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Title: Stand dynamics and topographic setting influence changes in live tree biomass over a 34-year permanent plot record in a subalpine forest in the Colorado Front Range

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ABSTRACT:

Climate-induced increases in tree mortality are reported for many forests worldwide. Understanding the potential effects on carbon pools requires long-term monitoring of changes in forest biomass. We measured above-ground biomass of living trees (AGB) over a 34 year period (1982-2016) in permanent plots spanning a range of forest stand ages, species compositions, and topographic settings in a subalpine forest in the Colorado Front Range. Stand-level and species-level AGB varied spatially and temporally in relation to stand age, successional processes and site moisture classification. Young (c. 122 years) postfire stands composed of lodgepole pine had lower average AGB than older (> 250 years) mixed-species stands. Mesic stands had higher AGB than xeric or hydric stands of similar age. At the level of individual species, significant shifts in AGB among species were primarily explained by successional replacement of shade-intolerant pines by shade-tolerant Engelmann spruce and subalpine fir. The permanent plot network recorded significant shifts in species dominance and tree densities from 1982-2016 reflecting successional patterns developing over several centuries as well as the effects of recent localized windthrow, insects, and pathogens. Despite increases in tree mortality, there was a general pattern of increasing AGB across the forest.

Keywords: Forest biomass, subalpine forests, permanent plots, forest dynamics, Colorado Front Range.

INTRODUCTION

Recent increases in tree mortality, documented in forests worldwide, are likely to profoundly affect above-ground forest biomass and therefore carbon storage in forests (van Mantgem et al. 2009, Allen et al. 2010, Peng et al. 2011, Brando et al. 2013, Williams 2013). While rising atmospheric CO₂ concentrations may favor tree growth, warmer temperatures may also induce drought stress leading to reduced tree growth and increased tree mortality. These net effects of warmer temperatures on site-specific forest productivity have proven difficult to predict (Camarero et al. 2015, Girardin et al. 2016). Whether future forests act as sinks or sources of carbon will depend on the capacity of new tree recruitment and tree growth to compensate for losses of trees in the forest overstory (Hartmann et al. 2018). Research examining the response of forests to increasing overstory tree mortality is needed to determine the consequences for future species composition and forest structure, including possible declines in living tree biomass (Hartmann et al. 2015, Luyssaert and Cornelissen 2018).

High elevation forests in the Colorado Rocky Mountains reflect the effects of a warming climate. Research has documented earlier snowmelt and warmer, drier summers in the subalpine zone of the Colorado Front Range (CFR) (Clow 2010, McGuire et al. 2012, Kittel et al. 2015, Smith et al. 2015), a phenomenon also observed across the U.S. West (Stewart 2005, Pederson et al. 2011). Previous research conducted in subalpine forests of the CFR has linked these trends of earlier snowmelt and warmer, drier summers to decreased primary productivity and increases in tree mortality rates (Hu et al. 2010, Smith et al. 2015). Furthermore, radial tree growth and seedling establishment in many subalpine forest habitats in the CFR have been shown to be moisture limited and unfavorably influenced by warmer temperatures (Villalba et al. 1994, Moyes et al. 2015, Kueppers et al. 2016, Andrus et al. 2018). Thus, it is reasonable to expect that

subalpine forest biomass in the CFR may already be altered by response to the warming climate trend of the late 20th to early 21st centuries.

Climatic presses and climatic pulses (*sensu* Harris et al. 2018) are affecting forest dynamics in the CFR. The current trajectory towards warmer, drier conditions (a climatic “press”) is affecting tree mortality and recruitment dynamics in the subalpine forests of the Southern Rocky Mountains Ecoregion (Smith et al. 2015, Conlisk et al. 2017, Andrus et al. 2018). Likewise, relatively discrete extreme climatic events (“pulses”) such as windstorms (Veblen et al. 1991, Wohl 2013), droughts (Bigler et al. 2007), wildfires (Schoennagel et al. 2007), and climatically-induced outbreaks of bark beetles (Chapman et al. 2012, Hart et al. 2014) are well-documented sources of pulsed increases in tree mortality in subalpine forests throughout the Southern Rocky Mountains Ecoregion. Substantial empirical evidence as well as modeling-based studies indicate that climatic presses and pulses are likely to significantly affect future biomass patterns of subalpine forests in the Southern Rocky Mountains Ecoregion (Temperli et al. 2015, Conlisk et al. 2017, Foster et al. 2018). However, assessment of the implications for carbon storage of climate-induced changes due to climatic presses and pulses requires better understanding of how above-ground biomass of living trees (AGB) in forests varies spatially in relation to abiotic site factors and temporally in response to stand dynamics and disturbance events.

