

Carbon accumulation in Colorado ponderosa pine stands

Jeffrey A. Hicke, Rosemary L. Sherriff, Thomas T. Veblen, and Gregory P. Asner

Abstract: Woody encroachment and thickening have occurred throughout the western United States and have been proposed as important processes in the US carbon (C) budget despite large uncertainty in the magnitude of these effects. In this study we investigated ponderosa pine encroachment near Boulder, Colorado. We reconstructed a time series of forest structure to estimate changes in C storage by the trees. Advantages of this technique include the ability to estimate changes in C stocks over time with a single series of measurements (i.e., no historical measurements), and the ability to calculate accumulation rate changes through time. Substantial variation occurred in the C amounts and accumulation rates among the three plots resulting from differences in slope, aspect, and soil conditions. Accumulation rates increased exponentially as trees increased in size and additional trees established within the plots, and were highly variable among plots (0.09–0.7 Mg C·ha⁻¹·year⁻¹ during 1980–2001). These rates were less than those used in studies of the US carbon budget, and only by assuming no mortality for the densest stand could we generate a projected rate in 2050 that was similar. Thus, time since the initiation of encroachment and rate of encroachment are variables that should be considered for accurately computing the continental C budget.

Résumé : L'empiètement et la densification des forêts survenus partout dans l'ouest des États-Unis seraient, croit-on, des processus importants dans le bilan du carbone (C) aux États-Unis malgré une forte incertitude quant à l'ampleur de leurs effets. Dans cette étude, nous avons examiné l'empiètement par le pin ponderosa dans les environs de Boulder, au Colorado. Nous avons reconstitué des séries temporelles de la structure de la forêt pour estimer les changements dans le stockage du C par les arbres. Cette technique comporte plusieurs avantages, incluant la possibilité d'estimer les variations temporelles des stocks de C à l'aide d'une série unique de mesures (c.-à-d. sans mesures antérieures) et la capacité d'estimer les variations temporelles du taux d'accumulation. Les variations entre les trois parcelles dans la quantité de C et le taux d'accumulation étaient importantes à cause des différences dans la pente, l'orientation et les conditions du sol. Le taux d'accumulation a augmenté de façon exponentielle à mesure que les arbres augmentaient de taille et que de nouveaux arbres s'établissaient dans les parcelles, et il a varié fortement d'une parcelle à l'autre (0,09 à 0,7 Mg C·ha⁻¹·an⁻¹ entre 1980 et 2001). Ce taux est inférieur à ceux utilisés dans les études sur le bilan du C aux États-Unis, et seulement en assumant une absence de mortalité pour le peuplement le plus dense pouvions-nous prédire un taux comparable en 2050. Par conséquent, le temps écoulé depuis le début de l'empiètement et le taux d'empiètement sont des variables qui devraient être considérées pour calculer avec précision le bilan continental du C.

[Traduit par la Rédaction]

Introduction

Woody encroachment is the process by which woody plants expand into grasslands or meadows, and has been identified in ecosystems throughout the world (e.g., Archer et al. 2001). A related process called "woody thickening" (also referred to as "infilling" or "densification") occurs when a forest increases in stem density (e.g., Covington and Moore 1994). Woody encroachment and thickening affect

biodiversity and ecosystem function by changing species composition as well as stand age and size structure, and by altering carbon (C) and nutrient cycling. For example, mesquite encroachment over the last 100 years in central Texas has been found to increase soil and plant C and nitrogen stocks (Hibbard et al. 2001, Asner et al. 2003).

In addition, woody encroachment and thickening have recently been identified as processes contributing to the proposed US carbon sink. Pacala et al. (2001) estimated that woody encroachment accounts for 0.12–0.13 Pg C·year⁻¹ (1 Pg = 10¹⁵ g) or 17%–43% of the total estimated C sink of 0.3–0.7 Pg C·year⁻¹. Pacala et al. (2001) relied on two modeling estimates of the contribution of woody encroachment to this proposed sink. The first was computed by a process-based ecosystem model, the Ecosystem Demographic model, and the second method was taken from Houghton et al. (2000), who used a bookkeeping model. Houghton et al. (2000) utilized values of burned and grazed area together with estimates of C accumulation rates resulting from fire exclusion to calculate the contributions of land-use change and fire exclusion to the US carbon budget. Accumulation rates in ponderosa pine forests were derived principally from

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ecosystem modeling (Keane et al. 1990, Covington and Moore 1994). Houghton et al. (2000) estimated a conterminous US carbon sink due to fire exclusion of $0.24 \text{ Pg C}\cdot\text{year}^{-1}$, with about half resulting from woody encroachment (used in the Pacala et al. (2001) study) and half from woody thickening.

In North America, woody encroachment is associated with several types of ecosystems, including mesquite shrublands in arid and semi-arid rangelands throughout the southwestern US (e.g., Archer 1994, Archer et al. 2001), pinyon-juniper woodlands in the West (e.g., Burkhardt and Tisdale 1976), aspen stands in the northern Great Plains (Köchy and Wilson 2001), and conifer forests, especially ponderosa pine and Douglas-fir across western North America (Steinauer and Bragg 1987, Mast et al. 1997, Hessburg et al. 1999, Turner and Krannitz 2001).

Causes of woody encroachment and thickening vary among the different ecosystems and possibly by location. Fire suppression has occurred since the 1920s in the US (Houghton et al. 2000). Increases in cattle grazing over the past 100 years have affected woody plant invasion (Miller and Wigand 1994, Mast et al. 1998). Climate is a third process that could contribute to woody encroachment and thickening by influencing the establishment of seedlings during favorable growing conditions (Savage and Swetnam 1990, Miller and Wigand 1994, Mast et al. 1998, Swetnam and Betancourt 1998). Other factors such as CO_2 fertilization, nitrogen deposition, and exotic species invasions may also play important roles (Miller and Wigand 1994, Köchy and Wilson 2001). The co-occurrence and coupling of these factors, their wide spatial variation, and lack of historical observations challenge our understanding of the controls over woody encroachment and thickening and make projections highly uncertain.

In conifer forests, fire is an important driver of forest structure, although different regions have different fire frequencies. Ponderosa pine forests in the pre-settlement Southwest were thought to be maintained as open, park-like woodlands by frequent, low intensity surface fires, but the past century of fire exclusion has resulted in more densely populated ponderosa pine stands (Cooper 1960, Covington and Moore 1994, Fulé et al. 1997). In contrast, other western US conifer forests, and even other ponderosa pine forests, have longer fire return times with naturally occurring stand-replacing fires, or a mixture of longer and shorter return intervals (Romme and Despain 1989, Shinneman and Baker 1997, Kaufmann et al. 2000, Veblen et al. 2000, Veblen 2003).

In this paper we estimated C accumulation resulting from ponderosa pine encroachment using plot-level measures of tree age and diameter. Plot-scale conifer production in the Cascade Mountains was calculated by Graumlich et al. (1989) from dendrochronological measurements. These authors compared production with CO_2 and climate data to determine that temperatures increased growth in this area. Similarly, we reconstructed the temporal behavior of stand age and size for three plots on different slope aspects at the grassland-forest ecotone near Boulder, Colorado, USA. This area has experienced pine encroachment during the last 150 years through higher elevation forest expansion into lower elevation grasslands. Tree establishment dates together with diameter measurements and allometric equations al-

lowed us to calculate a time series of C accumulation for each tree. This method provided a means of calculating C storage without relying on previous studies, an advantage for locations lacking historical information. Summing the C accumulation across each plot resulted in a time series of accumulation associated with trees on a per area basis. We did not address changes in soil C that are likely to affect the total C stocks of the plots (Jackson et al. 2002). We extend the work of past studies by utilizing field measurements to estimate time series of C at the tree level, and by focusing on C in addition to forest structural variables such as basal area. Thus, we can compare our results with ecosystem modeling studies used to calculate the impacts of encroachment and thickening on the continental-scale C budget. Since we studied only one site, our intent was not to characterize accumulation rates across the western US, but rather investigate results at a location experiencing documented change.

