NRC Research Press
ARTICLE

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

Rachel K. Chai, Robert A. Andrus, Kyle Rodman, Brian J. Harvey, and Thomas T. Veblen

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 aboveground biomass (AGB) of living trees over a 34-year period (1982–2016) in permanent plots with varying 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 (ca. 122 years) postfire stands composed of lodgepole pine (*Pinus contorta* var. *latifolia* Engelm. ex S. Watson) had lower mean 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 (*Picea engelmannii* Parry ex Engelm.) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.). The permanent plot network recorded significant shifts in species dominance and tree densities between 1982 and 2016, reflecting successional patterns developing over several centuries and 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.

Key words: forest biomass, subalpine forest, permanent plots, forest dynamics, Colorado Front Range.

Résumé : On rapporte une augmentation de la mortalité des arbres en lien avec le climat dans plusieurs forêts un peu partout dans le monde. Un suivi à long terme des changements dans la biomasse forestière est nécessaire pour comprendre les effets potentiels des réservoirs de carbone. Nous avons mesuré la biomasse aérienne (BA) des arbres vivants pendant une période de 34 ans (1982–2016) dans des placettes d'échantillonnage permanent représentatives d'une variété d'âges, de compositions en espèces et de configurations topographiques des peuplements forestiers dans une forêt subalpine située dans le Front Range du Colorado. La BA à l'échelle du peuplement et de l'espèce variait dans l'espace et dans le temps en relation avec l'âge du peuplement, les processus successionnels et la classification des stations basée sur l'humidité du sol. Les jeunes (∼122 ans) peuplements issus de feux et composés de pin tordu latifolié (*Pinus contorta* var. *latifolia* Engelm. ex S. Watson) avaient une BA plus faible que les peuplements mixtes plus vieux (>250 ans). Les peuplements établis sur des stations mésiques avaient une plus grande BA que les peuplements du même âge établis sur des stations xériques ou hydriques. À l'échelle de l'espèce, d'importantes variations interspécifiques de la BA s'expliquaient principalement par le remplacement successionnel des pins intolérants à l'ombre par l'épicéa d'Engelmann (*Picea engelmannii* Parry ex Engelm.) et le sapin subalpin (*Abies lasiocarpa* (Hook.) Nutt.), des essences tolérantes à l'ombre. Le réseau de placettes d'échantillonnage permanent a connu des variations importantes dans la dominance des espèces et la densité des arbres de 1982 à 2016. Ces variations reflètent des patrons successionnels évoluant sur plusieurs siècles ainsi que les effets récents et localisés des chablis, des insectes et des pathogènes. Malgré l'augmentation de la mortalité des arbres, la tendance générale allait dans le sens d'un accroissement de la BA à travers la forêt. [Traduit par la Rédaction]

Mots-clés : biomasse forestière, forêt subalpine, placettes d'échantillonnage permanent, dynamique forestière, Front Range du Colorado.

Introduction

Recent climate-induced increases in tree mortality have been documented in forests worldwide and are likely to profoundly affect aboveground forest biomass and, therefore, carbon storage (van Mantgem et al. 2009; Allen et al. 2010; Peng et al. 2011; Williams et al. 2013; Brando et al. 2014). Although rising atmospheric carbon dioxide (CO_2) 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 the increasing mortality of overstory trees 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).

Received 16 January 2019. Accepted 20 May 2019.

