformed linear models. Tests of the need for different models based on density class were not significant for any biomass category ($p > 0.40$), so data from all density classes were combined to generate the allometric equations presented here. Inside bark basal diameter was a slightly better predictor of belowground biomass than outside bark basal diameter for every biomass category (Table 2). Model fits were better for root crown and total coarse root biomass than for any of the root diameter classes.

Models based on outside bark basal diameter show a slight bias towards overprediction of belowground biomass (i.e., negative unstandardized residuals) at small basal diameters (<3 cm; Figs. 3*a*–3*e*). Much of this bias is eliminated with the use of inside bark basal diameter as a predictor variable (Figs. 3*f*–3*j*). Larger diameter trees exhibited much greater error variance than smaller diameter trees. Such

heteroscedasticity (i.e., unequal error variance over all observations) is common for biomass data (Parresol 1993).

Stand biomass estimates

Stand biomass estimates for our study area derived from allometric equations, plot measurements of tree basal diameter, and estimates of fine root biomass from coring varied widely (Table 3). Biomass ranged from 46 to 5529 kg·ha^{-1} for belowground biomass, from 176 to 9400 kg·ha^{-1} for aboveground biomass, and from 222 to 13 685 kg·ha^{-1} for total stand biomass. Biomass in all categories generally increased as stand density increased (Table 3; Fig. 4). Coarse root biomass (range of 31–3677 kg·ha^{-1}) averaged 62% of total belowground biomass. Low- and high-density stands had a slightly higher proportion of belowground biomass in coarse roots than moderate-density stands (61–69 versus 51–59%). Fine root biomass estimates ranged from 15 kg·ha^{-1} in the lowest density stand to 1852 kg·ha^{-1} in the highest density stand (Table 3). The proportion of total belowground biomass in fine roots was relatively constant for low- and high-density stands (31–39%) and slightly higher for moderate-density stands (41–49%).

Belowground to aboveground biomass ratios increased with increasing tree density, ranging from 0.21 to 0.68 for root to shoot biomass, from 0.16 to 0.45 for fine root to foliage biomass, and from 0.21 to 0.69 for coarse root to aboveground woody biomass. The proportion of total stand biomass contributed by belowground tissues increased with stand density from a mean of 19% in the low-density stands to 27% in the moderate-density stands and 32% in the high-density stands. Increases in the proportion of total biomass found belowground in higher density stands was primarily related to increased allocation to fine roots and 2–5 mm coarse roots, as the proportion contributed by root crowns and roots >5 mm remained remarkably constant across stands (Table 3). Increased allocation of biomass belowground with increasing density is also apparent in all three belowground to aboveground ratios (Table 3; Fig. 5).

Fine roots accounted for the most biomass belowground (31–49%) for all stands except the highest density stand (Table 3). The next most important category for total root biomass was 2–5 mm (13–26%) followed by root crown biomass (12–17%), although root crown biomass equaled or slightly exceeded biomass in the 2–5 mm category in the lowest density stands. Excluding the highest density stand, biomass allocation to different root diameter categories followed the order fine roots > 2–5 mm coarse roots ≥ root crowns > 10 mm coarse roots > 5–10 mm coarse roots.

Belowground stand biomass differed by stand density class for all root size categories ($p < 0.05$). Aboveground and total stand biomass and the ratio of coarse root to aboveground woody biomass also differed by density class ($p \leq 0.01$). Belowground, aboveground, and total stand biomass, as well as the various ratios of belowground to aboveground biomass, all increased with increasing tree density (Figs. 4 and 5). Results of post hoc tests for differences in density classes revealed that for all biomass categories, as well as the ratio of fine root to foliage biomass, the low-density group contained significantly less biomass (or a lower biomass ratio) than both the moderate- and high-density groups (Figs. 4 and 5*b*). An apparent trend of increasing biomass (or increasing biomass ratios) from moderate- to high-

