THESIS

ENGELMANN SPRUCE AND SUBALPINE FIR STAND DYNAMICS IN NORTH CENTRAL COLORADO

Submitted by

Drew Phillip Derderian

Department of Forest and Rangeland Stewardship

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Fort Collins, Colorado

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Master's Committee:

Advisor: Daniel Binkley

Mark Paschke
Monique Rocca

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ABSTRACT

ENGELMANN SPRUCE AND SUBALPINE FIR

STAND DYNAMICS IN NORTH CENTRAL COLORADO

Stemwood biomass and production were measured in a 600-year chronosequence of stands consisting of Engelmann spruce and subalpine fir in the Colorado Front Range. The stands were part of a chronosequence established and measured in 1984. The original chronosequence showed near-constant biomass of spruce after approximately 250 years of development. Spruce production also had remained nearly constant after an initial rise and fall during the first 250 years. Fir biomass decreased more than that of spruce after around 150 years. Fir biomass remained at lower consistent sub-dominate values through the end of the chronosequence. Fir's high production from early stand development decreased and remained constant after approximately 175 years of development. Changes over the most recent 29 years did not follow the patterns in the 1984 chronosequence: spruce biomass dropped by 70% with little change in fir biomass. This resulted in a 47% average decrease in total stand biomass since 1984. Stand biomass showed no relationship with stand age. Spruce beetle-kill appeared to have played a major role in live biomass decline in all stands. Net increment was negative in fir as increases in fir production were more than offset by fir mortality. The stands investigated have developed from post-fire initiation and, although there was no evidence of subsequent major disturbance in 1984, severe beetle infestation since then has altered expected trends in spruce-fir forest structure. Stand age pattern projections will likely continue to be altered by disturbances and changing disturbance regimes.

ACKNOWLEDGEMENTS

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INTRODUCTION

Tree biomass monitoring contributes valuable information toward predicting trends in the dynamics of a forest ecosystem. When divided into size classes and followed over time, tree biomass gives an indication of structure, productivity, fine-scale mortality, and the larger scale disturbance regimes of a forest stand. In forests that reach a steady-state quickly and in forests with frequent stand-replacing disturbance regimes, observing the development of stand structure can equip managers with an ability to predict biomass in similar forests over time. Changes in forest structure over longer periods of time are challenging to study. However, measurements of changing forest characteristics spatially can give indications of historical vegetation and help determine ecosystem patterns (Walker et al., 2010).

In stands of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) in the Colorado Front Range, direct observation of forest development is difficult as these ecosystems develop over centuries. An alternative is to use a chronosequence, a technique that uses space-for-time substitution to determine typical patterns of stand development (Walker et al., 2010). Greg Aplet and colleagues used the chronosequence approach in 1984 to examine forest structure and development in mixed stands of Engelmann spruce and subalpine fir that ranged in age from 175 to 700 years old (Aplet et al., 1988). These stands contributed to characterization of mixed-species dynamics and tested existing theories of community development of spruce-fir forests of the central Rockies (Aplet et al., 1989).

Insight into the development of the forest and pattern predictions, such as those provided by a chronosequence, can help to answer whether observed mortality is expected or outside of the range of variability experienced by these stands in the past. Identification of trends including

unexpected trajectories of change, can be useful in providing greater understanding of stand and disturbance dynamics and in facilitating best-practice management strategies. In Colorado, spruce-fir forests occupy approximately 20% of forested land (*Landfire vegetation data*, 2008) and continentally they range from central British Columbia and Alberta, Canada to Arizona and New Mexico, inhabiting subalpine zones (Alexander, 1984). Ecologically, spruce-fir forests are important as habitat for a wide range of species and, as the dominant forest-type in high-elevation areas, they source the greatest amount of water for streams and rivers from the Rocky Mountains. They are valued commercially for their wood production, particularly spruce, and provide prime recreation areas for skiing, camping and hiking. Finally, under the strains of climate change, forests have increased value in carbon storage. It is understandable that recent increases in mortality in Colorado Front Range spruce-fir stands, such as those recently observed (Colorado State Forest Service, 2013), can raise the concerns of forest managers and the public.