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High-elevation forests in the Rocky Mountains of Colorado, United States (USA), 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 western USA (Stewart et al. 2005; Pederson et al. 2011). Previous research conducted in subalpine forests of the CFR has linked these trends to decreased primary productivity and increases in the rates of tree mortality (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. 2017; Andrus et al. 2018). Thus, it is reasonable to expect that the biomass of the CFR subalpine forest may already be altered in 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 (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 (climatic pulses) such as windstorms (Veblen et al. 1991; Wohl 2013), droughts (Bigler et al. 2007), wildfires (Schoennagel et al. 2007), and climate-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 and 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 of climate-induced changes (due to climatic presses and pulses) on carbon storage requires better understanding of how aboveground biomass (AGB) of living trees in forests varies both 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 to steep gradients of elevation and moisture availability over short distances have been documented to strongly influence stand development patterns in subalpine forests in Colorado; therefore, site factors, as well as stand age, must be explicitly considered in examining spatial and temporal variation in forest biomass (Peet 1981). Existing studies in subalpine forests in Colorado provide a wide range of estimates of AGB. For example, estimates from 18 old (>200 years) stands of Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) yielded a range in AGB of 130 to 488 Mg·ha^{-1} (Binkley et al. 2003) but did not reveal clear relationships of AGB to potential drivers such as stand age and topographic setting. Lower mean AGB is commonly reported for stands composed of lodgepole pine (*Pinus contorta* var. *latifolia* Engelm. ex S. Watson) mixed with Engelmann spruce and subalpine fir than AGB reported for old spruce–fir forests (Arthur and Fahey 1992; Kueppers and Harte 2005; Bradford et al. 2008). However, existing AGB data do not fully represent the variation in species composition and topographic settings that define existing models of subalpine forest community types and successional dynamics across elevation and topographic-moisture gradients in Colorado (Peet 1981; Aplet et al. 1988; Rebertus et al. 1992; Donnegan and Rebertus 1999). Although comparable studies examined long-term change in forest composition and structure (Esser 2015; Bretfeld et al 2016), only a single study investigated changes in AGB over a multidecadal period (1984–2013) in subalpine forests in Colorado, and it focused on mixed-species stands of Engelmann spruce and subalpine fir affected by a severe outbreak of spruce bark beetle (*Dendroctonus rufipennis* (Kirby, 1837)) in the early 2000s (Derderian et al. 2016). Furthermore, the existing studies underrepresent the presence of young (<150 years) postfire stands, often dominated by lodgepole pine or limber pine (*Pinus flexilis* E. James), which are common throughout the subalpine zone because of widespread fires in the second 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 10 permanent plots located across a topographically complex subalpine forest landscape. This research addresses the following questions.

(*i*) How does stand-level biomass vary across a range of stand ages and topographic settings?

(*ii*) How have stand-level and species-specific biomass changes between 1982 and 2016 been influenced by successional processes?

Methods

Study area

Research was conducted in Colorado at the Niwot Ridge research station and nearby sites located in the Roosevelt National Forest and the city of Boulder watershed properties on the eastern slope of the CFR (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. The 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, high-elevation site in a continental location and therefore experiences broad variations in diurnal and seasonal temperatures (McGuire et al. 2012). The mean annual temperature is 1.98 °C, with mean monthly maximum temperatures of 20.0 °C peaking in July and mean monthly minimum temperatures reaching a low of −11.4 °C in January (data from C1 climate station at 3048 m above sea level, 1982–2016; McGuire et al. 2012). Over the period of 1989–2008, July maximum and minimum temperatures have increased (2 and 1.5 °C per decade, respectively; McGuire et al. 2012). At these high elevations, precipitation primarily occurs as snow from November to April. The mean annual precipitation is 705 mm (C1 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 (C1 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, 10 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 was installed in 1983, and three were installed in 1986 (Table 1). During plot installation, all live trees with diameter at breast height (DBH; breast height = 1.37 m) >4 cm were permanently tagged and identified by species, and DBH was recorded. Plot size was adjusted according to stand density 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, site moisture classification (Table 1)

Fig. 1. Map of the Niwot Ridge study area in Colorado, showing the location of permanent plots (triangles) and the C1 climate station (circle). BL, Brainard Lake; BW, Boulder watershed; MRS, mountain research station.