In the subalpine forest zone of Colorado (encompassing much of the Southern Rocky Mountains Ecoregion) AGB of living trees (or a proxy for it such as total stemwood biomass) has been estimated in relatively few studies representing only a limited proportion of the variability in stand ages, species composition, and topographic settings (e.g. Aplet et al. 1989, Arthur and Fahey 1992, Binkley et al. 2003, Kueppers and Harte 2005). Site conditions related

93 to steep gradients of elevation and moisture availability over short distances have been
94 documented to strongly influence stand development patterns in subalpine forests in Colorado so
95 that site factors as well as stand age must be explicitly considered in examining spatial and
96 temporal variation in forest biomass (Peet 1981). Existing studies in subalpine forests in
97 Colorado provide a wide range of estimates of AGB. For example, estimates from 18 old (> 200
98 years) stands of Engelmann spruce (*Picea engelmannii* Parry ex Engelmann) and subalpine fir
99 (*Abies lasiocarpa* (Hook.) Nutt.) yielded a range from 130 to 488 Mg/ha (Binkley et al. 2003),
100 but did not reveal clear relationships of AGB to potential drivers such as stand age and
101 topographic setting. Lower mean AGB is commonly reported for stands composed of lodgepole
102 pine (*Pinus contorta* Douglas ex Loudon var. *latifolia*) mixed with Engelmann spruce and
103 subalpine fir than old spruce-fir forests (Arthur and Fahey 1992, Kueppers and Hart 2005,
104 Bradford et al. 2008). However, existing data on AGB do not fully represent the variation in
105 species composition and topographic settings that define existing models of subalpine forest
106 community types and successional dynamics across elevation and topographic-moisture
107 gradients in Colorado (Peet 1981, Aplet et al. 1988, Rebertus et al. 1992, Donnegan and Rebertus
108 1999). While comparable studies examine long-term change in forest composition and structure
109 (Esser 2015, Bretfeld et. al. 2016), only a single study investigates changes in AGB over a multi-
110 decadal period (1984-2013) in subalpine forests in Colorado, and it focuses on Engelmann
111 spruce-subalpine fir stands affected by a severe spruce beetle outbreak in the early 2000s
112 (Derderian et al. 2016). Furthermore, the existing studies underrepresent the presence of young
113 (< 150 years) postfire stands, often dominated by lodgepole pine or limber pine (*Pinus flexilis*
114 James), which are common throughout the subalpine zone due to widespread fires in the second
115 half of the 19th century (Sibold and Veblen 2006).

The current study quantifies changes in AGB of living trees over a 34-year period (1982-2016) using ten permanent plots located across a topographically complex subalpine forest landscape. This research addresses the following questions: 1. How does stand-level biomass vary across a range of stand ages and topographic settings? 2. How have stand-level and species-specific biomass changes from 1982 to 2016 been influenced by successional processes?