Materials and methods

Study site

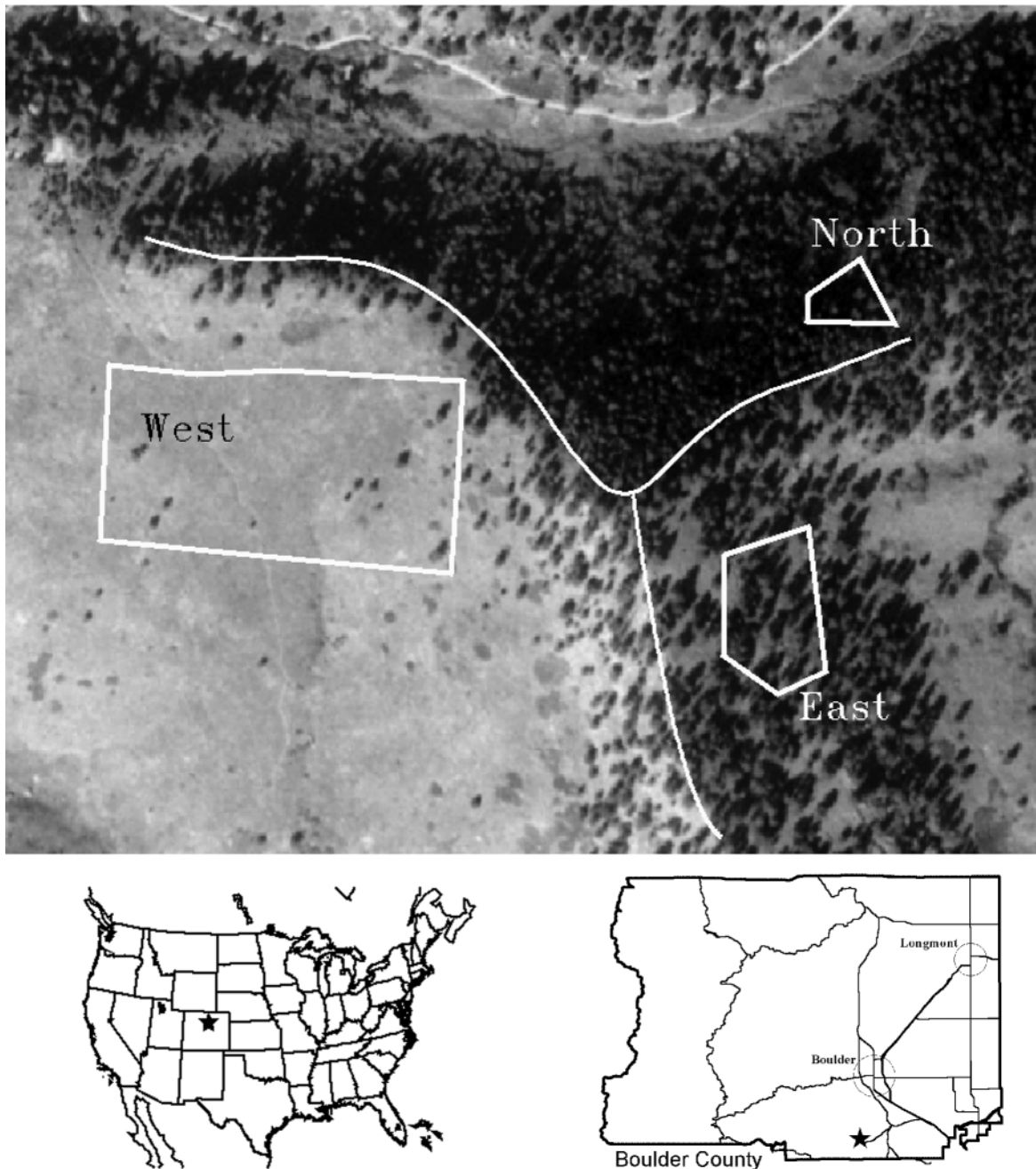
Our study site is located near Boulder, Colorado (39.94°N , 105.28°W) at an elevation of 2000 m. The area is at the montane forest-grassland ecotone, which occurs at similar elevations along a north-south line at the eastern base of the Rocky Mountains in northern Colorado. Vegetation of the montane zone varies from open park-like stands of ponderosa pine (*Pinus ponderosa* Dougl. ex Laws var. *scopulorum* Engelm.) at the forest-grassland ecotone to denser stands mixed with Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *glauca* (Beissn.) Franco) in more mesic sites and north-facing slopes. Mean temperatures reported by the nearby Boulder station range from 25°C in July to -10°C in January. Annual precipitation averages 395 mm, with the majority occurring in spring.

The site encompasses a north-south and an east-west ridge (Fig. 1). The original purpose of this field study was to characterize changes in stand structures and fire regimes in the northern Colorado Front Range along the environmental gradient from the lower ecotone to the upper limits of the ponderosa pine distribution; this site was the lowest elevation location of several identified for study. Because the fire regime study had somewhat different objectives than the study discussed in this paper, not all data useful for quantifying C accumulation were measured (e.g., tree heights). However, as demonstrated later, our results and conclusions are not sensitive to the assumptions made about the missing data.

Three plots were located on west-, east-, and north-facing aspects (hereafter "W plot", "E plot", and "N plot", respectively) to study differences in forest properties. The area was varied among plots to allow 60–80 trees to be sampled within each plot (Table 1). The W plot was located in a large meadow (Fig. 1) and had considerably higher herbaceous cover compared with the other two plots. The N and E plots were located higher on the ridge with steeper slopes than the W plot. Numerous rocky outcroppings were observed in the E plot.

In this region, the lowest elevation ponderosa pine stands were characterized by historically high fire frequencies (e.g., often 8–10 year return intervals to the same small stand or

Fig. 1. Aerial photograph from 1999 showing field site. Polygons indicate plot areas. Thick white lines indicate approximate locations of ridgelines. Maps show location of site in Boulder County, Colo. Increasing stem density can be seen from West to East to North plots.



tree, but highly variable) that maintained an open park-like forest structure prior to the early 1900s (Veblen et al. 2000). Studies at this site found a high surface fire frequency with low rates of ponderosa pine establishment until the early 1900s when fire suppression efforts became pronounced throughout the region (Fig. 2) (Veblen et al. 2000). The fire-scar record indicates a past regime of surface fires with a return interval of 12.5 years (17 fire years occurred from 1703 to 1916). Following a dramatic decline in fire occurrence in the late 1800s and complete cessation of fire after 1916, ponderosa pine establishment increased sharply at this site.

Precise historical records of grazing are unavailable, although grazing in the Boulder area has been reduced in the

past 30 years (Mast et al. 1998). Logging has occurred in the E and N plots, but only six stumps were recorded. Mast et al. (1997) documented woody encroachment in the area using historical and contemporary aerial photography; the authors calculated a 40% increase in forest cover between 1937 and 1988.

Tree measurements

On each plot we cored all trees greater than 4 cm in diameter at breast height (DBH) at 20 cm above the root–shoot boundary. Tree rings were crossdated or counted to identify approximate tree germination dates. Crossdating was accomplished visually using the master tree-ring chronology of

Table 1. Plot characteristics.

Plot	Area (ha)	No. of trees ^a	No. of saplings	No. of logs ^b	No. of stumps ^b	Mean diameter growth rate (cm-year ⁻¹) ^c	Median age (years) ^c
East	0.39					0.29	102
PIPO		86 (14)	16	9 (2)	6 (5)		
PSME		0	0	—	—		
JUSC		0	0	—	—		
West	1.9					0.39	65
PIPO		50 (1)	5	—	—		
PSME		7	5	—	—		
JUSC		8	2	—	—		
North	0.1					0.19	79
PIPO		54 (2)	22	3 (1)	6 (0)		
PSME		30 (1)	43	—	—		
JUSC		0	3	—	—		

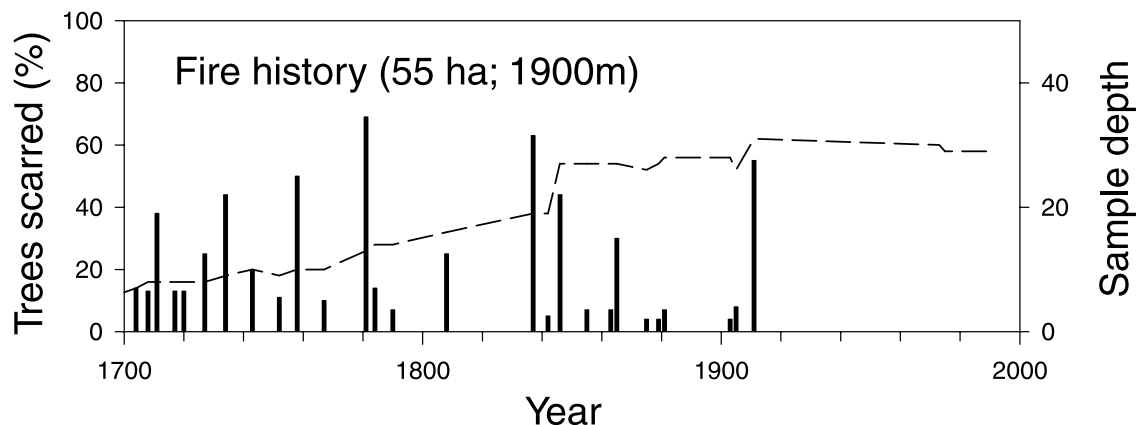
Note: PIPO, *Ponderosa pine*; PSME, *Pseudotsuga menziesii*; JUSC, *Juniperus scopulorum*.

