

EFFECTS OF TREE DENSITY AND STAND AGE ON CARBON ALLOCATION PATTERNS IN POSTFIRE LODGEPOLE PINE

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Abstract. Validating the components of the carbon (C) budget in forest ecosystems is essential for developing allocation rules that allow accurate predictions of C pools and fluxes. In addition, a better understanding of the effects of natural disturbances on C cycling is critical, particularly in light of alterations to disturbance regimes that may occur with global climate change. However, quantitative data about how postfire differences in ecosystem structure affect C allocation patterns are lacking. For this study, we examined how above- and belowground C pools, fluxes, and allocation patterns varied with fire-initiated differences in tree density and stand age in lodgepole pine stands in Yellowstone National Park of four forest types: low (<1000 trees/ha), moderate (7000–40 000 trees/ha), and high tree densities (>50 000 trees/ha) in 13-year-old stands, and in ~110-year-old mature stands. C pools in live biomass and detritus were estimated with allometric equations and direct sampling. Aboveground net primary productivity (ANPP) was estimated as aboveground biomass increment plus fine litterfall, and total belowground carbon allocation (TBCA) was estimated using a C balance approach. Our results indicate that the magnitude of C pools and fluxes varies greatly with fire-initiated differences in tree density and stand age. Coarse woody debris and mineral soil carbon accounted for the majority of total ecosystem C in young stands (91–99%), in contrast to mature stands where the largest amount of C was found in live biomass (64%). ANPP and TBCA increased with tree density (mean ANPP was 59, 122, and 156 g C·m⁻²·yr⁻¹, and TBCA was 68, 237, and 306 g C·m⁻²·yr⁻¹ for low-, moderate-, and high-density young stands, respectively), and with stand age (ANPP was 218 g C·m⁻²·yr⁻¹ and TBCA was 382 g C·m⁻²·yr⁻¹ for 110-year-old stands). ANPP and TBCA were positively correlated, and both variables were well correlated with leaf area index. Notably, the ratio of TBCA to (TBCA + ANPP) remained remarkably constant (0.63–0.66) across extreme gradients of tree density and stand age, differing only slightly for the low-density young stands (0.54). These results suggest that C allocation patterns in a postfire lodgepole pine ecosystem are independent of tree density and stand age.

Key words: aboveground net primary productivity (ANPP); carbon pools, fluxes, and allocation patterns; fire; lodgepole pine; *Pinus contorta*; total belowground carbon allocation (TBCA); Yellowstone National Park, Wyoming.

INTRODUCTION

Modeling terrestrial ecosystem metabolism, and changes that may occur due to alterations in global climate, is currently limited by an incomplete understanding of carbon (C) allocation patterns (Ryan et al. 1997b, Friedlingstein et al. 1999, Gower et al. 1999, Landsberg 2003). In particular, belowground C allocation is one of the poorest understood attributes of terrestrial ecosystems and represents a major uncertainty in global estimates of terrestrial productivity (Lauenroth 2000, Geider et al. 2001). Yet, belowground

net primary production (BNPP) often accounts for >60% of total NPP in forests (Nadelhoffer and Raich 1992, Gower et al. 2001, Law et al. 2001), and plant allocation of C belowground can be the single largest component of gross primary production (Davidson et al. 2002). Considerable progress has been made recently on new methods for estimating total belowground carbon allocation (TBCA) using a conservation of mass, C balance approach (Raich and Nadelhoffer 1989, Davidson et al. 2002, Giardina and Ryan 2002). The TBCA method provides accurate estimates of the total amount of C allocated belowground (root production + root respiration + C in root exudates + C allocated to mycorrhizae; Giardina and Ryan 2002). Used in conjunction with traditional measures of aboveground C allocation (e.g., aboveground net primary productivity [ANPP]), the TBCA approach pro-

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vides a unique opportunity to examine C allocation patterns in terrestrial ecosystems more fully.

In addition to uncertainties pertaining to allocation patterns, most ecosystem models that simulate terrestrial C cycling do not account for the effects of natural disturbance, making the accuracy of modeled C budgets questionable (Gower et al. 2001, Chen et al. 2002). Quantifying the important components of the C cycle during ecosystem recovery from fire is fundamental for determining how fire will alter local, regional, and global C budgets (Auclair and Carter 1993, Houghton 1996, Burke et al. 1997, Amiro 2001). Fire immediately changes C cycling, returning large amounts of CO₂ to the atmosphere (Harden et al. 2000), but it also leaves a long-term legacy in community composition and the distribution of stand age and tree density classes across the landscape. Aboveground production normally reaches a maximum with canopy closure and a peak in leaf area index (LAI), and declines thereafter with stand age (Gower et al. 1996a, Ryan et al. 1997a). Differences in tree density, in turn, likely represent gradients of competition for limiting resources, and C allocation has been shown to shift from above- to belowground with decreased nutrient availability (Gower et al. 1992, 1994, Haynes and Gower 1995, Keith et al. 1997). However, postfire patterns of C allocation throughout stand development and with gradients in tree density are not well quantified.

Here we present the results of a study designed to examine the indirect effects of fire (i.e., fire-initiated differences in tree density and stand age) on above- and belowground C pools, fluxes, and allocation patterns in a wildland setting under the influence of a natural disturbance regime. We measured above- and belowground C pools and fluxes in young (13-year-old) postfire lodgepole pine (*Pinus contorta* Dougl. ex Loud var. *latifolia* Engelm.) stands in Yellowstone National Park that span the natural range of variability in tree establishment following the 1988 Yellowstone fires (from <500 to >500 000 trees/ha). Comparable measurements were made in nearby mature (~110-year-old) stands. The objectives of our study were to: (1) determine how above- and belowground C pools and fluxes in young postfire stands differ with tree density, (2) determine how above- and belowground C pools and fluxes in young stands differ from mature forests with similar soils and topography, and (3) examine the effect of tree density and stand age on C allocation patterns.

We hypothesized that all C pools, with the exception of coarse woody debris (CWD), would increase with tree density in young stands and with stand age. C pools in live tree biomass (above- and belowground) have been shown to vary substantially with tree density in young stands (Litton et al. 2003b), and low-density young stands were expected to have smaller pools of C in litter and mineral soil as a result of smaller pools in live biomass and lower litterfall rates. CWD, a prod-

uct of prefire stand composition, fire intensity, and decomposition rates, was not expected to vary with density in young stands. However, we expected CWD pools would be lower in older stands where deadfall contributed by the present forest is a minor component of aboveground detritus and CWD inherited from the prefire stand would be expected to contain <15% of its original mass after 110 years (Fahey 1983).

We also predicted that ANPP and TBCA would increase with increasing tree density in young stands and with stand age, but that ANPP and TBCA in high-density young stands would approximate that in mature stands. As noted, productivity in forests normally peaks with maximum LAI at canopy closure and declines with age thereafter (Gower et al. 1996a, Ryan et al. 1997a). If LAI increases with stand density in young stands, then it follows that productivity will increase as well. High-density young stands exhibit stand characteristics that are similar to mature forests (e.g., closed canopies and high leaf area index [Reed et al. 1999]), and therefore, we expected ANPP would be similar in these stands. We hypothesized that TBCA would follow similar patterns as ANPP because conditions that promote high levels of ANPP tend to result in greater allocation of C belowground (Raich and Nadelhoffer 1989, Nadelhoffer and Raich 1992).

Finally, we hypothesized that the ratio of TBCA : TBCA + ANPP (i.e., fraction of the C flux allocated belowground) would be smaller in low- and moderate-density young stands and larger in high-density young stands and mature stands. Many recently disturbed forests have higher levels of nutrient availability than comparable undisturbed forests (e.g., Parsons et al. 1994), and increased nutrient availability has been shown to cause a shift in C allocation from below- to aboveground (Gower et al. 1992, 1994, Haynes and Gower 1995, Keith et al. 1997). This was expected to result in a proportionally smaller allocation of C belowground in low- and moderate-density young stands where less competition for limiting resources and higher nutrient availability were expected. However, in high-density young and mature stands where peak LAI and ANPP have likely already occurred, we expected a higher allocation of C belowground with increased competition for limiting belowground resources.

Study area

Yellowstone National Park (YNP) is an ideal natural laboratory for testing our hypotheses due to the great spatial variability in postfire tree establishment following the 1988 fires and the landscape mosaic of stand ages that exists as a result of a natural disturbance regime. In addition, confounding anthropogenic effects from management activities are minimal inside the park. YNP is located primarily on several high-elevation, relatively flat, forested plateaus in the northwest corner of Wyoming (Turner et al. 1994, 1997). As a result of recurring fire and insect epidemics, lodgepole

TABLE 1. Summary of site characteristics for study areas in Yellowstone National Park, Wyoming, USA.