METHODS

Study Area

Research was conducted at Niwot Ridge and nearby sites located in the Roosevelt National Forest and the City of Boulder Watershed properties on the eastern slope of the Colorado Front Range (40°3'20" N, 105°35' 22" W; Fig. 1). This area is characterized by a steep elevational gradient and thus a wide range of climatic conditions. Dominant tree species on Niwot Ridge and throughout the subalpine zone of the CFR are Engelmann spruce, subalpine fir, lodgepole pine, limber pine, and quaking aspen (*Populus tremuloides* Michx.) (Peet 1981; Veblen 1986). Niwot Ridge is a mid-latitude and high-elevation site in a continental location, and therefore experiences broad variations in diurnal and seasonal temperatures (McGuire et al. 2012). Average (1982 – 2016) annual temperature is 1.98 °C, with average monthly maximum temperatures of 20.0 °C peaking in July and average monthly minimum temperatures reaching a low of -11.4 °C in January (Climate Station C-1 at 3048 m; McGuire et al. 2012). Over the period of 1989-2008, July maximum and minimum temperatures have increased (2 °C and 1.5 °C per decade, respectively) (McGuire et al. 2012). At these high elevations, precipitation occurs primarily as snow from November – April. Average annual precipitation is 705 mm (C-1 Climate Data, 1982-2016; <http://niwot.colorado.edu/data/climate/c1-meteorological-data>). Between 1952 and 2010 precipitation declined during warm-season months of May through

September (C-1 Climate Data; Kittel et al. 2015). Thus, since the mid-20th century the climate of the study area has become warmer and drier during the summer growing season.

Between 1982 and 1986, ten large permanent forest inventory plots were installed across a range of subalpine stand types and topographic positions (Fig.1). Plots were established with the intent of including a wide range of stand ages and positions across elevation and topographic-moisture gradients (*sensu* Peet 1981) while avoiding areas that had been logged (Veblen 1986). Six plots were installed in 1982, one in 1983, and three in 1986 (Table 1). During plot installation, all live trees > 4 cm diameter at breast height (1.37 m; dbh) were permanently tagged, identified by species, and dbh was recorded. Plot size was adjusted according to stand density in order to capture a minimum of 215 live trees (Table 1). We classified site moisture as xeric, mesic, or hydric as inferred from slope steepness, slope aspect (south-facing being the driest), slope curvature, and percentage of surface occupied by rocks (Villalba et al. 1994; Table 1). For most plots, the site moisture classification (Table 1) was verified by tree radial growth responses to interannual climatic variability (e.g. wet and cool years are favorable for tree radial growth at xeric sites and the reverse for hydric sites; Villalba et al. 1994) and by soil moisture measurements during late summer (R. Andrus unpublished data). The successional states of the stands as derived from tree age structures (Veblen 1986; unpublished data) are: 1) young (c. 122 years) postfire stands of almost exclusively lodgepole pine (plots MRS1, 8, 9, and 10); 2) old seral postfire stands of Engelmann spruce and subalpine fir intermixed with lodgepole pine and limber pine (plots BW2, BW3, MRS4, MRS7); and 3) pure old (> 460 years) stands of Engelmann spruce and subalpine fir, considered to be in compositional equilibrium (*sensu* Veblen 1992; plots MRS5 and BL6).

Although bark beetle activity in surrounding areas of the Front Range increased starting

in the mid-1990s (Chapman et al. 2012), bark beetle-caused tree mortality was minimal in the permanent plots prior to 2008 (Smith et al. 2015). Bark beetles affecting the permanent plots since 2008 include: the mountain pine beetle (MPB, *Dendroctonus ponderosae*) in lodgepole pine and limber pine; spruce bark beetle (SBB, *Dendroctonus rufipennis*) in Engelmann spruce; and western balsam bark beetle (WBBB, *Dryocoetes confusus*) in subalpine fir. During a census of tree mortality conducted in 2007, only one tree was observed to have been killed by MPB and two others were under attack, whereas in the 2010 and 2013 mortality censuses c. 0.5% and 1.2%, respectively, were killed by bark beetles of different types (mostly WBBB) and by root rot (*Armillaria* spp.) The complex of attack by WBBB, *Armillaria* root rot, and other fungi, together known as “subalpine fir decline” (SFD), is a widespread cause of mortality for subalpine fir in Colorado associated with lower vigor trees and warmer, drier climatic conditions (Reich et al. 2016).