^aValues in parentheses for this column indicate how many ages were missing because of rotten cores.

^bValues in parentheses for this column indicate how many were identified by species; remainder were assumed to be PIPO.

^cIncludes only cored trees, all species.

Fig. 2. Fire history at site. Bars show percentage of trees scarred at site because of fire; sample depth (dashed curve) shows the number of recorder trees alive (i.e., trees that can record fire because of previous fire scarring). In spite of an increasing number of trees available to record fires, the actual number of recorded fires decreased in the 1900s.



Veblen et al. (2000). We determined the ages of nearly 100% of the living trees as well as ages and dates of tree death for standing dead trees and fallen trees if possible. For those cores that missed the pith, ages were estimated following Duncan (1989). To estimate the ages of trees too small to core (<4 cm DBH) and to estimate the number of rings missed because of coring height (~20 cm above the root-shoot boundary), we incorporated existing data on seedling ages in nearby areas (Veblen and Lorenz 1986, Mast et al. 1998). We used a value of 7 years for ponderosa pine following values reported for a nearby site (approximately 3 km distance) at the forest–grassland ecotone by Mast et al. (1998). Although Mast et al. (1998) did not report values for Douglas-fir and Rocky Mountain juniper for Boulder County, the authors found slightly longer and similar age-at-coring height relationships compared with those for ponderosa pine, respectively, in Rocky Mountain National Park. Based on this, we chose an age-at-coring height of 10 years for Douglas-fir and 7 years for juniper. As a sensitivity test,

we added 10 years to the age-at-coring height values in our subsequent calculations. This had no effect on the 2001 total C estimate for each tree, which was set by the measured tree diameter. It also only decreased C accumulation rates by 9%–13% through a longer modeled tree life-span. Missing ages were estimated from regression equations developed from trees with both age and DBH measurements (Table 1).

Our method may underestimate the number of trees alive prior to the 20th century because of decomposition or consumption by fire. Although these potentially missing trees may influence soil C fluxes, these trees do not contribute to today's forest C accumulation rates that we calculated (see below).

DBH was also recorded for each tree. All saplings less than 4 cm diameter were tallied, and tree species were identified. The majority were ponderosa pine, although Douglas-fir occurred in the N and W plots, and Rocky Mountain juniper (*Juniperus scopulorum* Sarg.) occurred in the W plot (Table 1). DBH, decay class, and species (where possible)

were recorded for stumps and logs as well. A decay classification of 1 (indicating no decay, e.g., needles present, intact bark) through 4 (indicating extreme decay, e.g., no bark, illegible annual rings) was used for recording the decomposition level of stumps and logs (a simplified version of Brown et al. 1982).

Calculation of carbon stocks

Estimating C stocks from DBH and tree establishment data required the following steps: (i) calculating time series of tree diameters using a model of ring width; (ii) converting tree diameters to C amounts using allometric equations; (iii) accounting for stumps and logs in the plots, and (iv) summing across trees in a plot. Several steps required specifying models and (or) parameters, and we tested the sensitivity of each using available alternatives as indicated in the following sections. In the Results section, we report the total uncertainty of C accumulation rates by varying our model and parameters selections together.

Tree diameter time series

We calculated a time series of tree diameter from germination date to 2001 using the measured DBH together with the tree age. We tested several models to estimate ring width and thus tree diameter. The simplest model assumed a constant ring width, corresponding to a linear increase in diameter. However, ring widths of ponderosa pine typically exhibit a negative exponential shape as the tree ages and the diameter increases, and so we modeled ring width as (Fritts et al. 1969)

$$[1] \quad W = a \exp(-bt) + k$$

where W is the ring width, t is time, and a , b , and k are constants corresponding to the initial ring width, the rate of decrease, and the final ring width, respectively. We chose b and k from a time series of ponderosa pine ring widths shown in Cook (1990), and determined a from the measured diameter. We report C stocks and accumulation rates using the negative exponential decrease model. However, we also tested the sensitivity of the C accumulation rate using the constant ring width model. The 1980–2000 C accumulation rates increased by 20%–41% with the constant ring width model compared with the method using an exponentially decreasing ring width, owing to the decreased biomass earlier in each tree's lifetime.

Carbon storage

We estimated tree biomass using allometric equations relating stem, branch, and foliage biomass to DBH. Gholz (1982) reported such equations based on measurements of several tree species in Oregon as

$$[2] \quad B = \exp(m + n \ln \text{DBH})$$

where B is the biomass, and m and n are constants reported by Gholz (1982). We substituted the allometric equations for *Juniperus occidentalis* for *J. scopulorum* since Gholz (1982) did not report information on the latter. Biomass values were converted to C by multiplying by 0.5 (Schlesinger 1997).

We tested our biomass estimates using diameter measurements and height estimates with an allometric equation reported by Edminster et al. (1980) for ponderosa pines in the

Colorado Front Range. Tree height was modeled using a Chapman–Richards equation following Jiang et al. (1999) as

$$[3] \quad H = h_1(1 - \exp h_2 \text{DBH})^{h_3}$$

where H is height, h_1 is the maximum height, and h_2 and h_3 control the shape of the curve. We set $h_3 = 0.75$ as reported by Jiang et al. (1999), but adjusted $h_1 (= 25)$ and $h_2 (= -0.02)$ to match heights from Edminster et al. (1980). The behavior of modeled biomass as a function of DBH was very similar using the Gholz (1982) and Edminster et al. (1980) allometric equations, with the resulting C accumulation rates differing by less than 15%.

Root biomass can be substantial in forests but can be related to aboveground biomass (e.g., Enquist and Niklas 2002). We used belowground allometric equations from Grier and Logan (1977) developed for Douglas-fir in Oregon. We also investigated using a constant proportion of belowground to total biomass, such as the 15.8% used by Birdsey (1992); this decreased 2001 C stocks and 1950–2001 accumulation rate estimates by 6–12%. We report both aboveground and total C stocks because we recognize the uncertainty associated with belowground biomass estimates.

To account for tree mortality, we assigned a value for the number of years since a tree died by the observed decay class: classes 1–4 corresponded to <10, 30, 50, and 100 years, respectively (R. Sherriff and T. Veblen, unpublished data) (we observed no class 1 stumps or logs and only ponderosa pine was identified as dead material). We used the regression equations described above to estimate the age of each stump and log from the measured DBH. The year of death, obtained from the decay class, and the age at death, calculated from the measured DBH, determined the diameter time series of each stump and log. After death, stumps and logs were removed from the live biomass calculations but decayed onsite according to

$$[4] \quad C = C_0 \exp(-t/\tau)$$

where C is the carbon amount, C_0 is the carbon at the time of mortality, t is time, and τ is the turnover time. Decomposition in the Front Range is slow because the climate is dry, and thus we set $t = 67$ years (Turner et al. 1995). We tested this assumption by setting $t = 30$ years, which decreased the final C accumulation rates by 3%. The long decay time, together with the relatively recent establishment of trees at this site, suggests that we accounted for the low mortality that had likely occurred. We also calculated the effect of varying mortality date by decay class on the accumulation rate. Halving the time since death (i.e., 15, 25, and 50 years) changed the accumulation rate by 4%.

We calculated the fraction of C stock and accumulation rate in 10-year age bins to assess how different stand ages contributed to the C estimates. We ignored the C contribution of the invaded grasslands in our calculations because it is negligible compared with those of a mature forest. For example, in a tallgrass prairie, Schimel et al. (1991) report aboveground C stocks of 0.4–1.6 Mg C·ha⁻¹. We also did not address changes in soil C (see Discussion).

To determine how C accumulation rates will change in the future, we allowed trees and saplings alive in 2001 to continue growing for an additional 50 years following the ring

Fig. 3. Tree establishment dates for all species. Only those trees that have been cored are shown; trees with estimated ages are not included.