Stand name	Density class [†]	Age class [‡]	Density (trees/ha)	Mean basal area (cm ²) [§]	Elevation (m)
Cascade Meadows	low	young	425	6.6 (1.3)	2486
Lewis Canyon North	low	young	533	8.8 (1.6)	2372
Cygnets Lakes	low	young	742	10.6 (1.3)	2508
Pitchstone Plateau	low	young	758	12.3 (1.4)	2368
Riddle Lake TH	moderate	young	7000	7.2 (0.5)	2429
Lewis Canyon South	moderate	young	8700	9.9 (0.9)	2363
Biscuit Basin	moderate	young	25 250	6.7 (0.5)	2223
Howard Eaton	moderate	young	39 167	3.5 (0.2)	2370
Riddle High	high	young	50 167	4.3 (0.2)	2417
Firehole Loop	high	young	73 455	2.2 (0.2)	2166
Gibbon Falls	high	young	75 500	2.8 (0.2)	2131
7-Mile Bridge	high	young	598 462	0.7 (0.0)	2076
Crawfish Creek	...	mature	1920	206.4 (12.3)	2278
Firehole River	...	mature	3360	113.8 (6.1)	2195
Midway Geysers	...	mature	2400	175.3 (8.0)	2213
West Thumb	...	mature	1320	397.6 (27.3)	2347

[†] For young stands: low density is <1000 trees/ha, moderate density is 7000–40 000 trees/ha, and high density is >50 000 trees/ha.

[‡] All young stands were 13 years old, and mature stands ranged from 100 to 120 years old.

[§] From basal diameter for young stands, and diameter at 1.3 m for mature stands. Numbers in parentheses are 1 SE of the mean.

pine forests currently cover some 80% of the park, although Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and whitebark pine (*Pinus albicaulis* Engelm.) can be locally abundant, and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) is thought to be the primary climax species (Despain 1990, Whitlock 1993). Site index at 100 years for lodgepole pine stands in YNP ranges from 9 to 20 (mean = 13, $n = 30$; Kashian 2002).

Study sites were located on rhyolitic soils, which are the result of major volcanic activity in the Quaternary Era (Despain 1990, Whitlock 1993). The soils are relatively infertile (mean values of 1.1% organic carbon and 0.05 meq N/100 g dry soil) and are classified in the Cryochrept or Cryumbrept families (Trettin 1986). In our stands, soils are sandy loams with low clay content (2–7%). Percent volumetric soil moisture during the 2000 and 2001 growing seasons ranged from 6 to 15% in young stands and 8 to 13% in mature stands (Litton et al. 2003a).

The climate in YNP is characterized by cool temperatures throughout the year and a dry growing season. At Yellowstone Lake (2360 m), 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).

METHODS

We used a full factorial design with four replicates of four forest types: low (<1000 trees/ha), moderate (7000–40 000 trees/ha), and high (>50 000 trees/ha) densities in 13-year-old stands, and ~110-year-old ma-

ture stands to investigate the effects of tree density and stand age, as influenced by fire, on above- and below-ground C pools, fluxes, and allocation patterns (Table 1). C pools in biomass (above- and belowground) and detritus (CWD, dead coarse woody roots, fine litter, and mineral soil organic matter) were estimated from allometric equations and direct sampling. TBCA was estimated using a C balance approach for non-steady state systems (Giardina and Ryan 2002), and ANPP was estimated as aboveground biomass increment plus fine litterfall. LAI was estimated in each stand with allometric equations to investigate empirical relationships between C flux (TBCA and ANPP) and photosynthetic activity. In addition, foliar and root N contents were sampled and soil inorganic nitrogen (N) availability was indexed with ion-exchange resin bags to estimate nitrogen availability in each stand.

We selected postfire lodgepole pine stands located on sites similar in environmental and topographic characteristics at elevations between 2000 and 2500 m (Table 1). Young stands (13 years old) spanned the range of variability in tree density that is present across the landscape following the 1988 Yellowstone fires (from <500 to >500 000 trees/ha). Mature postfire stands were 100–120 years old, with densities ranging from 1320–3360 trees/ha. Sampling was conducted on 0.25-ha plots located within larger (>2 ha), homogeneous, monospecific stands of lodgepole pine. All field work was conducted between June 2000 and August 2001.

Selecting stands from similar sites provided a sound rationale for comparing our density/age classes and interpreting any differences as being associated with tree density and/or stand age. We emphasize that, while differences in tree density and stand age are the result of fire, our study design does not explicitly test the

effects of fire on C pools, fluxes, and allocation patterns. In addition, our stand age comparison includes only two age classes. We use our mature stands as a reference for prefire conditions, and all stand age effects shown herein should be taken in light of this fact. In addition, density effects shown herein are constrained to 13-year-old lodgepole pine stands.

C pools

C pools in vegetation and detritus (g C/m²) were determined by multiplying biomass estimates of each component by their respective C content. Subsamples of detrital components were combusted in a muffle furnace to correct final biomass estimates for ash-free mass. Subsamples of all biomass components were ground in a Wiley Mill to pass through a 0.5-mm² mesh (size 40), and C content was measured on a LECO-100 CHN analyzer (LECO Corporation, St. Joseph, Michigan, USA).

Above- and belowground biomass estimates for lodgepole pine trees in young stands were reported by Litton et al. (2003b). Biomass was estimated using measurements of basal diameter in three belt transects per stand applied to allometric equations developed in YNP for predicting coarse root (≥ 2 mm) and aboveground biomass in 13-year-old lodgepole pine trees. Allometric equations were developed separately for above- and belowground biomass from untransformed variables using nonlinear regression techniques and biomass harvested from the aboveground ($n = 120$) and belowground ($n = 45$) portions of trees. Harvesting was conducted in stands from each density class, and the need for separate allometric equations based on tree density class was assessed using an extra sum of squares analysis for nested models (Bates and Watts 1988). Tests of the need for different allometric equations based on density class were not significant for either biomass category ($P > 0.40$). Moreover, biomass estimated using a single equation vs. separate equations for each density class revealed that, on average, aboveground and belowground biomass estimates from the two approaches differed by only 6%. Thus, single allometric equations based on data from all density classes were used to estimate aboveground biomass ($R^2 = 0.91$) and belowground biomass ($R^2 = 0.87$) in each stand. Fine root biomass (< 2 mm) was estimated with 15 cores (6.35 cm diameter) taken to a depth of 30 cm in each stand. Few fine roots were observed below 30 cm, which is consistent with the results of Pearson et al. (1984).

For mature trees, diameter at breast height (DBH), sapwood basal area, tree height, and height to the base of the live crown were measured on 50 randomly selected trees in each stand, and the data were used with allometric equations developed for lodgepole pine in southeastern British Columbia that estimate individual tree above- and belowground biomass (Comeau and Kimmins 1989). Stand biomass was then estimated as

stand density multiplied by mean tree biomass, which was first adjusted for the difference between stand mean basal area and the mean basal area of the intensively sampled trees using double sampling techniques (Cochran 1977). We validated the use of these *ex situ* allometric equations for mature lodgepole pine trees in YNP by applying the aboveground equations to five harvested trees. Biomass predicted from the allometric equations in Comeau and Kimmins (1989) was well correlated with harvested biomass values ($r^2 = 0.97$, $P < 0.01$, $n = 5$), and the intercept (3.9; 95% CI of -28.8 – 36.5) and slope (1.1; 95% CI of 0.7 – 1.5) did not differ from a 1:1 relationship.

Aboveground biomass for herbaceous and shrub species was estimated using allometric equations developed in YNP for predicting aboveground biomass from percent cover (r^2 values of 0.84 – 0.99 ; Turner et al. 2004). In each stand, we measured percent cover of all herbaceous and shrub species at the approximate time of peak biomass in twenty 0.25 -m² quadrats. Belowground biomass (i.e., fine roots) for herbaceous and shrub species was estimated using root cores (fifteen 6.35 cm diameter cores in each stand taken to a depth of 30 cm).