Fig. 2. Allometric relationship between (*a–e*) outside bark and (*f–j*) inside bark basal diameter and (*a* and *f*) root crown biomass, (*b* and *g*) >10 mm root biomass, (*c* and *h*) 5–10 mm root biomass, (*d* and *i*) 2–5 mm root biomass, and (*e* and *j*) total coarse root biomass for ≈13-year-old *Pinus contorta* var. *latifolia* in Yellowstone National Park, Wyoming. Regression parameters are listed in Table 2.
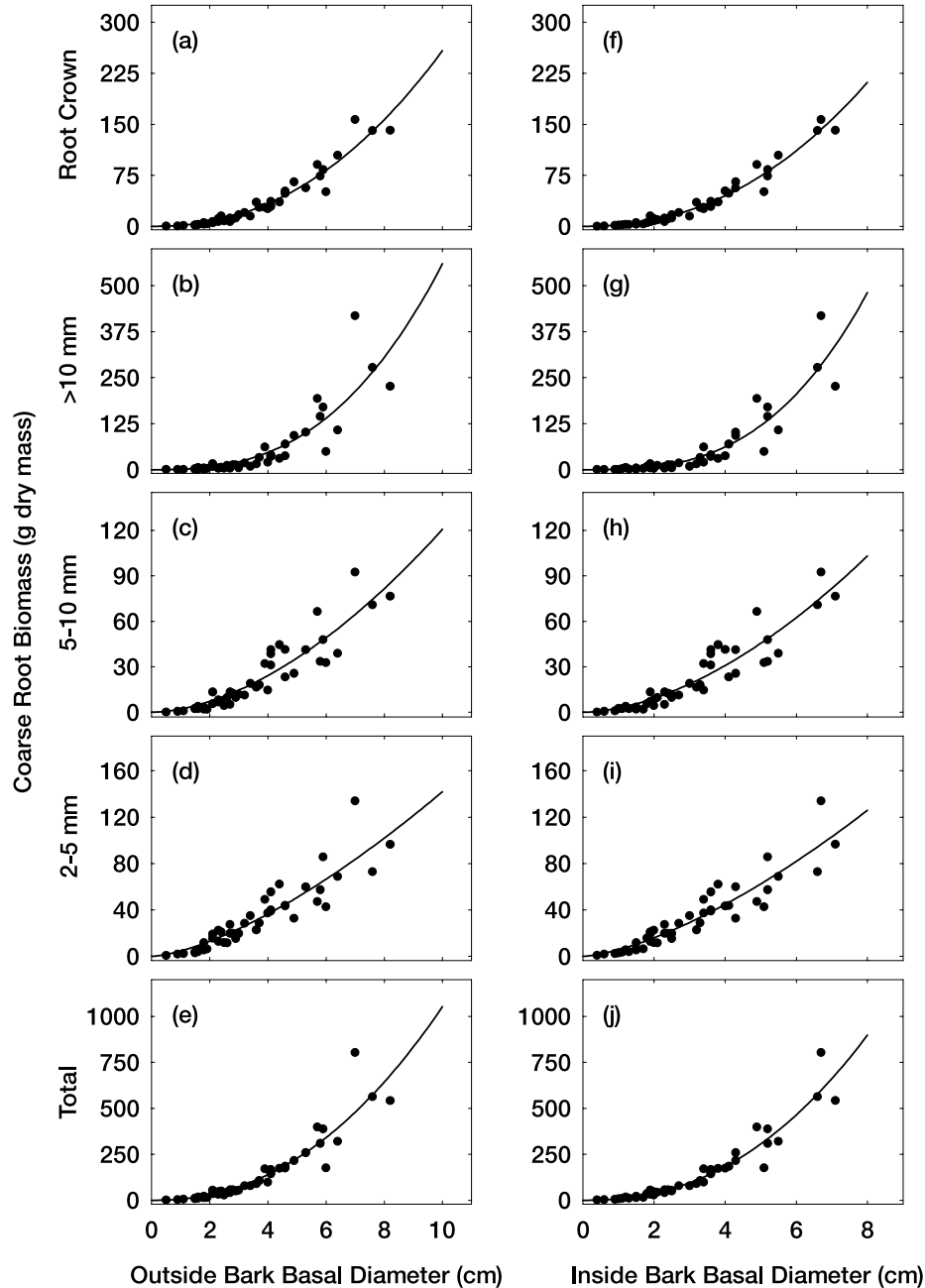
density classes was evident for all categories except the fine root to foliage biomass ratio, but significant differences between these classes were confined to coarse root and total belowground biomass categories and the coarse root to aboveground woody biomass ratio (Figs. 4 and 5).

Discussion

Belowground biomass allometry

Existing allometric equations for predicting belowground and aboveground biomass in lodgepole pine stands (Pearson et al. 1984; Comeau and Kimmins 1989) were developed in

older stands (≥70 years old) with larger trees (≥2 cm diameter at 1.3 m height). In addition, they require the measurement of tree or stand basal area at 1.3 m and (or) height to the base of the live crown, both of which are impractical in our young stands. Equations presented here require basal diameter and explain between 77 and 96% of the variance in root biomass. The utility of our allometrics as the trees grow larger over the course of stand development is uncertain.

Total coarse root biomass determined as the sum of individual component models always exceeds that determined with a single model for both individual trees and stands. Parresol (2001) outlined two procedures that guarantee the

Table 2. Regression equations for predicting total coarse root biomass (≥ 2 mm) and coarse root biomass by root diameter categories (g dry mass) from outside and inside bark basal diameter (cm) for ≈ 13-year-old *Pinus contorta* var. *latifolia* in Yellowstone National Park, Wyoming.