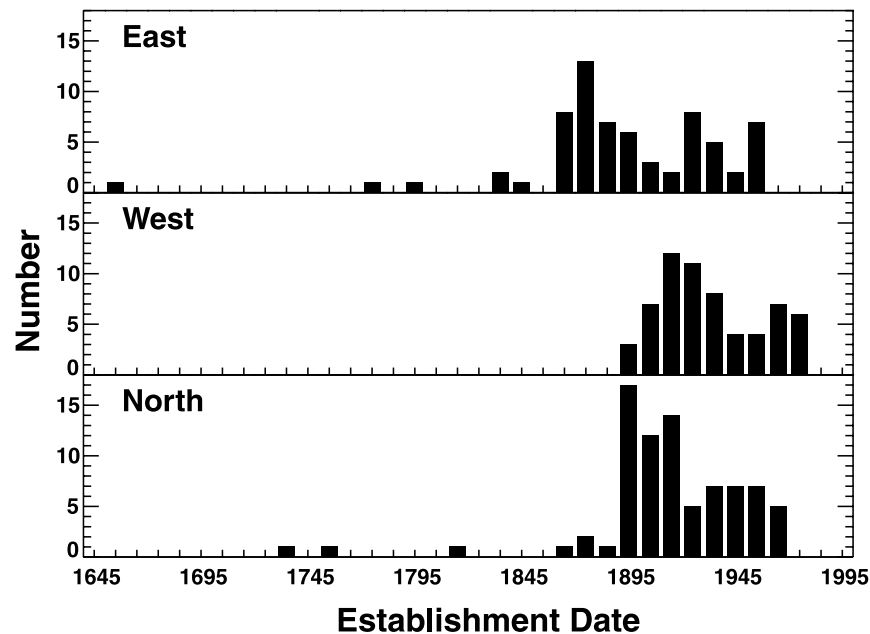
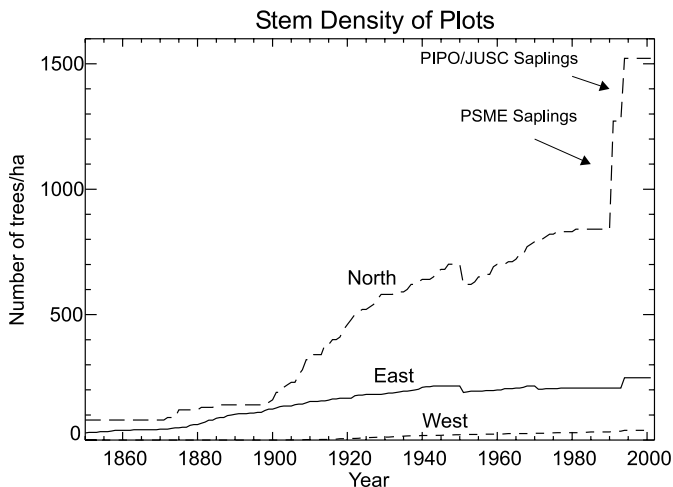


Fig. 4. Stem density (number·ha⁻¹) time series. Decreases indicate mortality as derived from stumps and logs. PIPO, *Ponderosa pine*; PSME, *Pseudotsuga menziesii*; JUSC, *Juniperus scopulorum*.

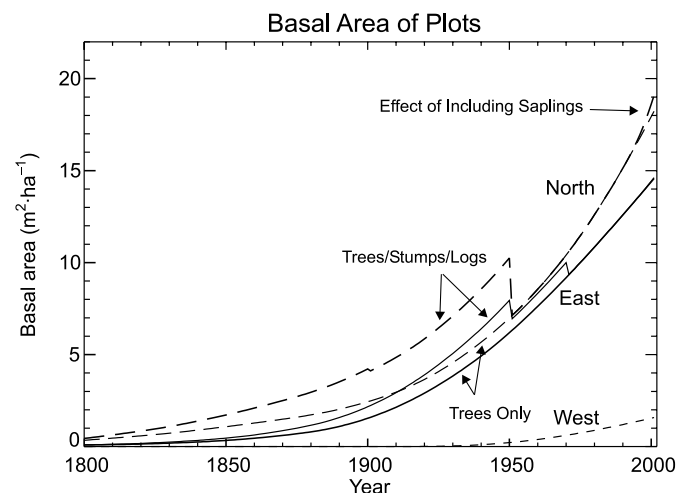


width model. Although it is likely that some of the trees and saplings alive in 2001 would die by 2050 and that additional tree establishment would occur in this time period, we did not account for these effects but report results using either trees alone or both trees and saplings since we feel these are likely to bound the actual behavior.

Results

Establishment dates of the measured trees, stumps, and logs occurred between 1660 and 1960 (Fig. 3). Most of the trees in the W and N plots germinated after 1900, whereas the majority of trees in the E plot established after 1870. No trees were detected before 1850 in the W plot, whereas several trees existed then in the E and N plots.

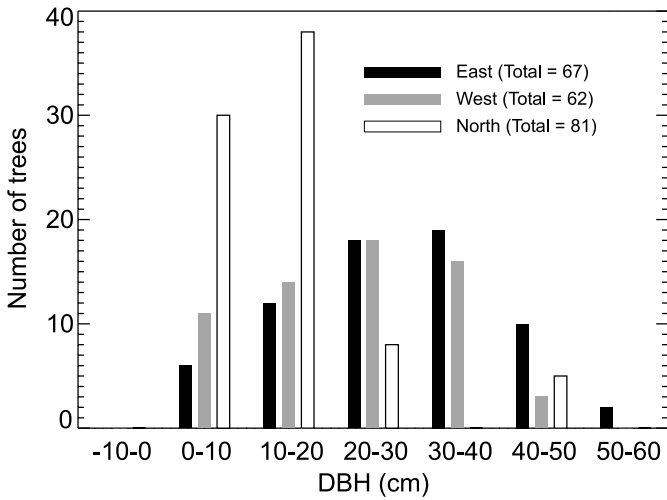
Fig. 5. Basal area (m²·ha⁻¹) time series. Shown are two time series per plot: trees and saplings only and trees, saplings, stumps, and logs. The effect of saplings on basal area is minimal as can be seen in the results from the North plot.



Stem density was highest in the N plot (Fig. 4) and lowest in the W plot. The rate of increase in stem density was also highest in the N plot and lowest in the W plot. A large number of saplings in the N plot established after 1980, whereas fewer saplings established in the E and W plots.

Despite the substantially greater number of stems in the N plot, the basal area was only slightly higher than in the E plot (Fig. 5). This resulted from the larger average stem diameter in the E plot (Fig. 6). In 2001, the E plot had a value of 15 m²·ha⁻¹, whereas we calculated roughly 19 m²·ha⁻¹ in the N plot. The large number of saplings present in the N plot added only minimal basal area (1 m²·ha⁻¹). The effect of mortality can be seen as the sharp decrease in the basal area around 1950 and again around 1970. Stumps and logs added

Fig. 6. Histogram of diameter at breast height (cm) measurements for East (black bars), West (gray), and North (white) plots. The North plot has more small trees, whereas the East and West plots have similar distributions.



an additional 3 m²·ha⁻¹ in the early 1900s in the N plot, with a smaller increase in the E plot.

The time series of aboveground C showed similar patterns among the three plots as the basal area (Fig. 7). Including stumps and logs increased the 1950 aboveground C somewhat in the E and N plots. The additional C stored onsite was reduced in time via decomposition.

Total tree C (above- and belowground) estimates were similar to basal area and aboveground C (Fig. 8). The N plot had the largest amount of C and accumulated C at the fastest rate among all plots. Carbon stocks of the E plot were slightly lower than those of the N plot, whereas the W plot contained very little C. Total C accumulation rates for 1980–2001 were 0.46 Mg C·ha⁻¹·year⁻¹ in the E plot, 0.09 Mg C·ha⁻¹·year⁻¹ in the W plot, and 0.70 Mg C·ha⁻¹·year⁻¹ in the N plot (Table 2). In a cumulative sensitivity study to estimate the range of rates, we varied the calculation assumptions discussed above together to change the rates either higher or lower. We computed the following ranges: E plot, 0.36–0.67 Mg C·ha⁻¹·year⁻¹; W plot, 0.08–0.11 Mg C·ha⁻¹·year⁻¹; N plot, 0.38–0.92 Mg C·ha⁻¹·year⁻¹.

Stand age structure varied among plots (Fig. 9). In the E plot, ages were evenly distributed over 120 years, while the W and N plots had few trees older than 100 years. Saplings in the E and N plots constituted a large fraction of the total number of trees. Figures 9b and 9c show the fraction of C amount and accumulation rate, respectively, per age-class. Despite large numbers of young trees, the older trees contributed most to the C stocks and accumulation rates. Particularly evident was the low number of trees greater than 150 years old (9 and 3 in the E and N plots, respectively) that contributed 25%–30% to the total C and 15% of the accumulation rate. Thus, we found that the growth of existing trees was more important in today's C budget than more recently established (encroaching) trees. However, as younger trees age, they will contribute proportionately more to the plot biomass than today.