Field Methods

Permanent Plot Remeasurement: Following the protocol used during initial plot installations (Veblen 1986), we conducted a complete re-census of all ten permanent plots in summer 2016. To calculate basal area increment and biomass of living trees, dbh of all live trees > 4 cm dbh were measured in 2016. This included stems that grew from seedlings or saplings into the tree size class and the diameter growth of trees tagged and measured at the dates of initial plot installation (Table 1). In addition to measuring dbh of all trees, in each plot we also measured height using a laser rangefinder for a subset of 25 to 88 trees (> 20 trees per species) stratified across the full range of tree diameters for the one to four tree species present within each plot.

A mortality census of newly dead trees (i.e. trees that had died since the previous census) was conducted for each plot at three-year intervals from plot installation until 1994 (i.e. 1985,

185 1988, 1991, and 1994), and then again in 2007, 2010, and 2013 (Smith et al. 2015). For the
186 current study, mortality was again measured in 2016 and we recorded evidence of mortality
187 agents (e.g. wind damage, insects, SFD). In the current study, tree mortality data are not
188 reported because they cover only an additional three-year period from the previous report on
189 mortality (Smith et al. 2015) but the observations of tree mortality cause (wind, insects) are used
190 in interpreting patterns of biomass changes. Annual examinations of all the plots revealed only
191 two noteworthy disturbance events since the date of plot installation. Some of the tallest trees in
192 stand MRS4 were windthrown by a series of winter storms in 2011-12 which caused widespread
193 treefalls in the northern Front Range (Wohl 2013). SFD caused sharp increases in the numbers
194 of dead subalpine fir in stand BL6, with minor effects in other stands.

195 **Biomass estimation and data analysis**

196 *Estimating live above-ground biomass:* Allometric equations for predicting AGB from tree dbh
197 and height were available for four of the five subalpine tree species present in the permanent
198 plots (Supplement Table S1). To calculate biomass of limber pine, for which published
199 allometric equations were not available, we used equations for the morphologically similar
200 southwestern white pine (*Pinus strobiformis* Engelm.) (Vargas-Larreta et al 2017). Because we
201 collected tree height data for only a subset of trees in each plot, we first used a semi-logarithmic
202 regression to estimate non-measured tree heights from dbh, as well as tree heights at time of plot
203 establishment, for each species in each plot (Supplement A Table S2 and Fig. S1). To compute
204 total above-ground tree biomass in megagrams per hectare (Mg/ha), we used dbh and height
205 estimates with species-specific allometric equations for each species in each plot for all live trees
206 (≥ 4 cm dbh) in 1982 and 2016 (Supplement Table S3). Biomass estimates in 2016 accounted for
207 recruitment of trees into the ≥ 4 cm dbh tree size class, growth of previously surveyed trees, and

loss of trees due to tree mortality. For all species, allometric equations were used to first estimate the biomass of the stemwood, bark, foliage, and branch components from dbh and height and then summed to obtain total biomass (Supplement Table S1). Due to the low numbers of quaking aspen, the biomass is not reported. The uncertainty of biomass estimation due to errors in the biomass equations and due to height allometry was quantified using a Monte Carlo approach following Chave et al. (2004) and Yanai et al. (2010) (Supplement Table S5).

Stand-level AGB values were compared graphically according to stand age and site moisture status. We also tested the relationships of stand age (old vs young) and site moisture classification (mesic vs xeric) with biomass values (AGB in 2016) using intraclass correlation coefficients - an indicator of the strength of the relationship between a categorical predictor and a continuous response variable - and a two-way ANOVA. Because the hydric stand MRS5 was the only stand in that site moisture class, it was not included in the statistical analysis.