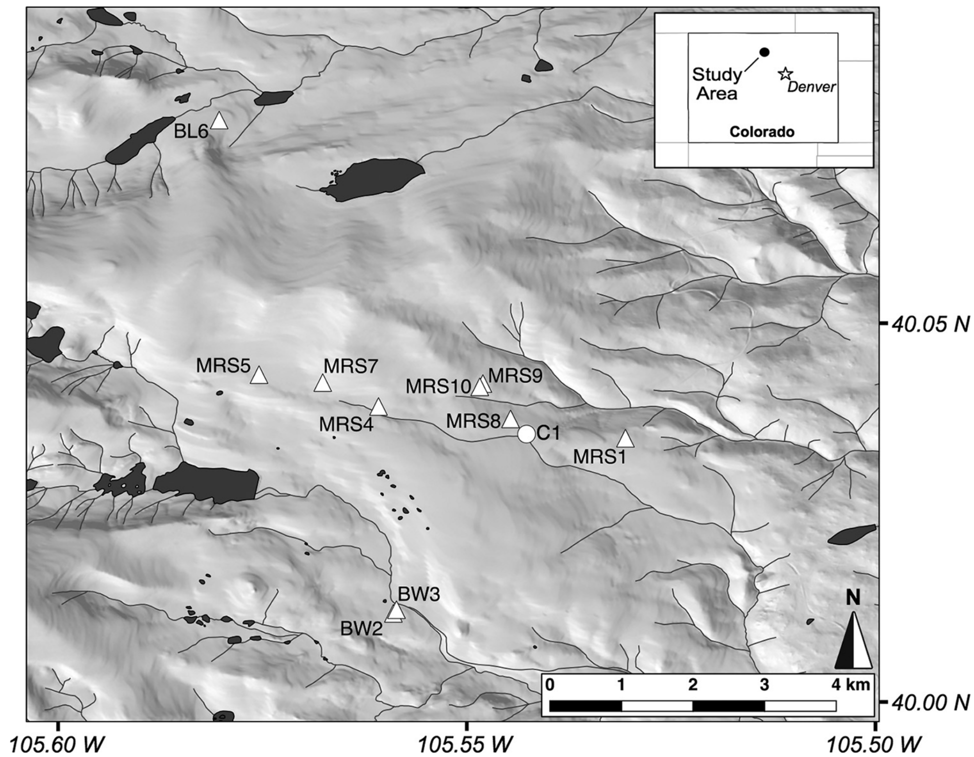


Table 1. Descriptors of the 10 permanent plots based on stand measurements in 2016.

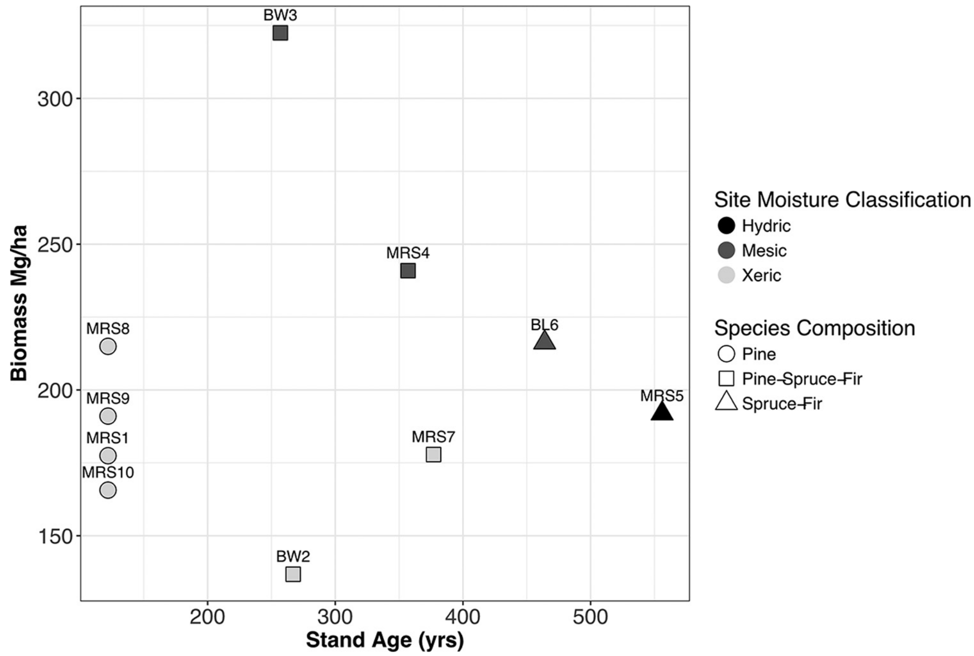
Plot	Year installed	Plot size (m²)	Initial tree density (stems·ha⁻¹)	Tree density in 2016 (stems·ha⁻¹)	Live basal area (m²·ha⁻¹)	Oldest tree (years)	Elevation (m)	Aspect	Slope (%)	Site moisture classification
Young postfire stands										
MRS1	1982	1134	7336	5758	59.79	122	2898	E	6	xeric
MRS8	1986	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
Old, seral postfire stands										
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
Old spruce–fir stands										
MRS5	1982	2916	1450	1522	52.81	556	3284	S	4	hydric
BL6	1982	1944	2124	1805	56.33	464	3219	NE	4	mesic

Note: MRS, mountain research station; BW, Boulder watershed; BL, Brainard Lake.