Projected basal area and C storage continued to rise into the future owing to sustained growth and a lack of mortality

Fig. 7. Time series of aboveground carbon (C) storage (Mg C·ha⁻¹) for each plot. Shown are two time series per plot: trees and saplings only and trees, saplings, stumps, and logs.

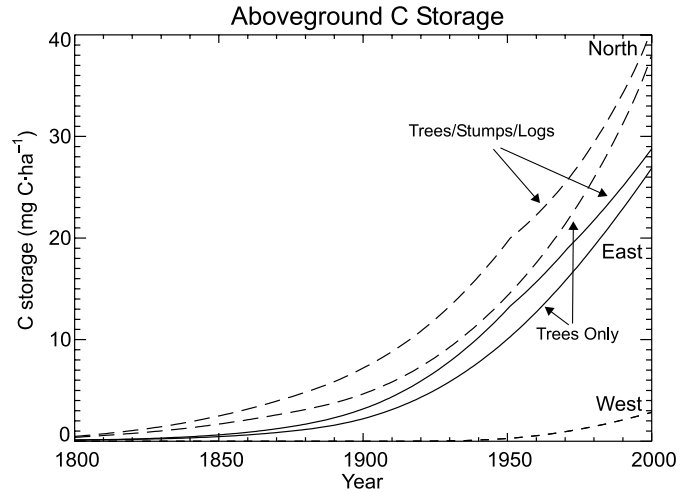
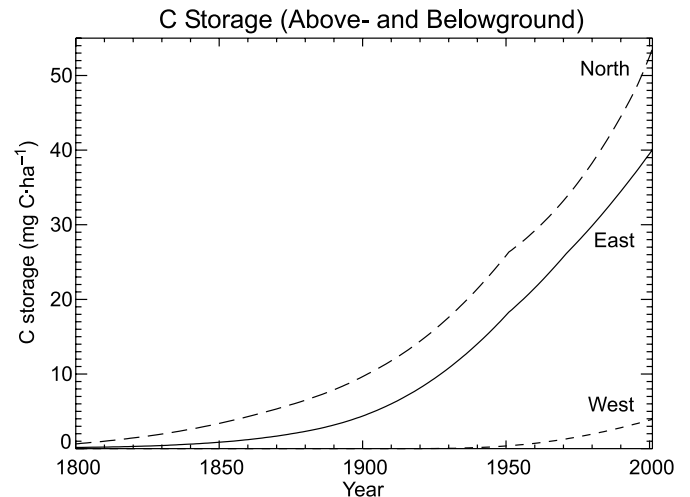


Fig. 8. Time series of total (above- and belowground) carbon (C) storage (Mg C·ha⁻¹) for each plot.



(Fig. 10). Including saplings that were alive in 2001 led to a substantial increase in modeled basal area and C storage in 2050 in comparison with values associated with trees alone. Projected basal area of trees and saplings in the N plot, ignoring any mortality that would likely occur, was similar to that reported by Covington and Moore (1994) for a modeled forest in Arizona, though offset by approximately 30 years. The 2030–2050 C accumulation rate increased substantially to either 1.12 or 2.81 Mg C·ha⁻¹·year⁻¹, depending on whether saplings were included. The lack of mortality, such as fire or insect damage, or additional establishment in this calculation implies that these numbers are uncertain; we report the values to demonstrate possible forest behavior and highlight this source of uncertainty in C accumulation predictions.

Discussion

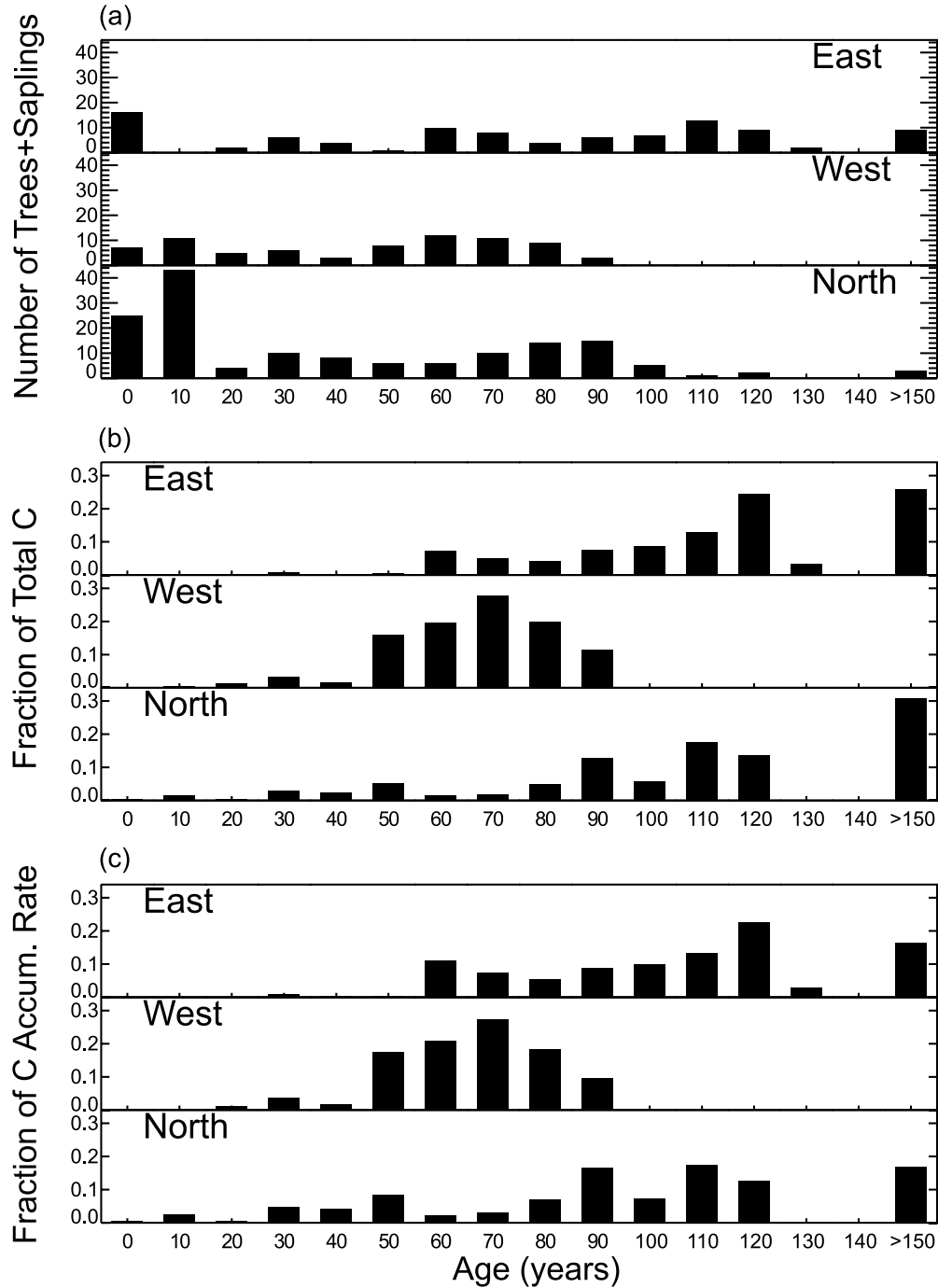
Changes in soil C might be expected to occur in association with woody encroachment. Although some studies of

Table 2. A review of carbon (C) accumulation rates.

Study	Location	Forest	Method	Accumulation rate (Mg C·ha ⁻¹ ·year ⁻¹)	Notes
Houghton et al. 2000	Western US	Pine, juniper, mesquite, cedar	Modeling and field measurements	0.25–2.5 ^a	Woody encroachment
Law et al. 2001	Oregon	Ponderosa pine	Modeling and field measurements	2.0–2.5 ^a	Woody thickening of established forests
Tilman et al. 2000	Minnesota	Ponderosa pine	Field measurements after logging	0.39 ^a	15-year old forest previously logged; above-ground only
Burrows et al. 2002	Queensland, Australia	Oak savanna Eucalypt	Field measurements Difference based on field measurements of C	1.8 ^a 0.53 ^b	Woody thickening of established forest Woody encroachment/thickening
Birdsey 1992	Conterminous US Colorado	All	Forest inventory	1.4 ^a	
Lal and Singh 2000	India	All	Forest inventory	0.0–0.89 ^a	
Asner et al. 2003	North Texas	Mesquite	Forest inventory Based on age and maximum potential biomass	0.31–1.05 ^b 0.36 ^b	Individual plant
This study	Colorado	Ponderosa pine	Remote sensing and field observations	0.02 ^b	Woody encroachment over 400 km ² region; aboveground only
			Field measurements	0.46, 0.09, 0.70 ^{a,c}	1980–2001
				0.62, 0.13, 1.12 ^{a,c} 0.72, 0.15, 2.81 ^{a,c}	2030–2050 (trees alive in 2001 only) 2030–2050 (trees and saplings alive in 2001)

^aTotal (above- and below-ground) accumulation.^bAboveground accumulation.^cEast-, west-, and north-facing plots, respectively.