In the Aplet et al. (1988) chronosequence, stand data suggested that some trends were directly associated with certain characteristics in competitive advantage in each of the two species, influencing dominance at various stand ages. A combination of shade tolerance, longevity, reproductive traits, and other characteristics sustained dominance of both species in their high elevation communities. The authors examined how these characteristics shaped stand development, as reflected in biomass and productivity. Total stemwood biomass remained nearly constant across all stand ages, suggesting an ongoing equilibrium of biomass in the absence of disturbance (Figure 1).

Measurements of the youngest stands in the chronosequence suggested that fir biomass was greater than that of spruce for the first 150 years. Further development of the stands included declining fir biomass and increasing spruce biomass through the next 450 years. This

shift in species biomass dominance was attributed to the greater longevity of spruce, which can exceed 500 years of age (Oosting and Reed, 1952). Fir's shorter life span resulted in increased mortality around 150 to 300 years of age. Essentially, the largest fir stems died as the largest spruce continued to grow for centuries. After the establishing cohort of fir declined, fir biomass appeared to sustain a lower and nearly constant value through the end of the chronosequence.

Spruce biomass and production, about 200 years after colonizing fir mortality, showed only a slight decline as the second-generation fir began replenishing the overstory and colonizing cohorts of spruce began to die. But overall, the biomass trend appeared to support either behavior toward asymptotic biomass accumulation or towards "long-period" oscillation (Aplet et al.,1988). Since Baker's (1949) shade tolerance classification, shade tolerance indices have not greatly changed and both species are still considered tolerant. Spruce is considered slightly less so, with spruce seedlings and saplings requiring more light than the minimum needed for fir (Kobe and Coates, 1997). Thus, early in stand development, fir mortality promotes continued establishment and growth of spruce.

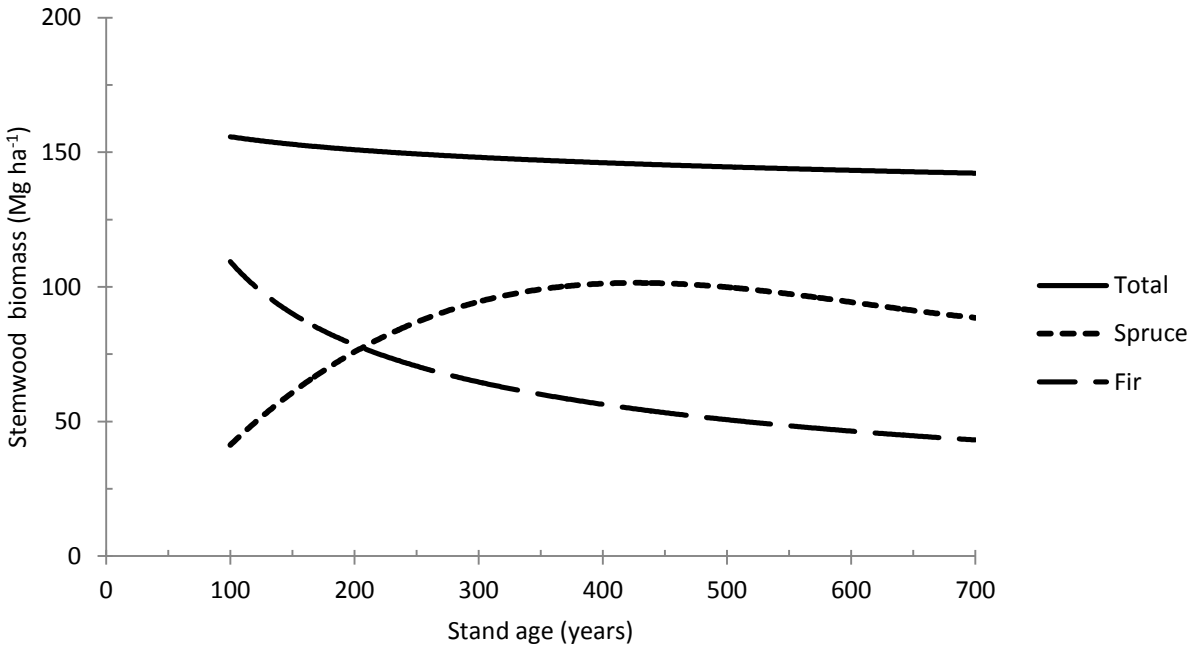


Figure 1: Moving average of the 1984 spruce-fir biomass chronosequence. Adapted from Aplet et al., 1989.