was verified by the responses of tree radial growth to interannual climatic variability (e.g., wet and cool years are favorable for tree radial growth at xeric sites, and dry and warm years are favorable for tree radial growth at hydric sites; Villalba et al. 1994) and by the measurements of soil moisture during late summer (R. Andrus, unpublished data). The successional states of the stands as derived from tree age structures (Veblen 1986; R. Andrus, unpublished data) are as follows (MRS, mountain research station; BW, Boulder watershed; BL, Brainard Lake): (*i*) young (ca. 122 years) postfire stands of almost exclusively lodgepole pine (plots MRS1, MRS8, MRS9, and MRS10); (*ii*) old, seral postfire stands of Engelmann spruce and subalpine fir intermixed with lodgepole pine and limber pine (plots BW2, BW3, MRS4, and MRS7); and (*iii*) 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), tree mortality caused by bark beetles was minimal in the 10 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* Hopkins, 1902) in lodgepole pine and limber pine, spruce bark beetle (SBB) in Engelmann spruce, and western balsam bark beetle (WBBB; *Dryocoetes confusus* Swaine, 1912) 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, ca. 0.5% and 1.2% of dead trees, 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 is known as "subalpine fir decline" (SFD) and is a widespread cause of mortality for sub-

Fig. 2. Aboveground biomass (AGB) in 2016 plotted against stand age. Color and symbol shape correlate to site moisture classification and forest type, respectively.



alpine fir in Colorado associated with trees of lower vigor 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 recensus of all 10 permanent plots during summer 2016. To calculate basal area increment and biomass of living trees, the DBH values of all live trees with DBH > 4 cm 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, we also measured height in each plot using a laser range finder for a subset of 25–88 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 3-year intervals from plot installation until 1994 (i.e., 1985, 1988, 1991, and 1994) and then again in 2007, 2010, and 2013 (Smith et al. 2015). For the current study, mortality was again measured in 2016, and we recorded evidence of mortality agents (e.g., wind damage, insects, and SFD). In the current study, tree-mortality data are not reported because they cover only an additional 3-year period from the previous report on mortality (Smith et al. 2015), but the observations of cause of tree mortality are used in interpreting patterns of biomass changes. Annual examinations of all the plots revealed only two noteworthy disturbance events since the date of plot installation: (*i*) some of the tallest trees in stand MRS4 were windthrown by a series of winter storms in 2011–2012 that caused widespread treefalls in the northern Front Range (Wohl 2013) and (*ii*) SFD caused sharp increases in the numbers of dead subalpine fir in stand BL6, with minor effects in other stands.