CWD, as defined here, includes all snags, downed wood, and stumps with a diameter > 7.5 cm. CWD produced during the 1988 stand-replacing fires was estimated in each stand with three 4×50 -m belt transects. DBH was measured on all trees, standing and down, that were alive at the time of the fire in 1988 and had stumps within the belt transects. Trees that were alive in 1988 often had at least some of their bark intact and displayed no stem charring. In contrast, trees that were already dead when the fires occurred in 1988 exhibited considerable charring of the stem. Allometric equations developed in southeastern Wyoming for predicting lodgepole pine aboveground biomass from DBH were applied to estimate stem and branch biomass (Pearson et al. 1984). Biomass predicted from the allometric equations in Pearson et al. (1984) is well correlated with harvested biomass for mature lodgepole pine in YNP ($r^2 = 0.94$, $P < 0.01$, $n = 5$). The Comeau and Kimmins (1989) allometric equations for predicting lodgepole pine biomass were not used for CWD because they necessitate the measurement of sapwood basal area and height to the base of the live crown. An exponential decay coefficient was used to adjust for mass loss over 13 years for downed CWD (Fahey 1983). No change in specific gravity occurs within 12 years for standing dead lodgepole pine trees (Fahey 1983). To estimate total CWD, we added estimates of CWD already present when the stands burned in 1988 by using information on pools ($\sim 23\%$ of total CWD in recently burned stands comes from prefire inputs) and losses by combustion ($\sim 8\%$ of CWD is consumed during fire) taken from measurements in YNP (Tinker 1999, Tinker and Knight 2000). CWD in mature stands was estimated from measurements taken at our Craw-

fish Creek site and other mature stands of similar age in YNP (Tinker 1999). C content of all CWD was assumed equivalent to that of live wood in our study area (46%).

We also estimated biomass in dead coarse woody roots in young stands (i.e., dead coarse roots, including root crowns, of trees killed during the 1988 fires). DBH of trees alive at the time of the fire was measured in three 4×50 m belt transects and used with allometric equations for predicting lodgepole pine coarse root biomass by size category (Pearson et al. 1984). As before, the allometric equations of Comeau and Kimmins (1989) were not used because they necessitate the measurement of sapwood basal area and height to the base of the live crown, and also because they do not separate root biomass estimates into size categories. Loss of mass after 13 years was determined using exponential decay coefficients developed for lodgepole pine roots by size categories (Yavitt and Fahey 1982). For mature stands, C remaining from coarse roots in the prefire stand after 100–120 years would be well incorporated into the mineral soil organic matter, which was sampled separately.

Biomass in fine litter (i.e., needles, bark, cones, and branches <7.5 cm diameter) was estimated by sampling the forest floor with 300-cm² frames. In young stands, 15 frames were sampled in one stand of each density class, and in mature stands the litter layer was sampled in each stand with five frames/stand. Within each frame, all litter down to the mineral soil was collected and dried to a constant weight at 70°C. Fine litter biomass estimates were corrected for ash-free mass by processing a subsample in a muffle furnace.

C pools in the mineral soil were estimated from percent C values, and measurements of soil bulk density taken with soil cores (6.35 cm diameter to a depth of 30 cm; 15 cores/stand for percent C and 5 cores/stand for bulk density). Cores for determining percent C in a given stand were composited, passed through a 2-mm sieve, and dried to a constant mass at 70°C. Composite samples were mixed thoroughly and four subsamples/stand were isolated, processed overnight on a roller mill, and analyzed for C content on a LECO-100 CHN analyzer. Soil bulk density was sampled in each stand using a standard core method (Culley 1993).

TBCA

TBCA ($\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) was estimated using a C balance, conservation of mass approach for non-steady state systems (Nadelhoffer et al. 1998, Giardina and Ryan 2002). Conservation of mass dictates that C outputs from the soil must equal C inputs minus any change (Δ) in C storage. The major output of C in forest soils is soil-surface CO₂ efflux (F_S), or soil respiration, as export of C via erosion and leaching is negligible in most forests (see Giardina and Ryan 2002). Inputs of C into the soil include aboveground litterfall (F_A) and C allocated belowground by plants (TBCA; the

sum of root respiration, root production, and C allocated to mycorrhizae and root exudates). Important storage components of C in soils include coarse roots (C_R), litter (C_L), mineral soil organic matter (C_S) and, in our system, dead coarse woody roots (C_{DCWR}). Thus, based on conservation of mass,

$$F_S = \text{TBCA} + F_A - (\Delta C_R + \Delta C_L + \Delta C_S - \Delta C_{DCWR}). \quad (1)$$

Solving for TBCA yields

$$\text{TBCA} = F_S - F_A + (\Delta C_R + \Delta C_L + \Delta C_S - \Delta C_{DCWR}). \quad (2)$$

ΔC_{DCWR} is subtracted here because it represents C allocated by the previous stand.

F_S was measured five times over the growing season in each stand at 30 points/stand, and once during the winter, in early March of 2003, at 10 points/stand (see Litton et al. 2003a for a detailed description). Yearly C flux from soils was estimated by linear interpolation of mean daily F_S between measurement periods during the growing season and by applying measured CO₂ efflux from snowpack across the entire snowpack period. Mean daily F_S was determined by adjusting mean measured F_S rates to mean daily soil temperature at 10 cm (Litton et al. 2003a). Linear interpolation of measured flux rates from a small number of measurement periods during the year has the potential to bias yearly flux estimates (Irvine and Law 2002). However, our linear interpolation should provide a relatively unbiased estimate of yearly flux rates because (1) the five growing season measurements were spread out over a very short growing season (~4 months), (2) corrections that were made to adjust flux rates to mean daily soil temperature incorporate seasonal Q_{10} values, which would at least partially account for any seasonal moisture effects, (3) the summer of 2000 in YNP was very dry and characterized by an absence of summer precipitation events, (4) our winter efflux rates in young and mature stands are consistent with reported winter flux rates for coniferous forests in the Rocky Mountains (Sommerfeld et al. 1996, McDowell et al. 2000, Striegl and Wickland 2001), and (5) our annual estimates of F_S agree relatively well with annual flux estimates from temperature response curves and continuous recording of soil temperature (Litton et al. 2003a).

F_S measurements were taken with a dynamic closed-chamber portable infrared gas analyzer (IRGA) coupled to a soil respiration chamber (PP-Systems EGM-2 IRGA and SRC-1 soil respiration chamber; PP-Systems, Herts, UK). In previous studies, the PP-Systems SRC-1 soil respiration chamber has been shown to yield 30–50% higher estimates of F_S compared to other chamber systems (Le Dantec et al. 1999, Janssens et al. 2000). Therefore, we compared F_S rates taken with the PP-Systems with rates measured with a LI-COR

dynamic closed-chamber IRGA system (LI-COR 6400 portable photosynthesis system and LI-COR 6400-09 soil respiration chamber; LI-COR, Lincoln, Nebraska, USA) in each of the 16 stands. We found no difference in stand mean F_S measured with the PP-Systems SRC-1 and LI-COR 6400-09 chambers in our study area ($P = 0.91$, paired samples t test; Litton et al. 2003a).

Tree F_A was measured in each stand with six 1-m² litterfall traps. Traps were placed in the field in early June of 2000 and collected in September 2000 and again in late May 2001. Dry conditions during the growing season and low temperatures over the winter would minimize any decomposition that may have occurred between collection periods. Litterfall biomass was separated into needles, reproductive material, and bark and branches, dried to a constant mass at 70°C, and the C content of each component was determined (see *Methods: C pools*, above). Herbaceous and shrub F_A were assumed equivalent to herbaceous and shrub ANPP (see *Methods: ANPP*, below), and these estimates were added to tree F_A estimates.

Eq. 2 differs from the original TBCA methodology of Raich and Nadelhoffer (1989) in that it directly estimates change in soil C storage, making it applicable to non-steady state systems such as our young, rapidly aggrading stands. It is important, therefore, to estimate changes in soil C pools accurately, as relatively small annual changes will potentially have substantial effects on the final TBCA estimate if the pools are large (Giardina and Ryan 2002).

For ΔC_R , we used intensive field measurements of individual tree basal diameter (DBH for mature trees), allometric equations developed for estimating coarse root biomass, and double sampling techniques. In young stands, 25 basal discs were harvested from randomly selected trees in July of 2001 in each stand, and an allometric equation was applied to the 1999 and 2000 rings for predicting total coarse root biomass from inside bark basal diameter (Litton et al. 2003b). The ΔC_R was then determined as the mean tree coarse root biomass increment between 1999 and 2000 multiplied by stand density and adjusted for the difference between stand mean basal area and the basal area of sampled trees. Estimates of Δ in coarse root biomass were multiplied by the C content of roots (46%). Mature stand ΔC_R was determined in a similar fashion. We used biomass estimates for mature trees in 2000 (see *Methods: C pools*, above) and determined the previous year's biomass by (1) estimating the 1999 DBH from mean radial increment (average of the previous five years) based on 50 cores taken at 1.3 m in each stand and (2) estimating the 1999 tree height by establishing a relationship between DBH (cm) and height (m) using trees that we sampled in our stands (height = $2.89 \times \text{DBH}^{0.59}$, $r^2 = 0.82$, $P < 0.01$, $n = 200$). We assumed that the height to the base of the live crown did not change over a one-year period.