Dependent variable	n	a (SE)	b (SE)	MSE	R^2
Outside bark basal diameter (cm)					
Total coarse root biomass (≥ 2 mm)	45	6.563 (2.145)	2.205 (0.175)	4032.79	0.87
2–5 mm coarse root biomass	45	4.658 (1.058)	1.484 (0.129)	144.14	0.83
5–10 mm coarse root biomass	45	2.127 (0.561)	1.754 (0.146)	80.05	0.85
>10 mm coarse root biomass	45	1.091 (0.667)	2.710 (0.319)	1753.20	0.77
Root crown biomass	45	1.507 (0.325)	2.234 (0.115)	100.50	0.94
Inside bark basal diameter (cm)					
Total coarse root biomass (≥ 2 mm)	45	7.691 (1.880)	2.289 (0.139)	2444.45	0.92
2–5 mm coarse root biomass	45	5.688 (1.064)	1.489 (0.114)	114.69	0.86
5–10 mm coarse root biomass	45	2.746 (0.614)	1.744 (0.133)	67.51	0.87
>10 mm coarse root biomass	45	1.028 (0.540)	2.957 (0.290)	1257.50	0.84
Root crown biomass	45	2.025 (0.315)	2.236 (0.089)	59.56	0.96

Note: Equations for all dependent variables are of the form $Y = aX^b$ where Y is the dependent variable (e.g., total coarse root biomass, g dry mass), X is outside or inside bark basal diameter (cm), and a and b are constants in the equation. SE is the asymptotic standard error of the parameter estimate, MSE is the mean square of the error, and R^2 is the coefficient of determination. All models were highly significant ($p < 0.005$).

additivity of nonlinear biomass equations. The first procedure calculates total biomass as the sum of the separately calculated best regression functions of the biomass components (i.e., our sum of individual component models), and the second assures additivity by setting restraints on regression coefficients. We did not use these techniques because our primary interest lay in estimating total coarse root biomass, and the single model was superior to all individual component models excluding root crown biomass.

For individual trees, our equations show a substantial difference between total biomass determined with a single model and as the sum of individual component models only for basal diameters <3 cm. Summing individual component models overestimates total biomass by 61% for a 1-cm tree, 14% for a 2-cm tree, and 4.5% for a 3-cm tree. Total coarse root stand biomass estimates are similar to the sum of individual component models in low- and moderate-density stands where the trees are larger on average (percent difference ranging from 1.4 to 3.6% at densities <39 000 trees·ha^{-1}). At higher densities, where a larger portion of the trees are in the smaller diameter class, total coarse root biomass estimated as the sum of individual component models exceeds the single model estimate by as much as 40% for the highest density stand (598 462 trees·ha^{-1}). The difference for stands that range in density from 39 000 to 75 500 trees·ha^{-1} is only 7.5–12.9%.

Our models of individual components are useful for estimating root biomass in different size categories and sum to a nearly unbiased total in all but the highest density stands (>100 000 trees·ha^{-1}), which are not common across the landscape. However, when total coarse root biomass values are required, we recommend using the single equation as we did in this study (Table 3).

Stand biomass estimates

Increasing biomass with stand age is a common attribute of forest ecosystems, although biomass can decline in very old forests (Peet 1981). The maximum stand biomass increment values in even-aged lodgepole pine stands in Wyoming

occur ≈ 40–60 years following stand initiation (Pearson et al. 1987). Therefore, it is not surprising that reported values of lodgepole pine forest biomass in older stands far exceed even our highest estimates of biomass in young stands (5.5 Mg·ha^{-1} for belowground biomass, 9.4 Mg·ha^{-1} for aboveground biomass, and 13.7 Mg·ha^{-1} for total stand biomass). Biomass estimates for lodgepole stands ranging from 75 to 240 years old in southeastern Wyoming were 26–56 Mg·ha^{-1} for belowground biomass, 96–144 Mg·ha^{-1} for aboveground biomass, and 123–185 Mg·ha^{-1} for total stand biomass (Pearson et al. 1984). In southeastern British Columbia in 70- to 78-year-old stands, the same values ranged from 37 to 79, from 117 to 313, and from 156 to 392 Mg·ha^{-1}, respectively (Comeau and Kimmins 1989).