Trends apparent in any chronosequence might not reflect the actual trajectory manifested in individual stands of the past, and past trajectories may not reoccur in the future (for stands of any given age). In general, an increase in observed tree mortality above expectations suggests recent and unanticipated change in the forest structure. Fine-scale disturbances, such as gap dynamics, and the coarse-scale disturbances of insect infestations and blowdown may result in frequent and dynamic oscillations in stand development (Veblen et al., 1991). The stands selected by Aplet et al. (1988) may also have been unrepresentative of the broader landscape, if larger areas experienced substantial disturbance within a 600 year period. The spruce-fir stands studied by Aplet et al. in 1984 in the Colorado Front Range were resampled for this study. Two questions were addressed: (1) did the 29-year trajectory of individual stands follow the trend identified in the 1984 chronosequence? and (2) did the age pattern among stands in 2013 match

the pattern from 1984? Determinants for changes in stand development are described within the framework of recruitment, growth and mortality at various structural ages.

METHODS

The methods of the original chronosequence were described in detail for the first sampling (Aplet et al., 1988; 1989). For analysis here, diameters, core data, and status from the original studies were used in addition to new data. During 2013 data collection, all but one of the initial original stands were re-sampled for current diameters and live/dead status.

Study Area

Stands were located in the headwater watersheds of the Cache La Poudre River and Laramie River in Larimer County, Colorado (Figure 2). Stands were selected to have similar environmental conditions and to span more than five centuries since stand-replacing events (Table 1). The 8 study stand ages were determined by the age of the oldest individual, assumed to be among the colonizing cohort following stand-replacing fire. Elevations of all plots were between 3000 meters and 3200 meters, most on north-facing aspects. In 1984 stand compositions were > 95% spruce and fir, with minor amounts of lodgepole pine (*Pinus contorta*).

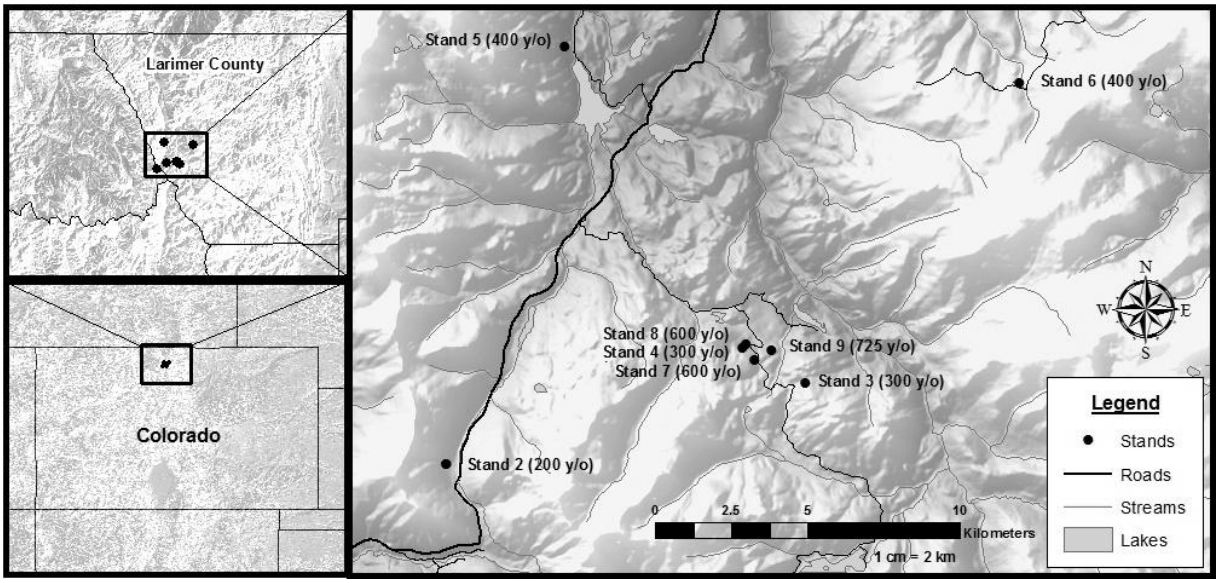


Figure 2: Map of study area and stand locations by age (years)

Data Collection

Stand ages, the time since each stand's post-disturbance initiation, were estimated based on ages of oldest trees in each plot. The youngest stand sampled in 1984 was not permanently marked and was not resampled in the present study. Stands were sampled with three subplots of either 0.05 or 0.1 ha. Diameter at breast height (dbh), species, and condition (live/dead) were recorded for living and dead trees > 5-cm dbh. Aplet et al. took a sub-sample of 33% of trees for age determination and measured height of two trees of each species per 5-cm dbh class.