We estimated ΔC_L by repeat sampling of the litter C pool (see *Methods: C pools*, above). In young stands, we sampled the litter C pool in 1998 and again in 2000, and Δ was estimated as the difference in pool sizes divided by two. For mature stands, we estimated change in pool sizes in each stand by sampling in 1999 and 2000. In all cases, sites for sampling in 2000 were located during the first year to ensure that similar areas were sampled during the following period.

Change in C_S in young stands was determined by first estimating stocks of mineral soil C in 2000 in each stand (see *Methods: C pools*, above). We then used identical techniques to estimate the mineral soil C pool in adjacent unburned stands (closest unburned stands with similar topography and prefire vegetation), and ΔC_S was estimated as the difference in pool sizes between the young stands and adjacent unburned stands divided by 12 (the number of years since the fire). For mature stands, C_S throughout the soil profile was assumed to be at steady state (i.e., $\Delta = 0$). The few studies that have addressed ΔC_S in forest ecosystems have documented rates of $<10 \text{ g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ (Richter et al. 1994, Bashkin and Binkley 1998). This represents a very small fraction ($<2\%$) of reported TBCA values for lodgepole pine (Smith and Resh 1999).

Estimates of C_S pools in our stands were limited to measurements taken from the top 30 cm of mineral soil. While C is certainly present below 30 cm, the size of the pool is most likely small and change in C storage below 30 cm was assumed negligible. Law et al. (2001) found that only 20% of C in the top one meter of mineral soil was found below 50 cm in a young *Pinus ponderosa* Laws. stand in Oregon. Within the top 30 cm of mineral soil in our study area, $\sim 62 \pm 1.6\%$ (mean ± 1 SE) of the C is found within the top 15 cm ($n = 4$). Even in highly productive sugarcane and Eucalyptus plantations in Hawaii, ΔC_S at lower depths (below 45 cm) is very slow (Bashkin and Binkley 1998).

C_{DCWR} in young stands was estimated using allometric equations to predict prefire standing biomass (see *Methods: C pools*, above). Decay coefficients were then applied 12 and 13 years after the stand replacing fire, and Δ was estimated as the difference in pool size between the years. The ΔC_{DCWR} was assumed to be zero for mature stands.

There are inherent uncertainties with the TBCA approach, including the inability to separate and quantify the various sinks of belowground allocation. Giardina and Ryan (2002) provide a comprehensive assessment of potential errors in technique and assumptions, and potential statistical problems arising from estimating TBCA and its components. One perceived statistical problem is that plot-level estimates of TBCA are based on subsamples, meaning that each plot-level estimate carries uncertainty that may increase the overall uncertainty of the final TBCA estimate. A second perceived statistical problem is that TBCA is a sum of components and, therefore, its final estimate must con-

tain the cumulative error associated with the variance in and between each component. However, Giardina and Ryan (2002) demonstrate that the variance of plot-level estimates of TBCA already contains all of the variance associated with subsampling and cumulative error.

ANPP

ANPP estimates ($\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) were calculated as the sum of tree, herbaceous and shrub aboveground net productivity. Tree ANPP was estimated as outlined in Clark et al. (2001):

$$\text{ANPP} = \Delta C_{\text{AB}} + F_{\text{AF}} \quad (3)$$

where ΔC_{AB} is the C increment in total aboveground biomass, and F_{AF} is C in aboveground fine litterfall (i.e., needles, small twigs, and reproductive materials). The ΔC_{AB} was calculated for young trees with an allometric equation for predicting individual tree aboveground biomass from basal diameter (Turner et al. 2004) and for mature trees with allometric equations for predicting individual tree stem, branch, and foliage biomass from DBH, sapwood basal area, tree height, and height to the base of the live crown (Comeau and Kimmins 1989). F_{AF} was estimated from six 1-m^2 litterfall traps/stand. Losses of C to consumers, volatiles, and leached organics were assumed negligible, and thus our estimates of ANPP are likely slight underestimates. No tree herbivory was observed in our stands, and the potential impact of ignoring volatiles and leached organics on estimates of NPP in forest ecosystems is estimated at 3–8% (Clark et al. 2001).

Herbaceous and shrub ANPP were estimated using allometric equations for predicting biomass from percent cover (see *Methods: C pools*, above). For these species, a given year's peak aboveground biomass is equivalent to aboveground productivity when converted to units of C. For shrubs, the allometric equations predict biomass in new foliage. The only shrub species that occurred with any frequency in our study area was *Vaccinium scoparium* (Leiberg ex Cov.), and we assumed that woody productivity was negligible in this small shrub.

LAI

Projected LAI (one-sided; m^2/m^2) for lodgepole pine trees in young stands was determined with allometric equations developed in situ for predicting individual tree foliage biomass from basal diameter ($r^2 = 0.89$, $P < 0.01$, $n = 120$), and projected leaf area from foliage biomass ($r^2 = 0.89$, $P < 0.01$, $n = 91$) (Turner et al. 2004). A single allometric equation, independent of tree density, was developed for predicting foliage biomass by harvesting foliage from trees in all density classes (see *Methods: C pools*, above). The allometric equation for predicting projected leaf area from foliage biomass was developed using the water displacement method (Chen et al. 1997) on foliage samples collected

from stands representing a wide range of densities. Individual tree foliage biomass and projected leaf area were determined for all trees in three belt transects/stand. Final LAI estimates come from dividing the sum of individual tree leaf area estimates (m^2) by the size of the sample area (m^2).

For mature stands, projected LAI for lodgepole pine trees was estimated from measurements of DBH on 50 trees in each stand and an allometric equation for predicting individual tree leaf area (m^2) from DBH for lodgepole pine trees in Wyoming that span a wide range of tree densities and diameters (Pearson et al. 1984). Mean tree leaf area was then multiplied by the tree density of each stand to determine total stand LAI after adjusting for mean stand basal area. Projected LAI was estimated by dividing total stand LAI by 2.5 (Waring and Running 1998).

Estimates of herbaceous and shrub LAI were added to estimates of tree LAI in each stand. Herbaceous and shrub LAI were estimated, by species, based on allometric equations for predicting biomass from percent cover (see *Methods: C pools*, above) and LAI coefficients that predict leaf area from biomass (Turner et al. 2004).

Nitrogen

Soil inorganic nitrogen availability ($\text{NH}_4^+ + \text{NO}_3^-$; $\mu\text{g N}/\text{bag}$) was indexed using ion exchange resin bags (Binkley and Matson 1983). Resin bags were constructed with two sections: one with anion resin (14 mL [1 tablespoon] of Sybron IONAC ASB-IPOH [Sybron Chemicals, Incorporated, Pittsburgh, Pennsylvania, USA]) and one with cation resin (14 mL of Sybron IONAC C-251 H^+). Each section of the resin bag contained 4–5 $\mu\text{mol}/\text{bag}$ and was $\sim 4 \times 4$ cm, with a band of heat-applied glue separating the pouches. For each site, 10 resin bags were tagged and placed at 2-m intervals at the interface of the litter layer and mineral soil in August of 2000. Two resin bags were also placed in double plastic bags at each site for controls. Resin bags were left in the field for one year. We emphasize that our estimates made with ion exchange resin bags are an index of inorganic soil N availability, and not a definitive value. However, resin bags have been used quite successfully to identify patterns among sites and treatments in previous studies (Skogley and Dobermann 1996).

Foliar nitrogen (%) was sampled in July of 2001 by randomly collecting one lateral branch from the terminal shoot of the closest tree every 2 m along a 30-m transect ($n = 15$ branches/site). For each site, the previous year's foliage was removed from each branch (foliage of the current year had not fully expanded), composited, dried to a constant mass at 70°C , and ground in a Wiley Mill to pass through a 0.5-mm^2 mesh (size 40). A subsample was then analyzed for N content on a LECO-100 CHN analyzer. N content of coarse

TABLE 2. C pools after stand-replacing fire in low-, moderate-, and high-density young stands (13 years old) and in mature stands (~110 years old) of lodgepole pine.