Biomass estimates for other young conifers are also greater than for 13-year-old lodgepole pine stands in YNP, perhaps because of the short growing season and infertile soils there. Twelve-year-old Scots pine (*Pinus sylvestris* L.) plantations in central Poland averaged 9.4 Mg·ha^{-1} for belowground biomass, 33.2 Mg·ha^{-1} for aboveground biomass, and 42.6 Mg·ha^{-1} for total stand biomass (Oleksyn et al. 1999). Eight-year-old loblolly pine (*Pinus taeda* L.) plantations from the Sandhills of North Carolina exhibited biomass estimates ranging from 6.1, 20.9, and 27.0 Mg·ha^{-1} on control plots to 13.5, 44.4, and 57.9 Mg·ha^{-1} on fertilized and irrigated plots for belowground, aboveground, and total stand biomass, respectively (Albaugh et al. 1998). For mixed loblolly and slash pine (*Pinus elliottii* Engelm.) plantations 8–12 years of age, biomass estimates ranged from 2.9 to 16.6 Mg·ha^{-1} for belowground biomass, from 16.1 to 91.0 Mg·ha^{-1} for aboveground biomass, and from 19.0 to 107.6 Mg·ha^{-1} for total stand biomass (Nemeth 1973).

Our total stand biomass estimates do not include biomass estimates for herbaceous and shrub species and estimates of belowground biomass in mycorrhizal tissues not contained in or on roots (i.e., hyphae, sporocarps, and sclerotia). After disturbance in pine forests, more carbon can be fixed in shrubs and herbaceous plants because of reduced competition from trees (Knight et al. 1994). Notably, understory fine

Fig. 3. Residuals (observed minus predicted values) of the nonlinear relationship between (*a*–*e*) outside bark and (*f*–*j*) inside bark basal diameter and (*a* and *f*) root crown biomass, (*b* and *g*) >10 mm root biomass, (*c* and *h*) 5–10 mm root biomass, (*d* and *i*) 2–5 mm root biomass, and (*e* and *j*) total coarse root biomass for ≈13-year-old *Pinus contorta* var. *latifolia* in Yellowstone National Park, Wyoming.
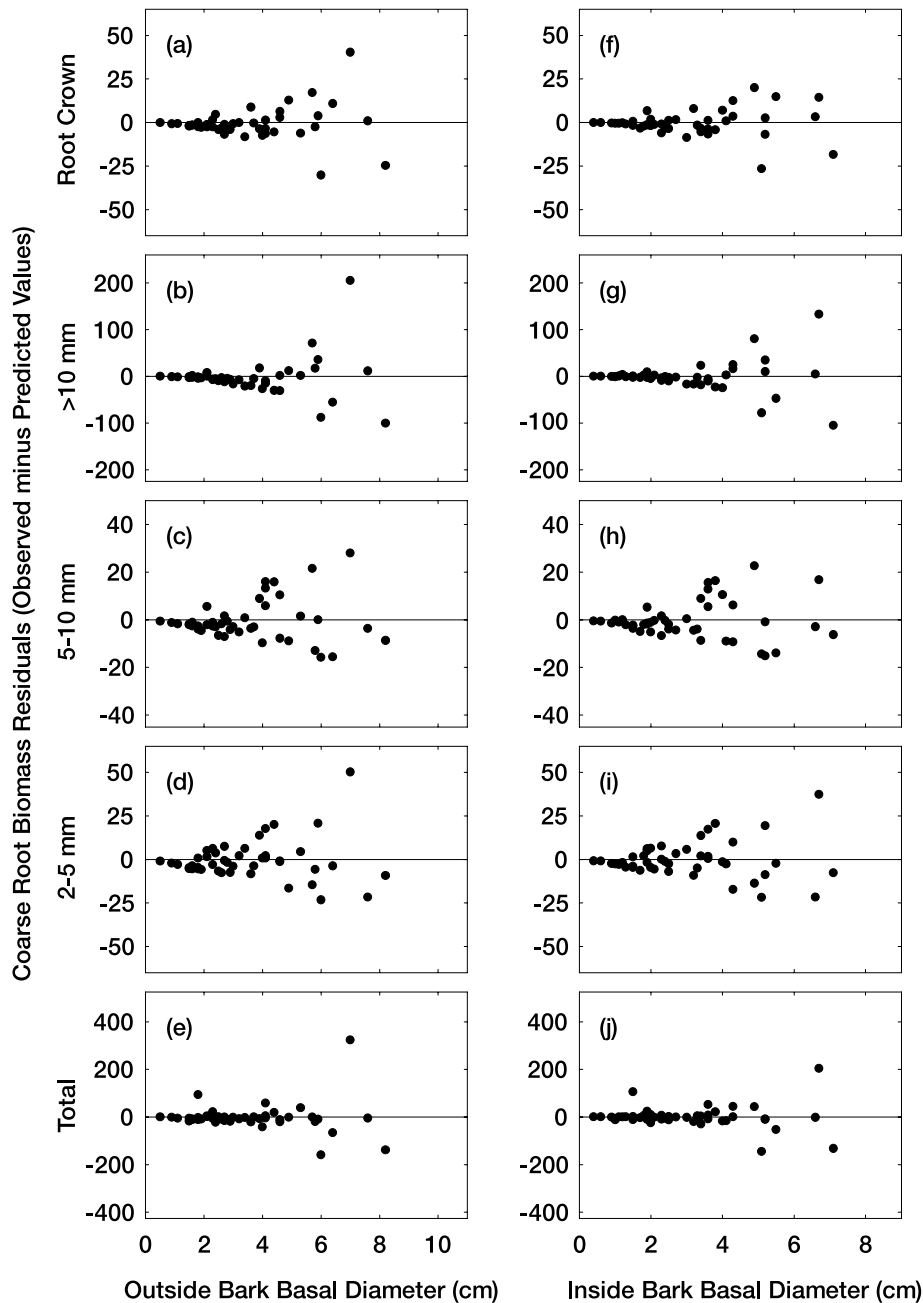
root productivity can equal or exceed overstory fine root productivity during early stages of stand development in pine forests (Gower et al. 1994). Postfire stands in YNP that contain low densities of lodgepole pine tend to have higher cover values of herbaceous and shrub species than stands with higher tree densities (C.M. Litton, unpublished data). However, nontree aboveground biomass did not differ significantly with density class (*p* > 0.24), so inclusion of herbaceous and shrub biomass here would not change our results substantially on a quantitative or a qualitative basis. Mycorrhizal biomass in hyphae, sporocarps, and sclerotia could be 3% of total stand biomass if allocation patterns in