RESULTS

Variability in Above-ground Biomass across Sites and Stand Ages

The ten permanent plots exhibited large differences in live tree above-ground biomass (AGB) (Fig. 2). The stand-level AGB in 2016 varied from 165 to 214 Mg/ha for the four young postfire stands and from 136 to 322 Mg/ha for the six older stands. On average, the four young postfire lodgepole pine stands had lower mean AGBs than the older stands including spruce and fir (means of 185 and 214 Mg/ha; Fig. 2). AGB in these young postfire stands also varied by site moisture classification. The less xeric young postfire stand (MRS8) had the highest biomass when compared to the other three young postfire stands (Fig. 2). We found marked differences in AGB for stands located adjacent to one another but in contrasting topographic settings. For example, the xeric stand BW2 located on a rocky morainal ridge had a substantially lower AGB

than that of BW3 in an adjacent area of low lying, concave topography despite both having originated from the same fire in c. 1748 (Figs. 2). Analogously, MRS4 and MRS7 are similarly-aged old postfire stands of pines mixed with more abundant Engelmann spruce and subalpine fir, but the xeric stand MRS7 had a much lower AGB than the mesic stand MRS4 (Fig. 2). The bog forest at MRS5, despite being the oldest stand, had one of the lowest AGB among the six older stands and contained large water-logged surfaces lacking any tree cover. In contrast, the mesic BL6 plot on a well-drained but mesic site had a higher stand density and total AGB than MRS5 (Fig. 2).

After excluding the hydric stand MRS5 to allow statistical comparison of the stands in groups of old vs. young and mesic vs. xeric site moisture conditions, we determined that AGB differed among groups. Median AGB in 2016 was greater in old stands (216 Mg/ha) than young stands (184 Mg/ha) and in mesic stands (241 Mg/ha) than xeric stands (178 Mg/ha. Site moisture status had a stronger influence on AGB than stand age as indicated by intraclass correlation coefficients of 0.69 and -0.06, respectively (Fig. S2). Two-way ANOVA showed a similar trend, where statistical significance ($F^{2,6} = 5.33$, $p = 0.047$) was primarily due to the differences between site moisture classes ($p = 0.024$). Plots showed less variation in AGB due to stand age ($p = 0.39$).

Changes in Above-ground Biomass from 1982 to 2016

In eight of the ten permanent plots, AGB increased from 1982 to 2016 (Fig. 3). For the young lodgepole pine-dominated stands (MRS1, MRS8, MRS9, MRS10), stand-level AGB increased 15 to 21% between 1982 and 2016 (Fig. 3). These young postfire stands exhibited 4 to 20% (Supplement Table S3) declines in trees per hectare from 1982 to 2016, yet consistently increased in biomass. Most tree mortality was unrelated to insect activity; insect attack

accounted for less than 1% of the total mortality from 1982 to 2016 in the young postfire stands. The number of trees in the smallest size classes declined, increasing the proportion of trees in the largest two size classes (Fig. 4a). Four of the older stands exhibited increases in AGB whereas two showed declines in AGB (Fig. 3). The two sites with the greatest increases in AGB were the mesic stand BW3 and the hydric stand MRS5 which increased by 12.9% and 18.0%, respectively. The increases in AGB in xeric stands BW2 and MRS7 were $\leq 10\%$. Stands MRS4 and BL6 experienced declines in AGB of 1.7% and 8.2%, respectively (Fig. 3).

Changes in AGB for individual species in the six older stands (Fig. 5) reflect trends in replacement of shade-intolerant pines by the more shade-tolerant Engelmann spruce and subalpine fir. In stand BW2, the number of limber pines in the intermediate and small size classes declined, while the abundance and biomass of shade-tolerant Engelmann spruce and subalpine fir increased (Figs. 4b, 5; Supplement Table S3). In the adjacent stand BW3 of similar age (c. 270 years) the increases in abundance and size of Engelmann spruce and growth of lodgepole pine into the > 30 cm dbh class offset declines in number of lodgepole pine in the smaller size classes (Fig. 4b; Supplement Table S3). In stand BW3, subalpine fir experienced a modest decline in abundance and AGB. In this stand, moderate to large-sized (> 30 cm dbh) lodgepole pine increased in abundance, and therefore exhibited the highest increase in AGB (Figs. 4b and 5). In stand MRS4 the more shade-tolerant Engelmann spruce and subalpine fir increased in abundance especially in the moderate and larger size classes whereas lodgepole pine declined in most size classes and disappeared from the smallest size class (Fig. 4b). Although biomass of Engelmann spruce and subalpine fir increased in stand MRS4, total AGB for the entire stand declined, reflecting a 24% decline for lodgepole pine from 1982 to 2016 (Figs. 3 and 5). In MRS7, Engelmann spruce and subalpine fir increased in biomass while the small

277 populations of lodgepole pine and limber pine declined in abundance and biomass (Figs. 4b and
278 5; Supplement Table S3).