Pool	Low-density young	Moderate-density young	High-density young	Mature
Aboveground vegetation C				
Pine foliage	10 (3)	134 (30)	182 (15)	300 (35)
Pine branches	7 (3)	58 (16)	38 (8)	481 (53)
Pine stems	6 (2)	99 (23)	159 (23)	7909 (1081)
Herbs and shrubs	53 (3)	42 (5)	33 (11)	37 (7)
Total aboveground	76	333	412	8727
Belowground vegetation C				
Pine coarse roots (≥ 2 mm)	3 (0.8)	56 (13)	105 (21)	2148 (185)
Pine fine roots (< 2 mm) [†]	2 (0.4)	42 (7)	58 (9)	68 (5)
Herb and shrub fine roots [†]	29 (2)	19 (4)	12 (3)	14 (4)
Total belowground	34	117	175	2230
Detritus				
Coarse woody debris [‡]	3301 (706)	3124 (912)	2543 (724)	1878
Dead coarse woody roots	562 (90)	548 (128)	538 (80)	...
Fine litter C [§]	77	64	319	868 (83)
Soil C [¶]	3586 (452)	2814 (349)	2383 (346)	3376 (388)
Total detritus	7526	6550	5783	6122
Total ecosystem C	7636	7000	6370	17079

Note: All pools are group means ($n = 4$) expressed in g C/m², and numbers in parentheses are 1 SE.

[†] Includes roots in the litter layer and in the mineral soil to a depth of 30 cm.

[‡] Snags, stumps, and downed woody material with a diameter > 7.5 cm.

[§] Needles, bark, cones, and branches < 7.5 cm diameter.

[¶] Soil organic matter in the top 30 cm of the mineral soil.

roots in each site was analyzed with material isolated from soil cores (see *Methods: C pools*, above).

Statistical analyses

The sample unit for this study was the stand and, thus, all variable measurements represent mean stand values or single values taken from a composite sample. All statistical analyses were performed in SPSS 10.0 for Windows (SPSS, Chicago, Illinois, USA) at an $\alpha = 0.05$. Stands were grouped into age and density classes (Table 1), and all data were tested for assumptions of normality and equality of variance. One-way ANOVA was used to test for effects of tree density and stand age on C pools, fluxes, and allocation patterns. The effect of age was assessed with a contrast model comparing the average of young stands to the mature stands, and density effects were assessed by constraining the analysis to young stands. Differences between individual density and age classes were analyzed with post hoc tests using Tukey's honestly significant difference (hsd) method or Dunnett's C method in the case of unequal variances. We used linear regression analysis to examine empirical relationships between estimates of TBCA, ANPP, and LAI.

RESULTS

C pools

The majority of ecosystem C in young stands (91–99%) was in detrital pools (CWD, C_{DCWR} , fine litter,

and C_S ; Table 2). Detrital C was distributed almost equally between CWD (44–48%) and C_S (41–48%). C_{DCWR} and fine litter comprised a small proportion of detritus (7–9% and 1–6%, respectively). The proportion of total ecosystem C in live vegetation was never $> 10\%$ in young stands. For all density classes in young stands, foliage accounted for the greatest proportion of live aboveground lodgepole pine biomass (43–48%), followed by stems (26–42%), and branches (10–30%). Herbs and shrubs were a small part of total aboveground C in young stands (8–13%), with the exception of the low-density class (70%). Roots accounted for 26–31% of total vegetation C, and fine roots made up the majority of root biomass for all but the high-density young stands.

Mature stands contained two to three times more C than young stands. For mature stands, the majority of ecosystem C was found in live vegetation (64%; Table 2). Most vegetation C was in stems (72%), with 20% in coarse roots, 4% in branches, 3% in foliage, and $\sim 1\%$ in fine roots. Herb and shrub above- and belowground biomass accounted for $< 1\%$ of vegetation C. The detrital C pool was roughly equivalent in mature and young stands, but in mature stands it accounted for a much smaller proportion of total ecosystem C (36%). C_S was almost twice as important as CWD in the mature stand detrital pool (55% and 31%, respectively), and fine litter accounted for the remaining 14%.

Carbon in lodgepole pine foliage, stems, coarse roots, and fine roots increased with tree density in

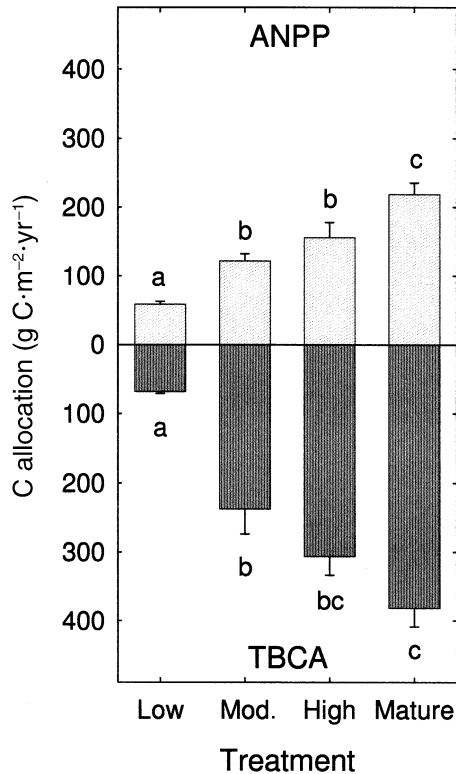


FIG. 1. Aboveground net primary productivity (ANPP) and total belowground carbon allocation (TBCA) vary with tree density in low-, moderate-, and high-density young stands (13 years old) of lodgepole pine ($P < 0.01$), and with stand age ($P < 0.01$). Bars are group means ± 1 SE ($n = 4$). Means with the same letter do not differ at $\alpha = 0.05$ (Tukey's hsd multiple-comparisons test after one-way ANOVA).

young stands ($P < 0.01$ for all categories, except branches where $P = 0.02$; Table 2). Likewise, C in all components of lodgepole pine vegetation increased with stand age from 13 years old to the mature forests ($P < 0.01$). C in herbaceous and shrub belowground biomass decreased with tree density ($P = 0.01$), but density had no effect on herbaceous and shrub aboveground C ($P = 0.18$). Differences in herb and shrub belowground biomass could well be a relict of the difficulties involved with sampling fine root biomass. Still, these results had very little effect on overall patterns of C pools, as herbs and shrubs accounted for $< 1\%$ of ecosystem C in all density and age classes (Table 2). There was no difference between 13-year-old and mature stands for both herbaceous and shrub belowground ($P = 0.14$) and aboveground C ($P = 0.53$).

For detrital C pools in young stands (Table 2), tree density had no effect on CWD ($P = 0.78$), C_{DCWR} ($P = 0.99$), or C_s ($P = 0.14$); and C_s did not vary with stand age ($P = 0.33$). We were unable to test for age effects on CWD, C_{DCWR} , and fine litter because of our sampling design. However, a trend of decreasing CWD and increasing fine litter with age was evident (Table 2).

TBCA

TBCA varied with tree density in young stands ($P < 0.01$) and with stand age ($P < 0.01$; Fig. 1). The group means for TBCA were 68, 237, 306, and 382 g C·m⁻²·yr⁻¹ for low-, moderate-, and high-density young stands and mature stands, respectively (Table 3). Within young stands, no difference was observed between moderate and high densities ($P = 0.21$), and high-density young stands did not differ from mature stands ($P = 0.23$). All of the individual components of TBCA (Eq. 2; Fig. 2 and Table 3) varied with tree density ($P < 0.01$), except F_A ($P = 0.30$) and ΔC_{DCWR}

TABLE 3. C fluxes after stand-replacing fire in low-, moderate-, and high-density young stands (13 years old) and in mature stands (~110 years old) of lodgepole pine.

Measure	Low-density young	Moderate-density young	High-density young	Mature
Aboveground net primary production (ANPP)†				
Biomass increment (ΔC_{AB})	6 (1)	61 (12)	93 (17)	113 (15)
Fine litterfall (F_{AF})	0.3 (0.2)	19 (3)	30 (4)	68 (2)
Herb/shrub ANPP	53 (3)	42 (5)	33 (11)	37 (7)
Total ANPP	59 (4)	122 (10)	156 (22)	218 (17)
Total belowground carbon allocation (TBCA)†				
Soil-surface CO ₂ efflux (F_S)	156 (2)	303 (41)	351 (23)	460 (25)
Aboveground litterfall (F_A)	59 (2)	69 (3)	72 (9)	106 (8)
Coarse root C (ΔC_R)	1 (0.2)	10 (2)	17 (3)	22 (3)
Litter C (ΔC_L)	3	13	24	6 (0.3)
Soil C (ΔC_S)	-18 (2)	-5 (7)	1 (3)	...
Dead coarse roots (ΔC_{DCWR})	15 (2)	15 (3)	14 (2)	...
Total TBCA	68 (3)	237 (36)	306 (27)	382 (27)

Note: All fluxes are group means ($n = 4$) expressed in g C·m⁻²·yr⁻¹, and numbers in parentheses are 1 SE.

† See Methods for a description of how ANPP, TBCA, and their components were estimated.