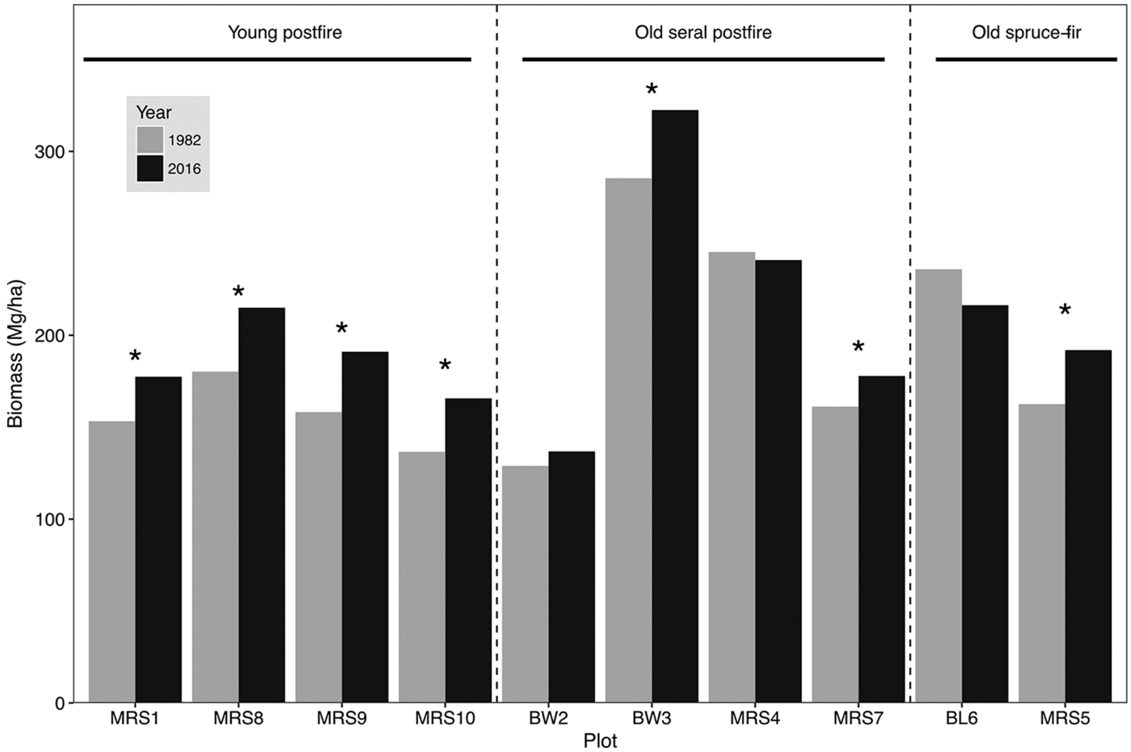
Live AGB estimation and data analysis

Allometric equations for predicting AGB from tree DBH and height were available for four of the five subalpine tree species present in the permanent plots (Ung et al. 2008; Supplementary Table S1[1]). To calculate biomass of limber pine, for which published allometric equations were not available, we used equations for the morphologically similar southwestern white pine (*Pinus strobiformis* Engelm.) (Vargas-Larreta et al 2017). Because we collected tree-height data for only a subset of trees in each plot, we first used a semilogarithmic regression to estimate nonmeasured tree heights from DBH, as well as tree heights at time of plot establishment, for each species in each plot (Supplementary Table S2[1] and Supplementary Fig. S1[1]). To compute total tree AGB in megagrams per hectare ($Mg \cdot ha^{-1}$), we used DBH and height estimates with species-specific allometric equations for each species in each plot for all live trees (DBH ≥ 4 cm) in 1982 and 2016 (Supplementary Table S3[1]). Biomass estimates in 2016 accounted for recruitment of trees into the tree size class of DBH ≥ 4 cm, growth of previously surveyed trees, and loss of trees due to tree mortality. For all species, allometric equations were used to estimate the biomasses of the stemwood, bark, foliage, and branch components from DBH and height, and these values were then summed to obtain total biomass (Supplementary Table S1[1]). The biomass of quaking aspen was not reported because of the low numbers of the species. The uncertainty of biomass estimation due to both height allometry and errors in the biomass equations was quantified using a Monte Carlo approach following Chave et al. (2004) and Yanai et al. (2010) (Supplementary Table S5[1]).

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 — indicators of the strength of the relationship between a categorical predictor and a continuous response variable — and a two-way analysis of variance (ANOVA). Because the hydric stand MRS5 was the only stand in that moisture class, it was not included in the statistical analysis.

[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2019-0023.

Fig. 3. Aboveground biomass (AGB) for each plot in 1982 and 2016. Asterisks (*) indicate plots that showed >10% change in biomass between 1982 and 2016.



Results

Variability in AGB across sites and stand ages

The 10 permanent plots exhibited large differences in live tree AGB (Fig. 2). The stand-level AGB in 2016 varied from 165 to 214 Mg·ha^{-1} for the four young postfire stands and from 136 to 322 Mg·ha^{-1} for the six older stands. On average, the four young postfire stands of lodgepole pine had lower mean AGBs than the older stands, including spruce–fir (means of 185 and 214 Mg·ha^{-1}, respectively; Fig. 2). AGB in the young postfire stands also varied by site moisture classification: the less xeric stand (MRS8) had the highest biomass when compared with the three other 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 ca. 1748 (Fig. 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 values among the six older stands and contained large water-logged surfaces lacking any tree cover. In contrast, the mesic stand BL6, on a well-drained but mesic site, had both higher stand density and higher 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, we determined that AGB differed among groups. Median AGB in 2016 was greater in old stands (216 Mg·ha^{-1}) than in young stands (184 Mg·ha^{-1}) and was also greater in mesic stands (241 Mg·ha^{-1}) than in xeric stands (178 Mg·ha^{-1}). AGB was more strongly influenced by site moisture status than by stand age, indicated by intraclass correlation coefficients of 0.69 and –0.06, respectively (Supplementary Fig. S2[1]). A two-way ANOVA showed a similar trend, in which 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 in terms of stand age (p = 0.39).