279 The two older spruce-fir stands lacking any pines (MRS5 and BL6) had similar size class
280 distributions to one another, indicating a continuous pattern of recruitment into all size classes
281 (Fig. 4c). However, total AGB of the hydric site MRS5 increased whereas that of BL6 declined
282 (Fig. 3). There was a substantial decline in the abundance and biomass of subalpine fir in BL6 as
283 compared to increases in MRS5 (Fig. 4c; Supplement Table S3).

284 DISCUSSION

285 Site and stand-level variability of biomass across the subalpine forest zone

287 In the current study, the observed patterns strongly suggest that stand-level AGB in
288 subalpine forests in the CFR varied by stand age and site moisture classification, although the
289 small sample sizes precluded demonstration of statistically robust patterns. Given that AGB
290 ranged from 165 to 214 Mg/ha in the four young postfire stands and that the only stand to attain
291 $\text{AGB} > 300 \text{ Mg/ha}$ is older than 270 years, attainment of high biomass requires greater stand age.
292 Variability in site moisture classification associated with topographic setting also strongly
293 influenced stand biomass. Among the six older stands, the highest AGB occurred at a mesic site
294 whereas lower AGB was associated with xeric and hydric moisture status. Despite a small
295 number of observations, the two-way ANOVA indicated nearly significant relationships of AGB
296 with stand age and site moisture status ($p = 0.047$). Mesic and old stands have higher median
297 AGB with a stronger relationship for site moisture classification compared to stand age. In
298 addition, the recent tree mortality caused by subalpine fir decline in BL6 reduced AGB in that
299 stand which otherwise would have contributed to a stronger relationship of AGB to site moisture
300 status and stand age.

The variability in AGB found in the current study for stands in different topographic settings is consistent with large differences in tree basal areas previously reported for different community types associated with elevation and topographic-moisture gradients in subalpine forests in Colorado (Peet 1981). Our results imply that drivers of spatial variability of AGB across larger areas of subalpine forests require stratification of study areas by community and topographic setting. Similarly, the lower mean AGB for young (e.g., c. 122 years old) post-fire stands versus the higher mean for stands older than c. 250 years implies that broader scale estimates of AGB also be stratified according to time since last stand-replacing fire. Improved understanding of spatial variation in AGB across the complex subalpine forest landscape could be enhanced by combining approaches based on remotely sensed data of biomass loads in relation to complex terrain (e.g. Swetnam et al. 2017) with field-based mapping of time-since last stand-replacing fire (e.g. Sibold and Veblen 2006). Furthermore, existing and additional field-based measurements such as those in the current study are needed for verification of remotely sensed estimates of AGB in subalpine forests in complex terrain and varying disturbance histories.

Changes in Above-ground Biomass over a 34-Year Period

Eight of the ten permanent plots remeasured in the current study exhibited small to moderate increases in stand-level AGB over the 1982-2016 period. The overall trend towards increased live biomass in these stands has occurred despite rising tree mortality rates since c. 2008 in the same permanent plots (Smith et al. 2015; Chai 2017). Thus, a recent trend of increasing tree mortality appears to be compensated for by increases in growth of the residual trees.