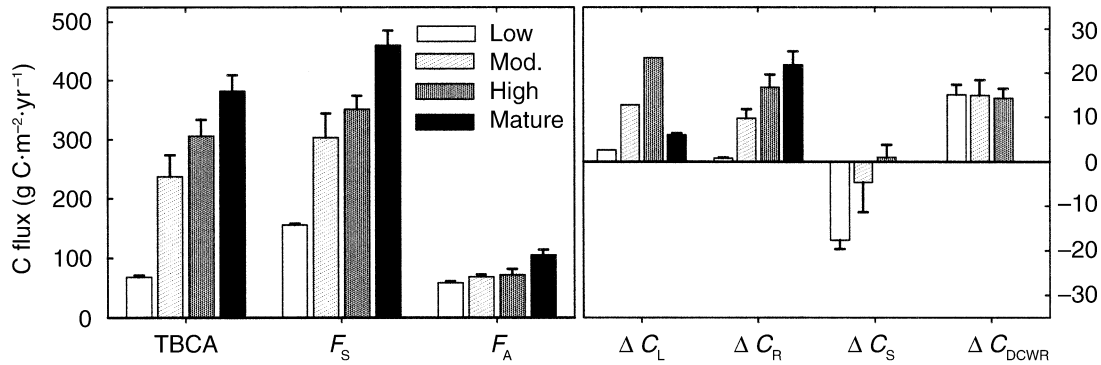


FIG. 2. Soil surface CO_2 efflux (F_s) is the largest component of total belowground carbon allocation (TBCA) for low-, moderate- (mod.), and high-density young stands (13 years old) and mature stands (~110 years old) of lodgepole pine. Litterfall (F_A) is the next largest component, and the importance of changes in soil C pools (litter C [ΔC_L], coarse root C [ΔC_R], soil C [ΔC_S], and dead coarse woody root C [ΔC_{DCWR}]) to the overall TBCA budget varies with density and age class. Bars show group means ± 1 SE ($n = 4$).

($P = 0.98$), and all components varied with stand age ($P < 0.01$, except for ΔC_S where $P = 0.04$). The coefficient of variation (cv) for TBCA ranged from 8% in low-density young stands to 31% in moderate-density young stands, with a mean cv across all density and age classes of 18%.

F_s was the largest component of TBCA for all density and age classes (Fig. 2 and Table 3). TBCA was roughly equivalent to F_s for all but the lowest density class (F_s accounted for 44% of TBCA in the low-density young stands, 78% in the moderate-density young stands, 87% in the high-density young stands, and 83% in the mature stands). Due to the overriding importance of F_s , ignoring Δ values in Eq. 2 (i.e., ignoring change in storage for soil C pools) would have underestimated TBCA by only -3% in the moderate-density young stands, -9% in the high-density young stands and -8% in the mature stands (a negative value indicates an underestimate). However, bias from ignoring Δ values in low-density young stands would have overestimated TBCA by $+44\%$, primarily concentrated in C_S ($+26\%$) and C_{DCWR} ($+23\%$). Low bias values in moderate- and high-density young stands are partially the result of a canceling effect within the various Δ pools. Ignoring ΔC_{DCWR} would have introduced a bias of $+5\%$ for moderate-density and $+6\%$ for high-density young stands. However, ignoring ΔC_L and ΔC_R would have biased TBCA by -6% and -4% , respectively, for moderate-density young stands and -8% and -6% , respectively, for high-density young stands. Ignoring ΔC_S in moderate- and high-density young stands would have affected the final TBCA estimate by $<1\%$. The majority of the bias in ignoring changes in soil C storage in mature stands would have come from ΔC_R (-6%).

ANPP

Like TBCA, ANPP increased with tree density in young stands ($P < 0.01$) and with stand age ($P < 0.01$; Fig. 1). Group means for ANPP were 59, 122, 156, and

218 $\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ for low-, moderate-, and high-density young stands and mature stands, respectively (Table 3). Within young stands, no difference was observed between moderate and high-density stands ($P = 0.25$). cv for ANPP ranged from 14% in low-density young stands to 28% in moderate-density young stands, with a mean cv across all density and age classes of 18%.

The fraction of total stand ANPP contributed by trees increased with tree density ($P < 0.01$) and stand age ($P < 0.01$; Table 3). Tree ANPP accounted for the majority of total ANPP on all but the low-density stands (10%, 64%, 79%, and 83% on low-, moderate-, and high-density young stands and mature stands, respectively), but ignoring herb and shrub productivity would have biased ANPP estimates in all density and age classes. Fine litterfall was an important component of tree ANPP (see Eq. 3 in *Methods*) in all but the low-density young stands, accounting for 5, 25, 26, and 39% of tree ANPP on low-, moderate-, and high-density young stands and mature stands, respectively (Table 3).

LAI

LAI was positively and linearly correlated with both ANPP ($r^2 = 0.86$; Fig. 3a) and TBCA ($r^2 = 0.85$; Fig. 3b), increasing with tree density in young stands ($P < 0.01$; LAI averaged 0.1, 1.3, and 1.8 m^2/m^2 in low-, moderate-, and high-density young stands, respectively) and with stand age ($P < 0.01$; LAI in mature stands averaged 2.7 m^2/m^2). LAI in the highest density young stand (2.2 m^2/m^2 ; ~600 000 trees/ha) was 80% of the mean LAI value for mature stands.

Nitrogen

Both foliar and root N concentrations decreased with tree density in young stands ($P = 0.01$ for foliar N and $P = 0.03$ for coarse root N), and with stand age ($P < 0.01$; Fig. 4a, b). Foliar N concentrations averaged 1.3, 1.2, 1.1, and 0.9% and coarse root N averaged 0.5, 0.3,

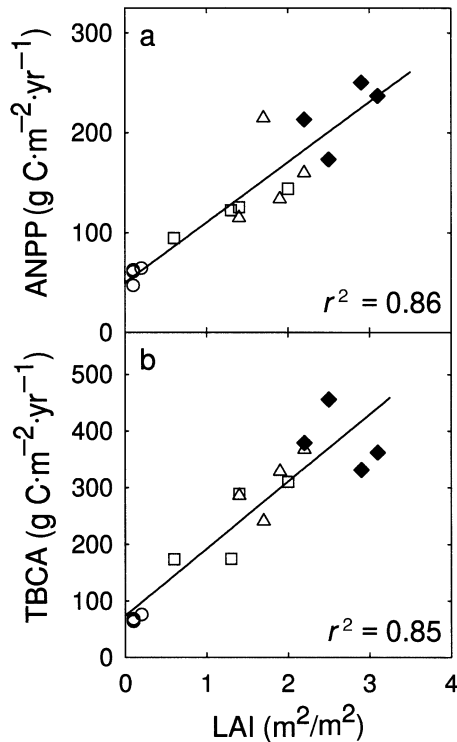


FIG. 3. (a) Aboveground net primary productivity (ANPP) and (b) total belowground carbon allocation (TBCA) are positively correlated with leaf area index (LAI) in postfire lodgepole pine stands differing in tree density and stand age. Open symbols are young stands (circles are low density, squares are moderate density, and triangles are high density), and solid symbols are mature stands. The regression equations are: $ANPP = 49.9 + 60.3 \times LAI$ ($r^2 = 0.86$, $P < 0.01$) and $TBCA = 73.8 + 118.5 \times LAI$ ($r^2 = 0.85$, $P < 0.01$).

0.4, and 0.2% for low-, moderate-, and high-density young stands, and mature stands, respectively.

Available inorganic soil N ($NH_4^+ + NO_3^-$) at the mineral soil/litter layer boundary decreased with tree density ($P = 0.03$), but did not vary with stand age ($P = 0.12$; Fig. 4c). Individually, NH_4^+ and NO_3^- both decreased with tree density in young stands ($P = 0.04$), and NH_4^+ increased with stand age ($P = 0.05$). In young stands, ~60% of available inorganic soil N was in the form of NO_3^- , while in mature stands NH_4^+ and NO_3^- availability were roughly equivalent (54% and 46%, respectively).

Carbon allocation patterns

We observed a positive linear correlation between TBCA and ANPP ($r^2 = 0.64$; Fig. 5). Both increased with tree density and stand age, and TBCA exceeded ANPP by an average of 57% (Figs. 1 and 5). Importantly, the ratio of TBCA : TBCA + ANPP remained relatively constant across extreme gradients of tree density and stand age ($62 \pm 2\%$ [mean ± 1 SE], $n = 16$), differing only slightly for the low-density young stands

($54 \pm 2\%$, $n = 4$), which are essentially non-forest at this point in stand development (Fig. 6).