Changes in AGB over the period 1982–2016

In eight of the 10 permanent plots, AGB increased between 1982 and 2016 (Fig. 3). For the young stands dominated by lodgepole pine (MRS1, MRS8, MRS9, and MRS10), stand-level AGB increased 15%–21% between 1982 and 2016 (Fig. 3). These young postfire stands exhibited 4%–20% (Supplementary Table S3[1]) declines in trees per hectare between 1982 and 2016; however, they consistently increased in biomass. Most tree mortality was unrelated to insect activity; insect attack accounted for <1% of the total mortality between 1982 and 2016 for the young postfire stands. The number of trees in the smallest size classes declined over time, increasing the proportion of trees in the two largest size classes (Fig. 4*a*). Four of the older stands exhibited increases in AGB, whereas two of the older stands 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 the xeric stands BW2 and MRS7 were ≤10%. 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 BW2, the number of limber pines in the intermediate and small size classes declined, whereas the abundance and biomass of shade-tolerant Engelmann spruce and subalpine fir increased (Figs. 4*b* and 5; Supplementary Table S3[1]). In BW3, the adjacent, similarly aged (ca. 270 years) stand, the increases in abundance and size of Engelmann spruce and the growth of lodgepole pine into the class of DBH > 30 cm offset declines in the number of lodgepole pine in the smaller size classes (Fig. 4*b*; Supplementary

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

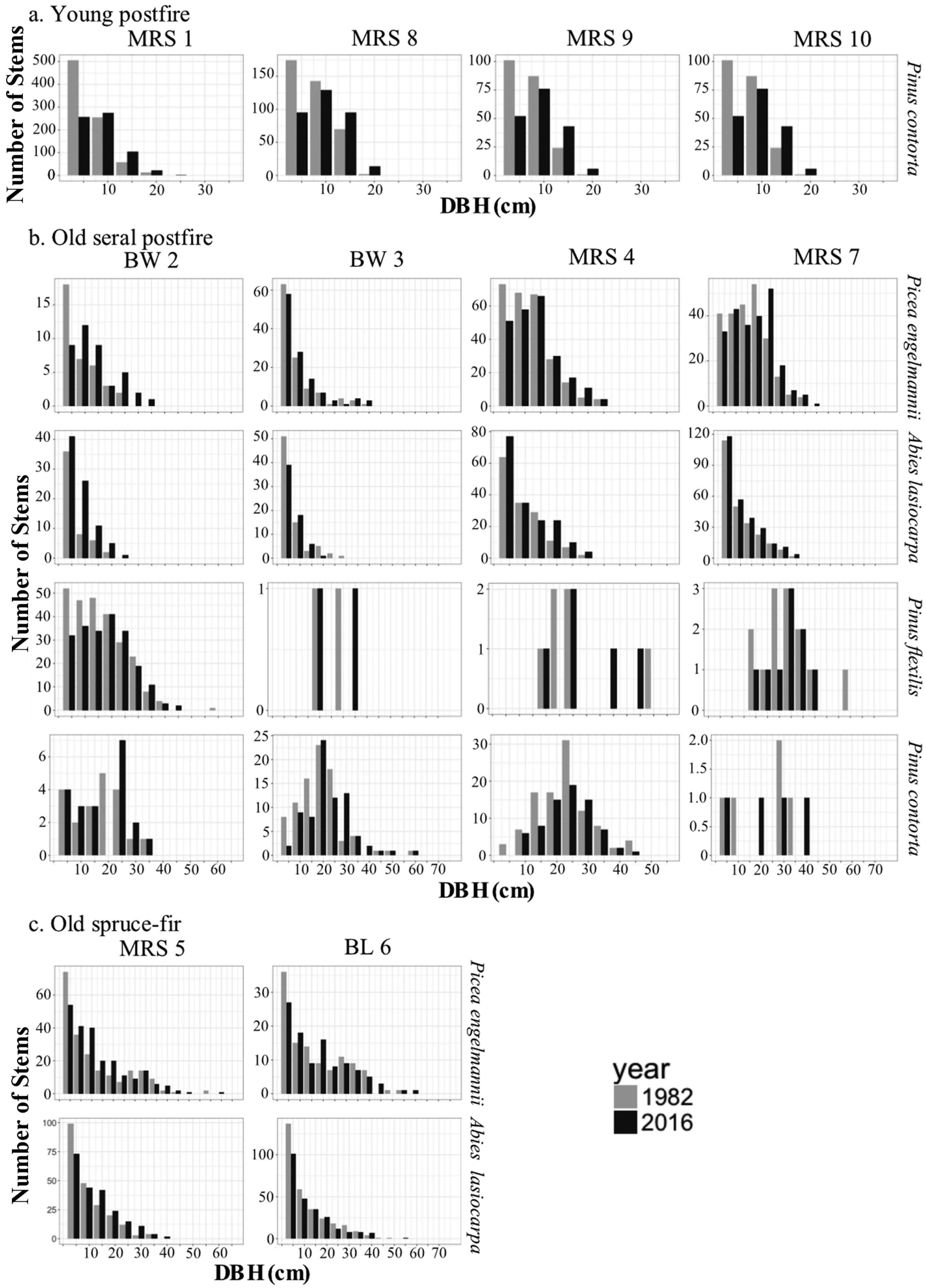
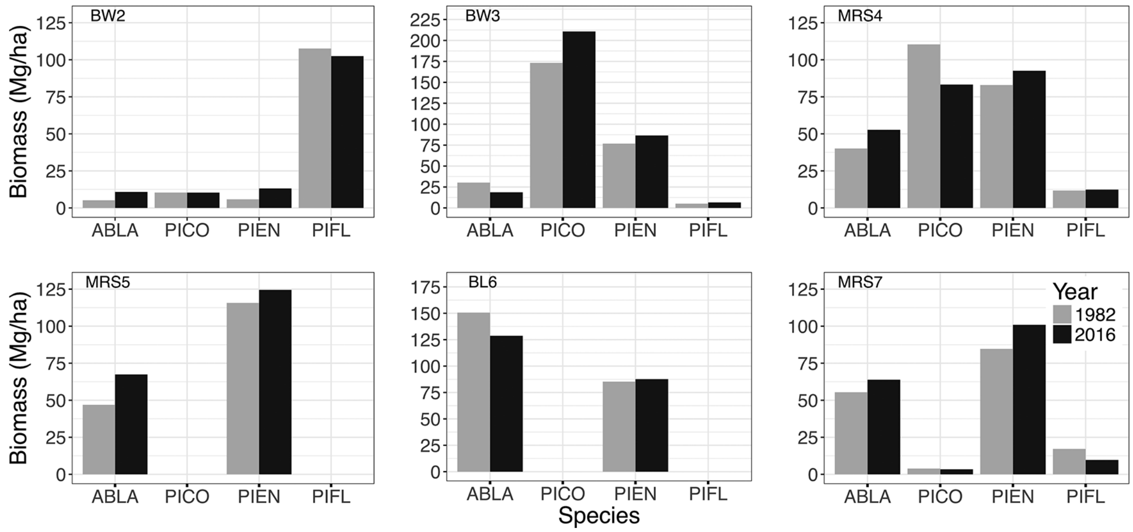