Increased biomass accumulation was observed in both young (c. 122 years old) and old (250 to > 550 years old) stands. In the four young postfire lodgepole pine stands AGB increased from 1982 to 2016 as intermediate-sized stems grew into the larger sizes classes and the live tree component of these stands continued to accumulate biomass. As expected for young stands in a stem-exclusion stage (*sensu* Oliver and Larson 1996), there was a decline in numbers of trees in the smallest size classes and a general shift towards larger maximum tree sizes that accounted for increased biomass. Among the six older stands, four stands exhibited increases in AGB while two declined in AGB. The declines in stand-level AGB were clearly associated with disturbance by a windstorm which affected stand MRS4 and the recent subalpine fir mortality from SFD in stand BL6. The other four old stands (BW2, BW3, MRS7, MRS5) exhibited small to moderate (up to 18%) increases in AGB from 1982 to 2016. The old stands with the highest increases in AGB were hydric and mesic sites (MRS5 and BW3) where the recent trend towards warmer and drier climate is less limiting for tree growth (Villalba et al. 1994). Thus, during the past several decades of a warming and drying climate on Niwot Ridge, the most favorable conditions for increased AGB are associated with mesic and hydric sites.

The changes in biomass observed over a 34-year period in the current study are compatible with the multidimensional framework proposed by Peet (1981) for characterizing longer-term forest development patterns in the CFR. For example, the increase in biomass observed in the young post-fire stands is consistent with the increasing trend in basal area and biomass postulated for Peet's (1981) stages 2 and 3 of development of lodgepole pine-dominated stands. Similarly, the sharp decline in biomass of stand BL6, a stand with a steady-state tree size distribution on a favorable mesic site, is consistent with the wide fluctuations in biomass as large trees become susceptible to fungal infection and insect attack in Peet's (1981) scheme.

However, testing of expected long-term trends in biomass was not feasible because our study was not designed as a chronosequence study and a 34-year period is too short for identifying trends over tree life spans of > 400 years. Nevertheless, our findings reinforce Peet's (1981) recommendation that studies of forest biomass must consider the influences of both site and successional conditions.

Although measurement of total carbon flux was not performed in the present study, the dominance of the living tree component in carbon pools and carbon fluxes in similar subalpine forests in Colorado (Kueppers and Harte 2005) implies that the increases in AGB of the living trees also increases carbon accumulation. The continued increases in plot-level AGB for old stands from 1982 to 2016 in the current study, as well as flux tower measurements of carbon fluxes in the surrounding forest from 1999 to 2012 (Hu et al. 2010), indicate that at a landscape scale these forests have been a carbon sink over the past several decades. Similarly, the results of the current study are consistent with a comprehensive literature review demonstrating that old forests can continue to accumulate carbon (i.e. function as carbon sinks; Luyssaert 2008). However, identifying the expected limits on the ability of old forests to accumulate more carbon was not an objective of the current study and clearly needs more research. Relevant to that research need, our study implies that local-scale topographic differences through their impacts on tree growth and biomass increment should be considered in assessing broader-scale forest carbon flux.

Over the 34-year census period, species-specific changes in biomass were largely explained by successional patterns of stand development and differential susceptibilities to stand-level disturbance events. The observed changes in size class frequency distributions for individual tree species were consistent with interpretations and predictions based on previously

collected tree population age structures (Veblen 1986) and Peet's (1981) general framework for describing forest development patterns in the CFR. In the four old postfire seral stands and two old spruce-fir stands, the shade-tolerant Engelmann spruce and subalpine fir were represented by abundant small trees and successively fewer trees in the larger size classes which is indicative of continuous recruitment into the main canopy. In contrast, limber pine and lodgepole pine exhibited declines in the numbers of trees in the smallest size classes. For these shade-intolerant species, this finding is consistent with their successional status when growing in stands mixed with the shade-tolerant species (Peet 1981, Veblen 1986). Thus, for the four, old seral postfire stands there was a consistent trend towards increased AGB for the shade-tolerant species. Although the numbers of lodgepole and limber pines in smaller size classes generally declined across all stands, the net change in AGB for the shade-intolerant pines was more variable reflecting differences among sites in overall size structures and rates of stand development. The site-specific changes in forest structure documented in the current study are also consistent with the results of resampling of sites in 2013 that were first sampled in 1972-73 in nearby Rocky Mountain National Park (Esser 2015, Bretfield et al. 2016). Although plots in those studies were not exactly relocated due to lack of permanent marking, the changes in forest structure and composition are similar to those shown in the current study based on re-measuring permanent plots.