DISCUSSION

C pools

As hypothesized, live lodgepole biomass increased with tree density in young stands and with stand age (Table 2). However, herbaceous and shrub aboveground biomass was independent of both tree density and stand age. Our results support previously reported patterns of herbaceous productivity in YNP (Reed et al. 1999).

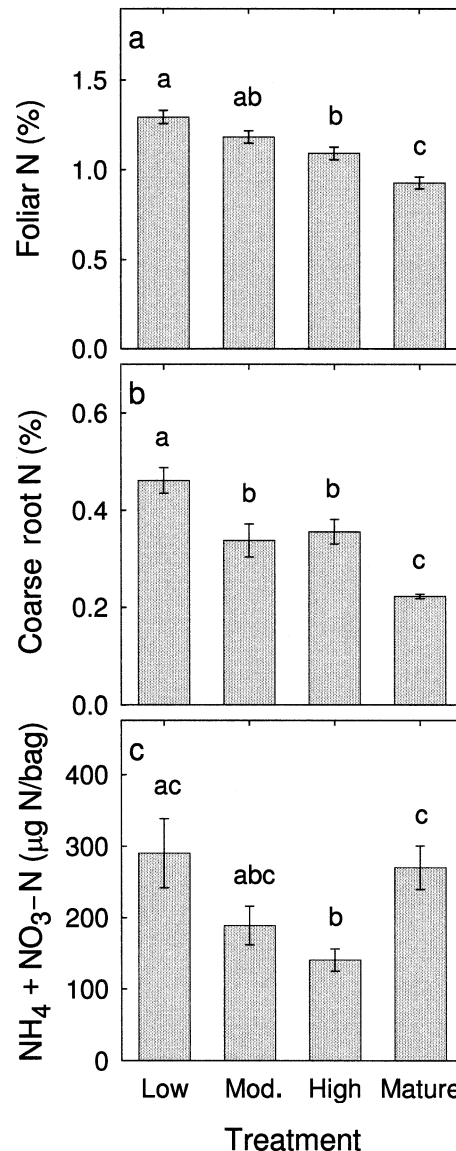


FIG. 4. Nitrogen concentration (%) in (a) one-year-old foliage and (b) coarse roots (≥ 2 mm) declines with tree density in young stands (low, moderate [mod.], and high) and with stand age in postfire lodgepole pine; (c) inorganic soil nitrogen ($NH_4 + NO_3$ -N) declines with tree density in young stands, but not with stand age. Bars are group means ± 1 SE ($n = 4$). Means with the same letter do not differ at $\alpha = 0.05$.

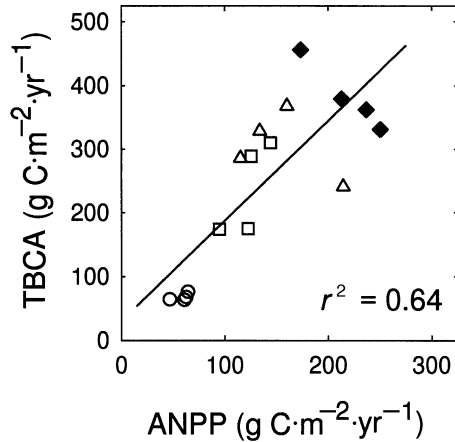


FIG. 5. Aboveground net primary productivity (ANPP) and total belowground carbon allocation (TBCA) in postfire lodgepole pine stands are positively correlated across gradients of tree density and stand age. Open symbols are young stands (circles are low density, squares are moderate density, and triangles are high density), and solid symbols are mature stands. The regression equation is: $TBCA = 30.7 + 1.57 \times ANPP$ ($r^2 = 0.63$, $P < 0.01$).

Tree density in young stands, as expected, had no effect on CWD pools. Overall, mature stands contained two to three times more C than young stands. Young stands had the vast majority of C in detrital pools (91–99%, divided almost equally between CWD and C_s), while most C in mature stands was in live biomass (64%; primarily in stems and coarse roots). Differences in the total amount of ecosystem C with stand age that we report here for lodgepole pine are similar to those reported for *P. ponderosa* in Oregon, where mature stands contained approximately two times more carbon than young stands (Law et al. 2001). Moreover, Law et al. (2001) reported very similar distributions of C with stand age for a *P. ponderosa* ecosystem, with 85% of total C in a young stand found in detritus and 61% in a mature stand found in live biomass.

Our estimates of fine litter C in young postfire stands in YNP (64–319 g C/m²) are lower than that reported for a 15-year-old stand of lodgepole pine in southeastern Wyoming (938 g C/m²) that initiated following logging (Smith and Resh 1999). The discrepancy is likely due to differences in stand history (i.e., postfire vs. postharvest), as much of the litter layer in our stands would have been consumed during the stand-replacing fires of 1988. Our estimate of fine litter C for mature stands in YNP (868 g C/m²) is within the range reported by Fahey (1983) for 105-year-old postfire stands of lodgepole pine in southeastern Wyoming (848–1661 g C/m² assuming that the litter layer is 49% C). Estimates of CWD pools in our young stands (2543–3301 g C/m²) fall within the lower end of a range reported by Tinker and Knight (2000) for seven to nine-year-old postfire lodgepole pine stands in YNP (1886–13 064 g C/m² assuming that CWD is 46% C).

TBCA, ANPP, and LAI

ANPP and TBCA increased with tree density in young stands and with stand age as initially hypothesized. However, we expected that ANPP and TBCA in high-density young stands would approximate that in mature stands due to similarities in LAI, a measure of photosynthetic capacity. In fact, LAI, ANPP, and TBCA in the highest density young stand (~600 000 trees/ha) fell within the lower range estimated for our mature stands, indicating that while standing biomass varied greatly, fluxes of C in these stands were similar. TBCA in the high-density class as a whole, however, did not differ significantly from mature stands (Fig. 1).

TBCA averaged 68–306 g C·m⁻²·yr⁻¹ in young stands and 382 g C·m⁻²·yr⁻¹ in mature stands. In contrast, TBCA was relatively constant at 481–539 g C·m⁻²·yr⁻¹ in 15 to 100-year-old lodgepole pine stands in south-central Wyoming (Smith and Resh 1999). Lower values in our stands of lodgepole pine can be explained at least partially by (1) differences in sampling and scaling techniques employed for estimating F_s , which is the major component of TBCA, and/or (2) our inclusion of changes in soil (ΔC_s), litter (ΔC_L), and dead coarse woody root C (ΔC_{DCWR}) in estimating TBCA. Regardless, values in lodgepole pine stands are at the low end of published estimates for belowground C allocation in other ecosystems. TBCA has been estimated at 188–395 g C·m⁻²·yr⁻¹ in control and fertilized 31-year-old plantations of *Pinus resinosa* Ait. in Wisconsin (Haynes and Gower 1995); 438–510 g C·m⁻²·yr⁻¹ in mature *Eucalyptus pauciflora* Sieb. ex Spreng in Australia (Keith et al. 1997); 554 g C·m⁻²·yr⁻¹ in mixed-aged *P. ponderosa* in Oregon (Law et al. 1999); 710–733 g C·m⁻²·yr⁻¹ in *Pseudotsu-*

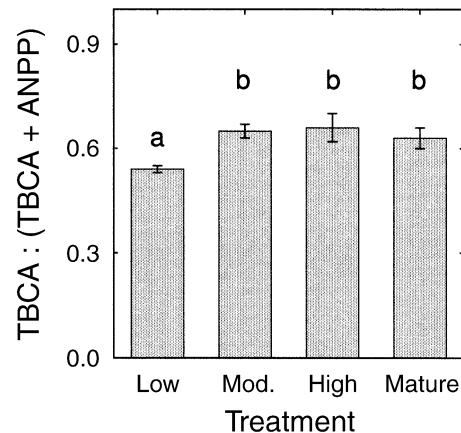


FIG. 6. The ratio of total belowground carbon allocation (TBCA) to TBCA + aboveground net primary productivity (ANPP) is remarkably constant (0.54–0.66) across gradients of tree density (low-, moderate- [mod.], and high-density young stands) and stand age. Bars are group means ± 1 SE ($n = 4$). Means with the same letter do not differ at $\alpha = 0.05$ (Tukey's hsd multiple-comparisons test after one-way ANOVA).

ga menziesii (Mirb) Franco in Washington (McDowell et al. 2001); and 1880 g C·m⁻²·yr⁻¹ in plantations of *Eucalyptus* in Hawaii (Giardina and Ryan 2002).