Fig. 9. Distribution among age-classes of (a) numbers of trees and saplings, (b) the fraction of carbon (C) storage in 2001, and (c) the fraction of C accumulation rate in 2001 at each of the plots. The older, larger trees in the East and West plots contribute relatively more to the C storage and accumulation rate than the younger, smaller trees.

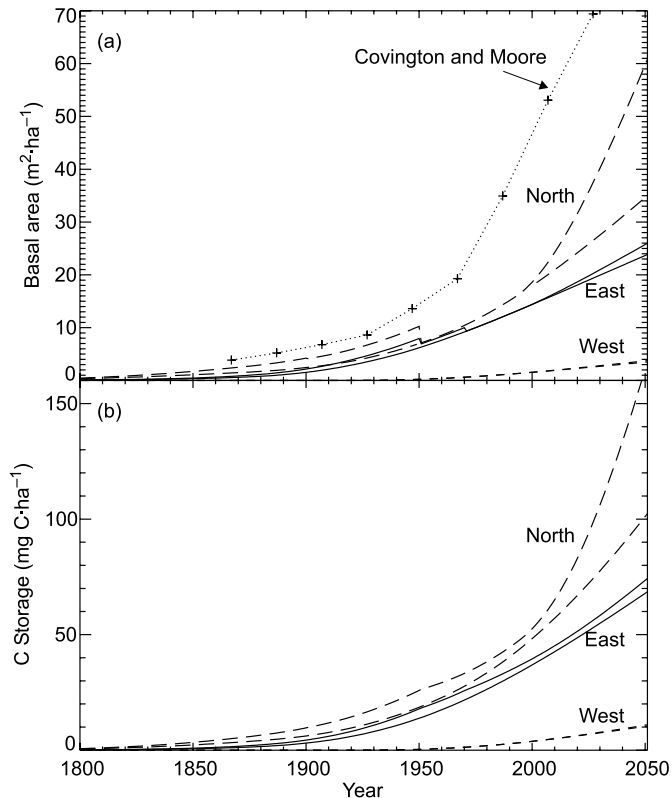


woody thickening have found modeled increases in soil C in response to fire exclusion (Liski et al. 1998), other studies have found little measured change (Tilman et al. 2000). Studies of mesquite encroachment in the southwestern US have found either marked increases in soil C (Hibbard et al. 2001) or little change (Connin et al. 1997). Barton and Wallenstein (1997) found more soil organic matter in a Pennsylvania savanna than in the expanding Virginia pine forest. A recent study by Jackson et al. (2002) found both increases and decreases in soil C after woody encroachment

by *Prosopis* (mesquite), *Larrea* (creosote), and *Juniperus* (juniper) spp. depending on rainfall inputs. Further research is needed to examine this issue for areas subjected to ponderosa pine encroachment and thickening.

Ponderosa pines bear cones as early as 7 years of age, although seeds from trees aged 60–160 years are more viable than those of younger trees (Burns and Honkala 1990). Thus, both encroachment and thickening were probably occurring at our study site, though it is difficult to differentiate these processes. At a given location, seedling establishment

Fig. 10. (a) Basal area ($\text{m}^2\cdot\text{ha}^{-1}$) projected to 2051 for East (solid curve), West (short dashed curve), and North (long dashed curve) plots. Also shown is modeled basal area from Covington and Moore (1994) for an Arizona ponderosa pine forest responding to fire exclusion. (b) Carbon storage ($\text{Mg C}\cdot\text{ha}^{-1}$) projected to 2051. Lower curve for each plot indicates behavior of trees living in 2001 only; upper curve shows behavior for both trees and saplings alive in 2001.



would likely be faster in forests experiencing woody thickening due to a preexisting seedbank. Our estimated C accumulation rates may thus be lower than a comparable location experiencing woody thickening alone.

Plot-level carbon storage

Carbon accumulation at the plot level results from two processes: the C accumulation per tree and an increase in the number of trees per plot. At the tree level, C accumulation is largely a function of stem diameter, which itself is a function of age and growth rate. However, not only does the C stored increase as the stem diameter increases, the rate of C accumulation also increases: older trees and (or) faster-growing trees store C at a faster rate than younger and (or) slower-growing trees. At the plot level, stem density becomes an important factor influencing C storage. Although we found that the oldest trees contribute most to today's C stocks, trees that established in later years did affect C storage, and faster encroachment rates drove greater accumulation rates. However, high stem densities may be coupled to lower growth rates, as in the N plot, as a result of increased competition for light, nutrients, and water.

Stands saturate with respect to C accumulation as mortality increases to balance tree establishment. At our field site,

however, mortality was not yet a factor, and we expect that C will continue to accumulate for several decades in the future, leading to increased accumulation rates (Fig. 10). However, we also expect mortality to accelerate as the stands mature. Table 3 compares characteristics of ponderosa pine forests from several studies. Our 2001 stand characteristics nearly match those reported by some studies, whereas our projected forest stand structure in 2051 (Fig. 10) was similar to mature ponderosa pine stands reported in other studies. Additional seedling establishment will likely occur in the next 50 years, and disturbances such as fire and insect outbreak are possible, making our predictions uncertain. However, we expect increased mortality compared with establishment and growth within the next several decades, decreasing the accumulation rate.

The three plots in our study had different age, growth rate, and tree establishment patterns that influenced C storage (Table 1, Fig. 3). The W plot, located in a meadow, had the lowest rate of encroachment (establishment) and C accumulation on a per-area basis. Ponderosa pine establishment favors open, disturbed, coarse-textured soil areas (Peet 1981). The higher herbaceous cover in the W plot may have increased competition with pine seedlings for resources, delaying tree establishment. The E plot situated higher on the ridge had more open forest structure and rockier soil, possibly allowing earlier establishment of pines. The slower tree growth in the N slope may be attributed to increased stem density and therefore competition for resources. Despite lower growth rates and younger trees (Table 1), however, the N plot had the highest C accumulation because of the rapid encroachment rate. The high spatial variability in C accumulation rates among plots implies that regional estimates of C accumulation need to account for this heterogeneity.

Comparisons with other studies

Table 2 lists C accumulation rates reported in published studies of forest structural changes. The rate used by Houghton et al. (2000), derived from Covington and Moore (1994), is substantially higher than our calculation for the late 1900s, although similar to our 2050 estimates for the densest stand that ignores any mortality. Law et al. (2001) estimated the C budget for a 15-year-old ponderosa pine forest in Oregon, computing an aboveground tree biomass of $5.8 \text{ Mg C}\cdot\text{ha}^{-1}$. The resulting average rate of aboveground C accumulation was $0.39 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$. The similarity of the Oregon accumulation rate and our rate from the E plot, despite the much younger tree ages at the Oregon site, was due to several factors. Faster tree growth in Oregon (0.67 versus $0.29 \text{ cm DBH}\cdot\text{year}^{-1}$) was likely due to greater precipitation (552 versus 395 mm). Furthermore, Law et al. (2001) studied a previously logged site, which would have facilitated seedling establishment synchronously across the site because of in situ seed banks. In contrast, our site experienced woody plant invasion.

Our C accumulation rates were typically less than published rates of other forest types. Tilman et al. (2000) investigated the effects of fire exclusion in a Minnesota oak savanna, and reported a C accumulation rate of $1.8 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$. Burrows et al. (2002) found that C storage increased at a rate of $0.53 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ across 57 permanent plots in Australian eucalypt forests, and attrib-

Table 3. A review of stand characteristics of ponderosa pine forests.