CONCLUSION

Estimates of tree biomass across a range of stand ages and topography in the CFR suggest that stand age and moisture limitations influence spatial patterns of stand-level above-ground biomass. Young (c. 122 years old) postfire stands of lodgepole pine averaged lower AGB than > 250-year-old stands of pines mixed with Engelmann spruce and subalpine fir or

pure stands of spruce-fir. Moisture limitations associated with topographic setting appeared to have a strong influence on stand-level AGB as reflected by high AGB at mesic sites and lower AGB at the more extreme xeric or hydric sites.

Substantial shifts in tree size structure distributions and AGB among species were observed between 1982 and 2016 and were primarily driven by successional replacement of shade-intolerant pines by shade-tolerant Engelmann spruce and subalpine fir. Stand-level AGB generally increased from 1982 to 2016 except in stands affected by recent (post-2010) disturbances (i.e., windstorms, insects and fungal pathogens). Despite a documented trend of rising tree mortality rates in the plots since 2008, continued increases in AGB suggest that mortality losses have been compensated for by growth of the residual trees. At the stand-level, during the 1982 to 2016 measurement period, the living tree component of these stands continued to accumulate carbon.

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TABLES

584 Table 1. Descriptors of the ten permanent plots based on stand measurements in 2016.

Plot	Year installed	Plot size (m ²)	Initial tree density (stems ha ⁻¹)	Tree density in 2016 (stems ha ⁻¹)	Live basal area (m ² ha ⁻¹) in 2016	Oldest Tree (yrs.)	Elev. (m)	Asp.	Slope (%)	Site moisture classification
<i>Young postfire stands</i>										
MRS1	1982	1134	7336	5758	59.79	122	2898	E	6	xeric
MRS8	1986	648	6111	5262	67.28	122	3023	NE	12	xeric
MRS9	1986	324	6635	5524	64.81	122	3091	SE	11	xeric
MRS10	1986	432	5949	5671	56.25	122	3090	SE	9	xeric
<i>Old postfire seral stands</i>										
BW2	1982	2592	1419	1373	41.24	267	2980	E	2	xeric
BW3	1982	810	3481	3222	87.41	257	2978	NE	3	mesic
MRS4	1982	1944	2644	2520	68.06	357	3171	S	7	mesic
MRS7	1983	2916	1700	1796	50.75	377	3255	S	14	xeric
<i>Old spruce-fir stands</i>										
MRS5	1982	2916	1450	1522	52.81	556	3284	S	4	hydric
BL6	1982	1944	2124	1805	56.33	464	3219	NE	4	mesic

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FIGURE LEGENDS

Fig.1: Map of the Niwot Ridge study area in Colorado showing the location of permanent plots (triangles) and the C-1 climate station (circle).

Fig. 2: Above-ground biomass (Mg/ha) in 2016 plotted against stand age. Color and symbol shape correlate to site moisture classification and forest type, respectively.

Fig. 3: Above-ground biomass (AGB) for each plot in 1982 and 2016 in megagrams per hectare (Mg/ha). An asterisk (*) was added for plots showing > 10% change in biomass from 1982 to 2016 to highlight the stands with the largest changes.

Fig 4: Numbers of trees in diameter at breast height (DBH in cm) classes in a) for the young postfire lodgepole pine stands; MRS1, MRS8, MRS9, MRS10. b) for each species in the old seral spruce, fir and pine stands; BW2, BW3, MRS4, MRS7. c) for each species in the old spruce-fir stands; MRS5, BL6. Bins are in increments of 5, starting at a dbh of 4. Plot sizes are given in Table 1.

Fig. 5. Above-ground biomass (AGB in Mg/ha) by species in each of the six old stands in 1982 and 2016. Species codes area as follows; ABLA: subalpine fir, PICO: lodgepole pine, PIEN: Engelmann spruce, PIFL: limber pine.

FIGURES

Fig. 1

Fig. 2

Fig. 3

618 Fig. 4

Fig. 5