TBCA in our stands was ~3 times F_A ($r^2 = 0.30$, $P = 0.03$; $TBCA = 3.25 \times F_A$), which is higher than earlier published estimates that indicated a 2:1 ratio of TBCA to F_A (Raich and Nadelhoffer 1989, Davidson et al. 2002). This difference is probably due to the low litterfall rates of our young stands and supports suggestions that global extrapolations of TBCA from F_A values should be limited to mature forests (Gower et al. 1996b, Nadelhoffer et al. 1998). We found that F_S was the major component of belowground C allocation in all but the lowest density stands, accounting for 78–87% of the final TBCA estimate, which agrees well with results from prior studies that have directly measured changes in soil C pools (Giardina and Ryan 2002, Stape 2002).

Our estimates of ANPP in young stands (59–156 g C·m⁻²·yr⁻¹) are consistent with published values for a 15-year-old lodgepole pine stand in south-central Wyoming (~140 g C·m⁻²·yr⁻¹; Smith and Resh 1999). Mean ANPP in our mature stands (218 g C·m⁻²·yr⁻¹) also agrees well with an independent estimate (210 g C·m⁻²·yr⁻¹) for a 100-year-old stand of lodgepole pine in southeastern Wyoming (Olsson et al. 1998). However, mean ANPP in our mature stands is 45% higher than that reported by Smith and Resh (1999) for a 100-year-old stand of lodgepole pine in south-central Wyoming (~150 g C·m⁻²·yr⁻¹). This difference can be explained at least partially by the assumption of canopy steady state by Smith and Resh (1999), where foliage NPP was predicted by measuring litter production alone. Foliage NPP in our study was measured as foliage biomass increment plus fine litterfall. Fine litterfall is accounted for because a large fraction of current year's foliage production and short-lived material such as flowers and twigs is shed before the end of a measurement period (Clark et al. 2001). If we eliminate fine litterfall from our estimate of ANPP (Table 3), then mean ANPP in our mature stands is almost identical to that reported in Smith and Resh (1999) for a 100-year-old stand. We are confident with our estimates of foliage productivity (foliage biomass increment plus fine litterfall), as our data agree well with a separate estimate of foliage NPP (data not shown; $P = 0.68$, paired-samples t test), which was calculated by multiplying stand foliage biomass by the fraction of biomass in current year's foliage (from harvesting five trees; $23 \pm 5\%$ [mean ± 1 SE], $n = 5$).

Trends in ANPP with tree density in our study closely match previous work done on young postfire lodgepole pine stands in YNP (Reed et al. 1999). In both studies, tree ANPP was shown to increase with tree density while no simple patterns were evident for herbaceous and shrub ANPP. A greater proportion of total ANPP was accounted for by herbs and shrubs in our low-density stands, but absolute herbaceous and shrub

ANPP values were very similar across all stands despite large differences in tree density and stand age. Apparently, herbaceous and shrub productivity remains relatively constant with changes in tree density and stand age. This may be a reflection of the infertile soils associated with our stands, as Reed et al. (1999) found that herbaceous and shrub productivity on a low-density fertile site (andesitic soils) was roughly equivalent to total ANPP on a high-density infertile site.

Strong correlations between ANPP and LAI have been reported in prior studies (Gholz 1982, Gower et al. 1992, 2001) and the general form of the relationship seems constant across diverse forest ecosystems (Fassnacht and Gower 1997). We found that LAI is also strongly correlated with belowground carbon allocation, and that the relationship of both ANPP and TBCA with LAI does not vary across extreme gradients of tree density and stand age (Fig. 5).

Carbon allocation patterns

Consistent patterns in C allocation were evident in our study (Figs. 5 and 6) despite considerable variation in tree density, stand age, soil inorganic N availability, and plant N concentrations. We hypothesized that increased competition for water and nutrients would result in proportionally greater belowground C flux in high-density young stands and mature stands. This was based on previous fertilization/irrigation experiments showing that increased availability of belowground resources can cause a shift in C allocation from below- to aboveground (Gower et al. 1992, 1994, Haynes and Gower 1995, Keith et al. 1997). In fact, N content in foliage and roots decreased with increasing tree density in our young stands and with stand age (Fig. 4a, b). In addition, our index of inorganic soil N availability decreased with tree density in young stands (Fig. 4c). Moreover, as tree density increased in young stands, soil moisture decreased (Litton et al. 2003a). Still, carbon allocation patterns were independent of gradients in N availability and soil moisture. Other studies have also found a lack of change in carbon allocation relative to limiting soil resources (Herbert and Fownes 1999).

It has been suggested that young forests allocate proportionally more C belowground to establish and maintain root and mycorrhizal biomass that can supply the growing plants with sufficient water and nutrients (Davidson et al. 2002). While the magnitude of above- and belowground fluxes did vary with stand age in our stands, overall allocation patterns were remarkably constant (Fig. 6). Our age sequence represents only two points in time and it is possible that the conservative C allocation patterns that we report may not hold over the entire course of stand development. ANPP has been shown to vary in an almost universal pattern with age, rising to a maximum with canopy closure and peak LAI and declining thereafter (Gower et al. 1996a, Ryan et al. 1997a). If TBCA does not vary with stand age in the same manner as ANPP, then C allocation patterns

should differ with age. Working in a chronosequence of lodgepole pine stands in south-central Wyoming, Smith and Resh (1999) found that ANPP exhibited the classic pattern with stand age and that TBCA was essentially constant through age 100. However, the ratio of TBCA : TBCA + ANPP remained very consistent (~ 0.73 – 0.80) across this same age sequence. These consistent patterns of C allocation with stand age agree with the results of our study. However, their mean allocation ratio was 24% higher than ours, due at least partially to (1) their omission of understory ANPP, which, excluding low-density stands, accounted for an average of 25% of total ANPP in our lodgepole pine stands, and (2) differences in estimates of TBCA due to the assumption of steady state for soil C pools in Smith and Resh (1999).

Caution should be used when inferring C allocation patterns from standing biomass. Trees accumulate large amounts of biomass in long-lived woody components and, therefore, patterns of standing biomass may not be consistent with annual C flux (Friedlingstein et al. 1999). Partitioning of standing biomass varied with density in our young stands, with higher tree densities associated with a significantly higher proportion of total tree biomass belowground (Litton et al. 2003b). However, the conservative C allocation patterns that we observed for these stands indicate that partitioning of standing biomass is not always indicative of annual C flux.

We are lacking only measurements of aboveground plant respiration (R_a) to be able to estimate gross primary production (GPP) in our stands, and thus, the fraction of GPP allocated belowground. Previous work has shown that total respiration is approximately equivalent to total dry matter production (Ryan et al. 1994, Waring et al. 1998). Assuming that the same is true for the aboveground component in our stands of lodgepole pine, TBCA accounts for a constant fraction of GPP across gradients of tree density and stand age ($46 \pm 2\%$ [mean ± 1 SE], $n = 16$). Similar results have been reported for *Pinus radiata* (D. Don) plantations, where 41% of GPP was allocated belowground (Ryan et al. 1996). Comparable values (45–52%) have also been reported for a variety of other forest types (Malhi et al. 1999).

We were unable to estimate net ecosystem exchange (NEE) in our study because we lacked, in addition to R_a , quantitative data on respiration rates and long-term dynamics of CWD. This is a very large C pool in our fire-dominated ecosystem and is presumably an important component of total ecosystem C in all areas subject to natural disturbance regimes where large wood is not removed. CWD is likely to play a key role in determining the net exchange of C between forested ecosystems and the atmosphere.

CONCLUSIONS

Predicting how changes in climate and disturbance regimes will affect the exchange of C between forest

ecosystems and the atmosphere is crucial for understanding current and future global C metabolism. Yet, little quantitative data exist on the effects of natural disturbance on terrestrial C pools and fluxes, and forests are often treated in models as being structurally similar. We have demonstrated that disturbance has important and lasting effects on the *magnitude* of C pools and fluxes in lodgepole pine ecosystems through fire-initiated differences in tree density and stand age. However, overall *patterns* of C allocation are apparently independent of tree density and stand age, which, if true for other terrestrial ecosystems, could greatly simplify modeling efforts and enhance their predictive capabilities.

The approach outlined in this study could be used to enhance the scope and accuracy of terrestrial C models by identifying allocation patterns that allow for the estimation of belowground C dynamics from commonly measured aboveground variables (e.g., ANPP or LAI). In addition, increased understanding of the effects of natural disturbance on the net exchange of C in forests via changes in stand structure and age will enable more accurate C modeling and better predictions of the effects of global change biology on terrestrial C cycling. The ability to incorporate the indirect effects of natural disturbance in modeling efforts is especially important in light of predictions that disturbances, particularly fire, will increase in frequency and intensity with projected changes in climate.

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