Study	Location	Description	Stem density (number·ha ⁻¹)	Basal area (m ² ·ha ⁻¹)	Aboveground C (Mg C·ha ⁻¹)
Gholz 1982	Eastern Cascade Mountains, Ore.	Mature and undisturbed forest	490 (<10 cm DBH); 215 (>10 cm DBH)	26.1	68
Law et al. 2001	Eastern Cascade Mountains, Ore.	15-year old forest, previously logged	1032 (<5 cm DBH); 344 (>5 cm DBH)	—	5.7
Fulé et al. 1997	Arizona	Mature forest	604.9 ^a	—	108
		Presettlement	65	11.7	—
		Contemporary (subjected to fire exclusion)	720	18.2	—
Covington and Moore 1994	Arizona	Presettlement	30	8.4	—
		Contemporary (subjected to fire exclusion)	1870	27.2	—
Kaufmann et al. 2000	Front Range, Colo.	Undisturbed	131–390	9.4–20.7	—
East plot, this study	Front Range, Colo.	Woody encroachment	207 (>4 cm DBH); 41 (<4 cm DBH)	14.6	29.2
West plot, this study	Front Range, Colo.	Woody encroachment	33 (>4 cm DBH); 6 (<4 cm DBH)	1.6	2.9
North plot, this study	Front Range, Colo.	Woody encroachment	841 (>4 cm DBH); 681 (<4 cm DBH)	19.1	41.4

^aMean stem density based on a mix of old and mature plots weighted by area (B.E. Law, Oregon State University, personal communication).

uted the changes to grazing and altered fire regimes. Continental-scale changes in forest C have been reported by several authors using forest inventory data. Birdsey (1992) calculated the C accumulation rate of all US forests, finding that US forests were accumulating C at a rate of 1.4 Mg C·ha⁻¹·year⁻¹. Birdsey (1992) estimated that forests in Colorado were accumulating C at a rate of 0–0.89 Mg C·ha⁻¹·year⁻¹. Also using inventory data, Lal and Singh (2000) reported C accumulation rates of 0.31–1.05 Mg C·ha⁻¹·year⁻¹ for several naturally occurring forest types across India.

Mesquite encroachment throughout the southwestern US has also been identified as a potentially significant C sink. Asner et al. (2003) estimated the change in aboveground C stocks associated with mesquite encroachment over a 400 km² region in north Texas. At the individual plant level, mesquite accumulates aboveground C at a rate of 0.36 Mg C·ha⁻¹·year⁻¹. Over the entire 400 km² region, Asner et al. (2003) found an aboveground C accumulation rate of only 0.02 Mg C·ha⁻¹·year⁻¹, which included woody vegetation removal throughout the region. At the continental scale, the relative importance of mesquite, ponderosa pine, and other woody plant (e.g., pinyon-juniper) encroachment in the C cycle depends on the accumulation rates and the area of expansion. To better understand patterns of spatial heterogeneity of woody vegetation changes at the regional scale, additional studies are required to investigate this phenomenon across ecosystems.

Causes behind accumulation rate differences compared with these other forest types include: (i) higher growth rates due to different climate regimes and (or) species; (ii) differences in potential biomass (e.g., mesquite woodlands); (iii) differences in time since tree establishment, which affect tree biomass and therefore growth rates.

Implications for a US carbon sink

We analyzed only three plots on one site in Colorado, and found large variability in accumulation rates. It is likely that rates vary substantially across the region in response to differing climate, soils, and land use. However, past estimates (Houghton et al. 2000) have relied upon limited modeling studies. Our results are based on field measurements, and so we feel that it is appropriate to investigate how our rates affect regional estimates, despite large uncertainties. Additional studies to quantify the regional variability of C accumulation are needed but are outside the scope of this paper.

Our largest estimate of 1950–2001 C accumulation rates was 59% of the total Rocky Mountain region woody encroachment value (including several forest types) used by Houghton et al. (2000), and 26% of the rate based on the ponderosa pine results of Covington and Moore (1994). As discussed above, however, the rate increased as the forests mature, and so the difference may be attributable to the different times since encroachment initiation. The large difference indicates that this time since initiation is an important variable when calculating the woody encroachment effect on the C budget. The difference also indicates that these effects change in time and that today's effect may be more or less than the future effect depending on the maturity of the invading forest. We contend that 2–3 Mg C·ha⁻¹·year⁻¹ is close

to the upper bound of the C accumulation rate in ponderosa pine forests, and that many areas experiencing forest invasion may have much lower values.

While the regional contribution of ponderosa pine forest change may have been overestimated by Houghton et al. (2000), it is difficult to quantify the magnitude of this overestimate. The authors calculated that 153×10^6 ha in the Rocky Mountains have experienced woody encroachment (out of a total encroachment area in the conterminous US of 224×10^6 ha), although the contributions from the different forest types (juniper, mesquite, ponderosa, and others) were not specified. Ponderosa pine forests cover 22×10^6 ha in the western US (Houghton et al. 2000), and it is probable that only some of that distribution is experiencing woody encroachment, although much of the distribution may be experiencing woody thickening.

Note that if the regional-scale contribution of woody encroachment to the proposed US carbon sink were overestimated, then it is possible that the contribution would increase as the encroaching forests mature. However, this result depends on the relative fraction of areas with increasing versus decreasing accumulation rates (e.g., young versus mature forests). Given the wide variation of age structure and fire history within and between ponderosa pine forests (Shinneman and Baker 1997, Veblen 2003), these sources of variability are likely to be important.

Conclusions

Forest structural measurements allowed us to calculate tree establishment dates and a time series of stem densities of all trees in three plots that have experienced woody encroachment over the last 150 years at the Colorado Front Range forest–grassland ecotone. By using field data to calculate tree establishment dates and diameters, we estimated C storage rates without requiring measurements from multiple dates. We calculated the C associated with each tree, then summed across each plot to compute plot-level values. We found substantial variation in the C accumulation rates among these plots. The different slopes and aspects among the plots resulted in different tree establishment dates, stem densities, and growth rates, probably due to differences in moisture, solar radiation, grazing, and competition with grasses.

Our contemporary maximum C accumulation rates were much smaller than those used to estimate C storage by ponderosa pine forests in a study of the US carbon budget by Houghton et al. (2000). Only by projecting C accumulation rates 50 years into the future and ignoring any mortality could we generate similar rates as those used by Houghton et al. (2000). It is clear that the C accumulation rate changes substantially through time as encroaching forests mature, first increasing with time then decreasing as mortality balances growth.

Woody encroachment and thickening are important processes when calculating the C budget of the US; recent estimates report that these processes are responsible for 17%–43% of the total sink (Pacala et al. 2001). Although we showed here that recent estimates of these processes may be too high (Houghton et al. 2000, Pacala et al. 2001), additional studies are required to identify the spatial variation in

the C accumulation rates, both within a forest type and among different tree species. Furthermore, analyses of soil C changes associated with forest encroachment are needed to understand this important process. Quantifying these effects will reduce the large uncertainty associated with woody encroachment and thickening in the US carbon cycle.

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References

- Archer, S. 1994. Woody plant encroachment into southwestern grasslands and savannas: rates, patterns, and proximate causes. *In* Ecological implications of livestock herbivory in the West. Edited by M. Vavra, W. Laycock, and R. Pieper. Society for Range Management, Denver, Colo. pp. 13–68.
- Archer, S., Boutton, T.W., and Hibbard, K.A. 2001. Trees in grasslands: biogeochemical consequences of woody plant expansion. *In* Global biogeochemical cycles in the climate system. Edited by E.-D. Schulze, S. Harrison, M. Heimann, E. Holland, J. Lloyd, I. Prentice, and D. Schimel. Academic Press Inc., San Diego. pp. 115–133.
- Asner, G.P., Archer, S.A., Hughes, R.F., Ansley, J.N., and Wessman, C.A. 2003. Net changes in regional woody vegetation cover and carbon storage in Texas drylands, 1937–1999. *Global Change Biol.* **9**(3): 316–335.
- Barton, A.M., and Wallenstein, M.D. 1997. Effects of invasion of *Pinus virginiana* on soil properties in serpentine barrens in southeastern Pennsylvania. *J. Torrey Bot. Soc.* **124**: 297–305.
- Birdsey, R.A. 1992. Carbon storage and accumulation in United States forest ecosystems. USDA Forest Service General Technical Report GTR-WO-59, Washington, DC.
- Brown, J.K., Oberheu, R.D., and Johnston, C.M. 1982. Handbook for inventorying surface fuels and biomass in the Interior West. USDA Forest Service General Technical Report INT-129.
- Burkhardt, J.W., and Tisdale, E.W. 1976. Causes of juniper invasion in southwestern Idaho. *Ecology*, **57**: 472–484.
- Burns, R.M., and Honkala, B.H. 1990. Silvics of North America: 1. Conifers. U.S. Department of Agriculture, Forest Service, Washington, DC.
- Burrows, W.H., Henry, B.K., Back, P.V., Hoffmann, M.B., Tait, L.J., Anderson, E.R., Menke, N., Danaher, T., Carter, J.O., and McKeon, G.M. 2002. Growth and carbon stock change in eucalypt woodlands in northeast Australia: ecological and greenhouse sink implications. *Global Change Biol.* **8**: 769–784.
- Connin, S.L., Virginia, R.A., and Chamberlain, C.P. 1997. Carbon isotopes reveal soil organic matter dynamics following arid land shrub expansion. *Oecologia*, **110**: 374–386.
- Cook, E. 1990. A conceptual linear aggregate model for tree rings. *In* Methods of dendrochronology. Edited by E.R. Cook and L.A. Kairiukstis. Kluwer, London. pp. 98–104.