our study area are similar to those reported for 35-year-old Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) in western Oregon (Fogel and Hunt 1979).

Biomass allocation patterns

The fraction of biomass in roots in young lodgepole pine stands is high compared with other values in the literature. Our estimates of the proportion of tree biomass in roots ranged from 17 to 40% (mean = 26%), values that exceed or are on the high end of the range reported for various species of pines (13–25%; Knight et al. 1994). About 22% of total biomass is located belowground in 75- to 240-year-old

Table 3. Summary of stand biomass (kg dry mass·ha^{-1}) estimated from allometric equations for ≈13-year-old stands of *Pinus contorta* var. *latifolia* in Yellowstone National Park, Wyoming.

Biomass category	Low density				Moderate density				High density			
	Cascade Meadow	Lewis Canyon N	Cygnet Lakes	Pitchstone Plateau	Riddle Lake TH	Lewis Canyon S	Biscuit Basin	Howard Eaton	Riddle High	Firehole Loop	Gibbon Falls	7-Mile Bridge
Fine root[a]	15 (7)	34 (8)	48 (6)	50 (5)	537 (14)	861 (11)	1 269 (10)	1076 (12)	1 116 (11)	1036 (12)	1 141 (10)	1 852 (13)
2–5 mm	8 (4)	13 (3)	21 (3)	23 (2)	159 (4)	235 (3)	532 (4)	577 (7)	625 (6)	650 (7)	845 (7)	2 482 (18)
5–10 mm	5 (2)	9 (2)	15 (2)	16 (2)	101 (3)	160 (2)	338 (3)	334 (4)	370 (4)	361 (4)	475 (4)	1 146 (8)
>10 mm	11 (5)	22 (5)	36 (5)	46 (5)	178 (5)	372 (5)	609 (5)	428 (5)	514 (5)	431 (5)	567 (5)	656 (5)
Root crown	8 (4)	13 (3)	22 (3)	27 (3)	131 (3)	238 (3)	442 (4)	369 (4)	426 (4)	380 (4)	504 (4)	847 (6)
Coarse root[b]	31 (14)	55 (12)	92 (13)	110 (12)	549 (15)	989 (13)	1 854 (15)	1564 (18)	1 800 (17)	1614 (18)	2 139 (19)	3 677 (27)
Total root	46 (21)	89 (20)	140 (19)	160 (17)	1086 (29)	1850 (24)	3 123 (25)	2640 (30)	2 916 (28)	2650 (30)	3 280 (29)	5 529 (40)
Aboveground	176 (79)	353 (80)	582 (81)	775 (83)	2722 (71)	6016 (76)	9 400 (75)	6191 (70)	7 538 (72)	6224 (70)	8 140 (71)	8 156 (60)
Total stand	222	442	722	935	3808	7866	12 523	8831	10 454	8874	11 420	13 685
Root/shoot[c]	0.26	0.25	0.24	0.21	0.40	0.31	0.33	0.43	0.39	0.43	0.40	0.68
Fine root/foliage[d]	0.20	0.23	0.20	0.16	0.45	0.34	0.31	0.37	0.32	0.36	0.30	0.43
Coarse root/ aboveground woody[e]	0.29	0.25	0.25	0.21	0.36	0.27	0.35	0.46	0.44	0.46	0.47	0.69