Table S3[1]). In BW3, subalpine fir experienced a modest decline in abundance and AGB. In this stand, moderate- to large-sized (DBH > 30 cm) lodgepole pine increased in abundance and therefore exhibited the highest increase in AGB (Figs. 4*b* and 5). In MRS4, the more shade-tolerant Engelmann spruce 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. 4*b*). Although

Fig. 5. Aboveground biomass (AGB) by species in each of the six old stands in 1982 and 2016. ABLA, subalpine fir; PICO, lodgepole pine; PIEN, Engelmann spruce; PIFL, limber pine.



the biomasses of Engelmann spruce and subalpine fir increased in MRS4, total AGB for the entire stand declined, reflecting a 24% decline in lodgepole pine between 1982 and 2016 (Figs. 3 and 5). In MRS7, the biomass of Engelmann spruce and subalpine fir increased, whereas the abundance and biomass of the small populations of lodgepole pine and limber pine declined (Figs. 4*b* and 5; Supplementary Table S3[1]).

The two older spruce–fir stands lacking any pines (MRS5 and BL6) had similar size class distributions to one another, indicating a continuous pattern of recruitment into all size classes (Fig. 4*c*). However, total AGB of the hydric stand MRS5 increased, whereas total AGB of BL6 declined (Fig. 3). There was a substantial decline in the abundance and biomass of subalpine fir in BL6 compared with increases in the abundance and biomass of subalpine fir in MRS5 (Fig. 4*c*; Supplementary Table S3[1]).