- Cooper, C.F. 1960. Changes in vegetation, structure, and growth of southwestern pine forests since white settlement. *Ecol. Monogr.* **30**: 129–164.
- Covington, W.W., and Moore, M.M. 1994. Southwestern ponderosa forest structure: changes since Euro-American settlement. *J. For.* **92**: 39–47.
- Duncan, R.P. 1989. An evaluation of errors in tree age estimates based on increment cores in Kahikatea (*Dacrycarpus dacrydioides*). *N.Z. Nat. Sci.* **16**: 31–37.
- Edminster, C.B., Beeson, R.T., and Metcalf, G.E. 1980. Volume tables and point-sampling factors for ponderosa pine in the Front Range of Colorado. Rocky Mountain Forest and Range Experiment Station, Research Paper RM-218. U.S. Forest Service, U.S. Department of Agriculture.
- Enquist, B.J., and Niklas, K.J. 2002. Global allocation rules for patterns of biomass partitioning in seed plants. *Science*, **295**: 1517–1520.
- Fritts, H.C., Mosimann, J.E., and Bottorff, C.P. 1969. A revised computer program for standardizing tree-ring series. *Tree-Ring Bull.* **29**: 15–20.
- Fulé, P.Z., Covington, W.W., and Moore, M.M. 1997. Determining reference conditions for ecosystem management of southwestern ponderosa pine forests. *Ecol. Appl.* **7**: 895–908.
- Gholz, H.L. 1982. Environmental limits on above-ground net primary production, leaf-area, and biomass in vegetation zones of the Pacific Northwest. *Ecology*, **63**: 469–481.
- Graumlich, L.J., Brubaker, L.B., and Grier, C.C. 1989. Long-term trends in forest net primary productivity: Cascade Mountains, Washington. *Ecology*, **70**: 405–410.
- Grier, C.C., and Logan, R.S. 1977. Old-growth *Pseudotsuga-Menziesii* communities of a western Oregon watershed: biomass distribution and production budgets. *Ecol. Monogr.* **47**: 373–400.
- Hessburg, P.F., Smith, B.G., and Salter, R.B. 1999. Detecting change in forest spatial patterns from reference conditions. *Ecol. Appl.* **9**: 1232–1252.
- Hibbard, K.A., Archer, S., Schimel, D.S., and Valentine, D.W. 2001. Biogeochemical changes accompanying woody plant encroachment in a subtropical savanna. *Ecology*, **82**: 1999–2011.
- Houghton, R.A., Hackler, J.L., and Lawrence, K.T. 2000. Changes in terrestrial carbon storage in the United States. 2: The role of fire and fire management. *Glob. Ecol. Biogeogr.* **9**: 145–170.
- Jackson, R.B., Banner, J.L., Jobbágy, E.G., Pockman, W.T., and Wall, D.H. 2002. Ecosystem carbon loss with woody plant invasion of grasslands. *Nature*, **418**: 623–626.
- Jiang, J., Peng, C.H., Apps, M.J., Zhang, Y.L., Woodard, P.M. and Wang, Z.M. 1999. Modelling the net primary productivity of temperate forest ecosystems in China with a GAP model. *Ecol. Model.* **122**: 225–238.
- Kaufmann, M.R., Regan, C.M., and Brown, P.M. 2000. Heterogeneity in ponderosa pine/Douglas-fir forests: age and size structure in unlogged and logged landscapes of central Colorado. *Can. J. For. Res.* **30**: 698–711.
- Keane, R.E., Arno, S.F., and Brown, J.K. 1990. Simulating cumulative fire effects in ponderosa pine Douglas-fir forests. *Ecology*, **71**: 189–203.
- Köchy, M., and Wilson, S.D. 2001. Nitrogen deposition and forest expansion in the northern Great Plains. *J. Ecol.* **89**: 807–817.
- Lal, M., and Singh, R. 2000. Carbon sequestration potential of Indian forests. *Environ. Monit. Assess.* **60**: 315–327.
- Law, B.E., Thornton, P.E., Irvine, J., Anthoni, P.M., and Van Tuyl, S. 2001. Carbon storage and fluxes in ponderosa pine forests at different developmental stages. *Global Change Biol.* **7**: 755–777.
- Liski, J., Ilvesniemi, H., Makela, A., and Starr, M. 1998. Model analysis of the effects of soil age, fires and harvesting on the carbon storage of boreal forest soils. *Eur. J. Soil Sci.* **49**: 407–416.
- Mast, J.N., Veblen, T.T., and Hodgson, M.E. 1997. Tree invasion within a pine/grassland ecotone: an approach with historic aerial photography and GIS modeling. *For. Ecol. Manage.* **93**: 181–194.
- Mast, J.N., Veblen, T.T., and Linhart, Y.B. 1998. Disturbance and climatic influences on age structure of ponderosa pine at the pine/grassland ecotone, Colorado Front Range. *J. Biogeogr.* **25**: 743–755.
- Miller, R.F., and Wigand, P.E. 1994. Holocene changes in semiarid pinyon-juniper woodlands. *BioScience*, **44**: 465–474.
- Pacala, S.W., Hurtt, G.C., Baker, D., Peylin, P., Houghton, R.A., Birdsey, R.A. et al. 2001. Consistent land- and atmosphere-based U.S. carbon sink estimates. *Science*, **292**: 2316–2320.
- Peet, R.K. 1981. Forest vegetation of the Colorado Front Range: composition and dynamics. *Vegetatio*, **45**: 3–75.
- Romme, W.H., and Despain, D.G. 1989. Historical perspective on the Yellowstone fires of 1988. *BioScience*, **39**: 695–699.
- Savage, M., and Swetnam, T.W. 1990. Early 19th-century fire decline following sheep pasturing in a Navajo ponderosa pine forest. *Ecology*, **71**: 2374–2378.
- Schimel, D.S., Kittel, T.G.F., Knapp, A.K., Seastedt, T.R., Parton, W.J., and Brown, V.B. 1991. Physiological interactions along resource gradients in a tallgrass prairie. *Ecology*, **72**: 672–684.
- Schlesinger, W.H. 1997. *Biogeochemistry: an analysis of global change*. Academic Press, San Diego, Calif.
- Shinneman, D.J., and Baker, W.L. 1997. Nonequilibrium dynamics between catastrophic disturbances and old-growth forests in Ponderosa pine landscapes of the Black Hills. *Conserv. Biol.* **11**: 1276–1288.
- Steinauer, E.M., and Bragg, T.B. 1987. Ponderosa pine (*Pinus ponderosa*) invasion of Nebraska sandhills prairie. *Am. Midl. Nat.* **118**: 358–365.
- Swetnam, T.W., and Betancourt, J.L. 1998. Mesoscale disturbance and ecological response to decadal climatic variability in the American Southwest. *J. Climate*, **11**: 3128–3147.
- Tilman, D., Reich, P., Phillips, H., Menton, M., Patel, A., Vos, Peterson, E.D., and Knops, J. 2000. Fire suppression and ecosystem carbon storage. *Ecology*, **81**: 2680–2685.
- Turner, D.P., Koerper, G.J., Harmon, M.E., and Lee, J.J. 1995. A carbon budget for forests of the conterminous United States. *Ecol. Appl.* **5**: 421–436.
- Turner, J.S., and Krannitz, P.G. 2001. Conifer density increases in semi-desert habitats of British Columbia in the absence of fire. *Northwest Sci.* **75**: 176–182.
- Veblen, T.T. 2003. An introduction to key issues in fire regime research for fuels management and ecological restoration. *In* Conference on Fire, Fuel Treatments, and Ecological Restoration: Proper Place, Appropriate Time, Fort Collins, Colo., 16–18 April 2002. *Edited by* P.N. Omi and L.A. Joyce. U.S. Dep. Agric. For. Serv. Rocky Mt. Res. Stn. Proc. RMRS-P-29. pp. 259–275.
- Veblen, T.T., and Lorenz, D.C. 1986. Anthropogenic disturbance and recovery patterns in montane forests. *Physical Geography*, **7**: 1–24.
- Veblen, T.T., Kitzberger, T., and Donnegan, J. 2000. Climatic and human influences on fire regimes in ponderosa pine forests in the Colorado Front Range. *Ecol. Appl.* **10**: 1178–1195.