Note: Numbers in parentheses are percentages of total stand biomass.
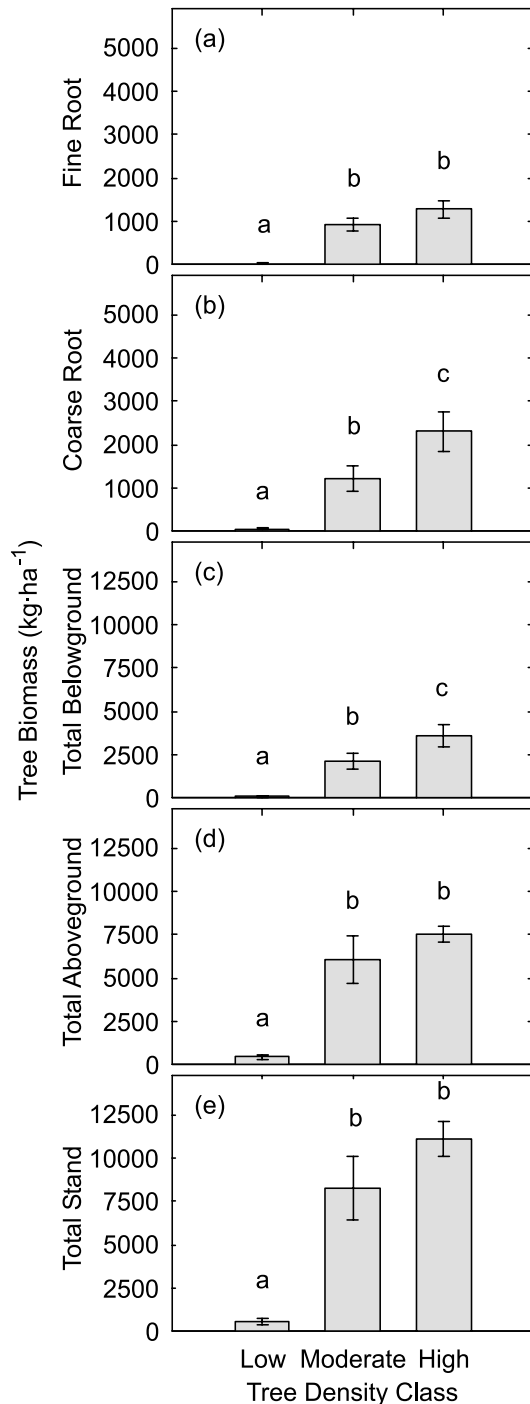
[a]Estimated from coring.

[b]Total coarse root biomass estimates were calculated from a single model (as opposed to the sum of individual component models). Note that the sum of biomass estimates and percentages from individual components does not equal the estimate and percentage from the single model. See Discussion for explanation.

[c]Root to shoot biomass ratio (i.e., total belowground to total aboveground biomass ratio).

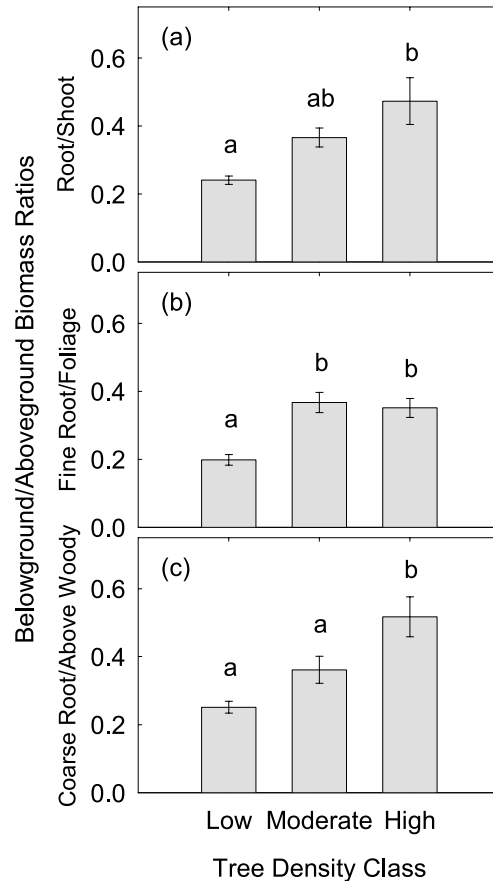[d]Fine root to foliage biomass ratio.

[e]Coarse root to aboveground woody (i.e., stem plus branch wood and bark) biomass ratio.

Fig. 4. (*a*) Fine root, (*b*) coarse root, (*c*) total belowground, (*d*) total aboveground, and (*e*) total stand tree biomass (dry mass, mean ± 1 SE) for different density classes in young stands of *Pinus contorta* var. *latifolia* in Yellowstone National Park, Wyoming. Means with the same letter do not differ at $\alpha = 0.05$.