Discussion

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

In the current study, the observed patterns strongly suggest that stand-level AGB in subalpine forests of the CFR varied by stand age and site moisture classification; however, the small sample sizes precluded demonstration of statistically robust patterns. Given that AGB ranged from 165 to 214 Mg·ha^{-1} in the four young postfire stands and the only stand to reach AGB >300 Mg·ha^{-1} is over 270 years old, attainment of high biomass requires greater stand age. Variability in site moisture classification associated with topographic setting also strongly influenced stand biomass. Among the six older stands, the highest AGB occurred at a mesic site, whereas lower AGB was associated with xeric and hydric moisture status. Despite a small number of observations, the two-way ANOVA indicated nearly significant relationships of AGB with stand age and site moisture status (p = 0.047). Mesic and old stands have higher median AGB with a stronger relationship to site moisture classification than to stand age. In addition, the recent tree mortality caused by SFD in BL6 reduced AGB in that stand, which otherwise would have contributed to a stronger relationship of AGB to site moisture 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., ca. 122 years old) postfire stands vs. the higher mean for stands older than ca. 250 years implies that estimates of AGB on a broader scale should also be stratified according to time since the 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 the 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 with varying disturbance histories.

Changes in AGB over a 34-year period

Eight of the 10 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 rates of tree mortality since ca. 2008 in the same permanent plots (Smith et al. 2015; Chai 2017). Thus, increases in growth of the residual trees appear to compensate for the recent trend of increasing tree mortality.

Increased biomass accumulation was observed in both young (ca. 122 years old) and old (250 to >550 years old) stands. In the four young postfire stands dominated by lodgepole pine, AGB increased between 1982 and 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 the number 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 exhibited increases in AGB and two exhibited decreases in AGB. The declines in stand-level AGB were clearly associated with a windstorm disturbance that affected MRS4 and the recent SFD-related mortality of subalpine fir in BL6. The other four old stands (BW2, BW3, MRS7, and MRS5) exhibited small to moderate (up to 18%) increases in AGB between 1982 and 2016. The old stands with the highest increases in AGB were hydric and mesic sites (MRS5 and BW3) where the recent trend towards a warmer, 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 the 34-year period in the current study are compatible with the multidimensional framework proposed by Peet (1981) for characterizing forest development patterns in the CFR over a longer term. For example, the increase in biomass observed in the young postfire stands is consistent with the increasing trend in basal area and biomass postulated for Peet's (1981) stages 2 and 3 of development of stands dominated by lodgepole pine. Similarly, the sharp decline in biomass of BL6, a stand with a steady-state tree-size distribution on a favorable mesic site, is consistent with the wide fluctuations in biomass in Peet's (1981) scheme as large trees become susceptible to fungal infection and insect attack. 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 between 1982 and 2016 in the current study, as well as flux-tower measurements of carbon fluxes in the surrounding forest between 1999 and 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 et al. 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 forest carbon flux on a broader scale.

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, seral postfire 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, the shade-intolerant limber pine and lodgepole pine exhibited declines in the number of trees in the smallest size classes. 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 pine and limber pine 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 a 2013 resampling of sites that were first sampled in 1972–1973 in nearby Rocky Mountain National Park (Esser 2015; Bretfeld et al. 2016). Although plots in those studies were not exactly relocated because of a lack of permanent marking, the changes in forest structure and composition are similar to those shown in the current study based on remeasuring 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 AGB. On average, young (ca. 122 years old) postfire stands of lodgepole pine had lower AGB than both pure spruce–fir stands and >250-year-old stands of pines mixed with Engelmann spruce and subalpine fir. Moisture limitations associated with topographic setting appeared to have a strong influence on stand-level AGB, 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 over the 1982–2016 period, except in stands affected by recent (post-2010) disturbances (i.e., windstorms, insects, and fungal pathogens). Despite a documented trend of rising rates of tree mortality in the plots since 2008, continued increases in AGB suggest that the growth of residual trees has compensated for mortality losses. At the stand level during the 1982–2016 measurement period, the living tree component of these stands continued to accumulate carbon.

Acknowledgements

We thank Brandon Quick Bear, Logan Barrett, Alexandra Orrego, Evelyn Flamenco, Joao Fernandes, and Shala Wallace for their research assistance and P. Blanken and H. Barnard for their helpful comments on an earlier draft of the manuscript. This research was supported by National Science Foundation (NSF) Award No. 1262687, the Niwot Ridge Long-Term Ecological Research Project (NSF Award No. 1027341), and University of Colorado's Undergraduate Research Opportunities Program. We also thank Robert Peet, an anonymous reviewer, and an anonymous Associate Editor of the *Canadian Journal of Forest Research* for comments that improved the manuscript.

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