Fig. 5. (*a*) Root to shoot, (*b*) fine root to foliage, and (*c*) coarse root to aboveground woody biomass ratios (mean ± 1 SE) for different density classes in young stands of *Pinus contorta* var. *latifolia* in Yellowstone National Park, Wyoming. Means with the same letter do not differ at $\alpha = 0.05$.

The root to shoot biomass ratio in our stands ranged from 0.21 to 0.68, which exceeds the value of 0.18 reported for temperate coniferous forests (Jackson et al. 1996). For all but the low-density stands, our root to shoot values are higher than the mean of 0.26 reported for gymnosperms (Cairns et al. 1997) and 0.24–0.26 for conifers (Cannell 1982; Körner 1994). The root to shoot biomass ratio includes the effect of biomass accumulation in woody tissue over time and is an indication of cumulative biomass storage patterns. The fine root to foliage biomass ratio is more indicative of the current year's pattern in carbon allocation, and values in our stands (0.16–0.45) were somewhat lower than root to shoot ratios. Like the root to shoot biomass ratios, fine root to foliage biomass increased with increasing stand density, indicating that tree density affects belowground biomass allocation (Table 3).

Fine roots have been reported to make up approximately 3–7% of total biomass in pine forest ecosystems (Knight et al. 1994). This is true in our study area only for the low-density stands (5–8%). The moderate- and high-density stands had higher proportions of total biomass in fine roots (10–14%), in spite of the fact that we sampled fine root biomass late in the summer when it can be at low seasonal values in coniferous forests (Vogt et al. 1980; Gholz et al. 1986).

lodgepole pine stands with tree densities <2500 trees·ha⁻¹ (Pearson et al. 1984). In 110-year-old stands with >9000 trees·ha⁻¹, however, the proportion of biomass found belowground increases to ≈32%. Comeau and Kimmins (1989) found 25% of stand biomass belowground in xeric stands and 20% in mesic stands of 70-year-old lodgepole pine.

Our findings suggest that biomass allocation is strongly affected by stand density in young coniferous forests. Belowground biomass in our stands of lodgepole pine, as a whole and as a proportion of total stand biomass, increases as stand density increases (Table 3; Figs. 4a–4c and 5). Stand density has also been shown to be an important factor controlling biomass dimensions in mature lodgepole forests. Biomass ratios differed for two 110-year-old stands of lodgepole pine growing on a common site but differing in tree density (2217 and 14 640 trees·ha^{-1}; Pearson et al. 1984). The root to shoot biomass ratio in the low-density stand was 0.27 compared with 0.50 for the high-density stand.

The fraction of biomass located belowground can also vary with moisture and nutrient availability and with tree age in young conifer stands. Biomass partitioning between belowground and aboveground components varies across gradients of moisture and nutrients in 8-year-old loblolly pine stands (Albaugh et al. 1998). The 3-year average proportion of biomass located belowground was 35, 31, 25, and 23% for control, irrigated, fertilized, and irrigated and fertilized plots, respectively. The proportion of biomass found belowground in 8- to 12-year-old mixed loblolly and slash pine plantations was somewhat lower (15%) and it did not vary with stand age (Nemeth 1973). In contrast, the proportion of tree biomass found in roots in ponderosa pine trees (*Pinus ponderosa* Dougl. ex P. & C. Laws.) decreased with increasing tree age from 55% in 3- to 9-year-old trees to only 10% in 21- to 40-year-old trees (Grulke and Retzlaff 2001). Likewise, the proportion of total woody biomass in coarse roots has been shown to decreased steadily from a maximum of 47% at age 2 to 13% at age 34 in slash pine plantations (Gholz and Fisher 1982).

Causal patterns in biomass allocation

Our work on young lodgepole pine forests and previous studies on young and mature coniferous forests indicate that the root to shoot biomass ratio increases with increasing stand density and decreases with increasing age. Competition for moisture and nutrients, whereby trees allocate more carbon belowground to compete for limiting resources, could explain the pattern of increasing root to shoot biomass with stand density. However, previous studies have shown that as trees age, they allocate less biomass belowground (Gholz and Fisher 1982; Grulke and Retzlaff 2001) and older trees normally correspond to increases in tree size. Since our high-density stands were characterized by smaller trees and our low-density stands by larger trees, increases in the root to shoot biomass ratio with stand density could merely be the result of inherent differences in individual tree allocation patterns that exist as a result of differences in tree size. If small trees allocate more biomass belowground than large trees, then stands characterized by small trees (high-density stands) will have a larger percentage of their biomass belowground and higher root to shoot values regardless of competition.

Some data exist to support the idea that increased root to shoot values are a result of increased competition for limiting belowground resources in mature stands. Lodgepole pine stands growing on xeric sites allocate a substantially larger proportion of net primary productivity belowground than those found on mesic sites, and thus, xeric sites exhibit higher root to shoot ratios (Comeau and Kimmins 1989). In addition to moisture, nutrient availability has been correlated with belowground biomass allocation in coniferous forests. For Douglas-fir stands, a higher proportion of total biomass exists belowground in areas of low productivity (Keyes and Grier 1981; Kurz 1989), and decreases in moisture and (or) nutrient availability result in an increased allocation of productivity belowground (Gower et al. 1992). Notably, both moisture and nitrogen availability declined as stand density increased in our study area (C.M. Litton, unpublished data).

Our biomass data for individual trees, excluding fine root biomass estimates, clearly indicate that biomass allocation patterns vary with tree size (Fig. 6, solid circles and solid line), and this pattern causes the differences that we observed in stand-level biomass allocation with tree density. A lack of variation in the tree-level belowground to total biomass ratio with tree size would have indicated that allocation patterns in stands were the result of competition for belowground resources. Differences in individual tree biomass allocation with tree size are not likely a result of sampling bias because in creating the allometric equations, we sampled trees of all sizes in each density class and our data show that allometry does not vary with density ($p > 0.40$; extra sum of squares analysis for nested models (Bates and Watts 1988)).

Is there any effect of stand density and competition on belowground biomass allocation? We suspect that any differences due to belowground competition would be more apparent in biomass pools with rapid turnover (fine roots). Because our analysis was based on individual trees, we estimated individual tree fine root biomass assuming that fine root biomass for the tree of average basal diameter could be estimated by dividing the stand-level estimate of fine root biomass by tree density. We then added this estimate to coarse root biomass to estimate total belowground biomass for an individual tree of average basal diameter in each of the 12 stands (Fig. 6, open circles and dashed line). This analysis also indicates that biomass allocation patterns across gradients of stand density are largely determined by tree size. The proportion of total root biomass in fine roots does not vary with stand density ($p = 0.65$; mean of 34% in low-density stands, 45% in moderate-density stands, and 36% in high-density stands), suggesting that the assumptions that we made to estimate fine root biomass did not bias the analysis. Simply stated, denser stands are characterized by smaller trees and smaller trees have a larger proportion of total biomass belowground than larger trees.

Conclusions

Given the paucity of data, belowground biomass is often estimated as a proportion of total stand biomass using variables such as root to shoot ratios. Mean values that span a great variety of tree species, stand densities, age-classes, and site quality are used to make inferences about broad-scale biomass patterns and carbon dynamics. The use of average values makes the reliability of such assessments questionable. Incorporation of belowground biomass estimates from direct measurement or with the use of allocation patterns and ratios that take into account important stand variables

Fig. 6. Relationship between tree size and the ratio of below-ground biomass to total biomass for individual trees. Below-ground biomass was calculated for coarse roots only (w/o fr, solid circles and solid line) and with estimates of fine root bio-mass (w/ fr, open circles and dashed line). For the coarse roots only analysis, allometric equations were used to estimate coarse root and aboveground biomass across a range of tree sizes. For total belowground biomass (coarse plus fine roots), fine root bio-mass was estimated for the individual tree of average basal di-ameter in each of the 12 stands by dividing stand-level fine root biomass estimates by stand density. We then applied allometric equations for estimating coarse root and aboveground biomass to the tree of average basal diameter and added our estimate of bio-mass in fine roots.
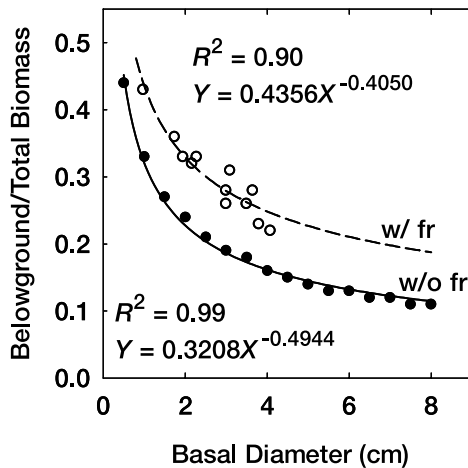
will greatly improve assessments of biomass allocation in vegetation across large spatial and temporal scales.

The results from this and previous studies suggest that biomass allocation patterns in coniferous forests change across gradients of stand age and density. Increased below-ground biomass allocation with increasing stand density in young stands appears to be determined primarily by inherent differences associated with tree size, not competition for belowground resources. Studies of this kind help to fill gaps in current knowledge about the effects of stand structure and age on biomass allocation and carbon storage and cycling. Increased understanding of biomass allocation rules through-out stand development and over gradients of stand density will make modeling efforts more practical and reliable.

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