Table 1: 2013 stand and plot details show the eight stands and their similar characteristics. Stands were selected in the same elevation range with mostly North-facing aspect. Adapted from Aplet et al., 1989.

Stand	Stand age in 2013 (years)	Aspect	Slope°	Elevation (m)
2	205	E	11	3150
3	305	NW	23	3250
4	305	N	25	3250
5	405	E	25	2900
6	405	NE	13	3150
7	605	NE	13	3200
8	605	NE	22	3150
9	730	NW	15	3150

Re-sampling of plots occurred during June and July of 2013, twenty-nine years after original data was gathered. Datasheets containing stand/plot identification, tree numbers, species, and 1984 dbh were used as references in the field. Most of the original trees were easily identified with their aluminum tags still attached. Plots were re-sampled for dbh of living trees and standing dead trees. New trees entering the > 5-cm dbh class were recorded by species and measured. Trees with missing tags were reliably identified based on size and location within plots. Small missing trees were assumed to have died and fallen.

Analysis

Data was entered and manipulated in Microsoft Excel©. Original raw heights and affiliated dbh measurements for spruce and fir in each stand were combined, testing stand dbh-height relationship. I used the relationship between dbh and height in 1984 to estimate heights based on dbh in 2013 using Curve Expert© to find logistic power regressions for each species. Spruce and fir heights and dbh were correlated ($n = 390$ $r^2 = 0.86$; $n = 307$ $r^2 = 0.88$). Dbh and height estimates from 1984 and 2013 were used to re-calculate 1984 standing stemwood volume and the new standing stemwood volume with equations from Myers and Edminster (1972). Stemwood volumes were converted to mass using spruce and fir densities of 368 kg m^{-3} and 433 kg m^{-3} (Wenger, 1984).

Stemwood production in 1984 was determined from 10-year growth increments on cores, and production between 1984 and 2013 was determined from changes in measured dbh (29-year average). Spruce, fir, and total live biomass sums were averaged for the three subplots in each stand, and extrapolated to a hectare scale. 2013 stemwood production values were calculated by summing 2013 fir, spruce, and total live stemwood biomass, subtracting 1984 values, and dividing the 29 years of growth to obtain yearly average gross increment.

Recent mortality was calculated as the average decrease in biomass based on the biomass of trees that died between 1984 and 2013. All trends over time were examined with curve-fitting routines in Curve Expert©. Regression analyses were used to determine the biomass and production age patterns. Paired t-tests were used to examine the differences in stand means of 1984 and 2013 with a significance set at ($p < 0.05$).

RESULTS

In 1984, average tree (> 5cm) density across all ages was approximately 950 fir/ha and 650 spruce/ha. In 2013, overall average density showed a slight decline in fir to 915/ha, and a very large decrease for spruce to 323/ha. Live tree stemwood biomass dropped from 155 Mg/ha to 82 Mg/ha (Table 2). Subalpine fir stemwood biomass remained nearly constant between 1984 and 2013 (non-significant change of -2 Mg/ha). Stand 2 showed very high fir mortality, with a 2/3 decline in fir biomass between 1984 and 2013 (Figure 4A). Spruce stemwood biomass declined by 70% (Table 2) from 1984 values, to an average of 31 Mg/ha (Figure 4B). Average forest structure as a result of this decline has 47% less live biomass than 1984 (Table 2).

The six graphs in Figure 3 show fir, spruce, and total trends in biomass identified in the 1984 chronosequence and linear regressions. No trends in stemwood biomass with stand age were significant, for either species and for either sampling date. However, average fir biomass in 2013 was similar to 1984, with little to no change, while spruce and total biomass declined. Spruce and total biomass trends showed similar slopes in relation to age, as they had in the past, but with a notable reduction in biomass across stand ages.

Gross stem increment between 1984 and 2013 demonstrated changes in both values and trends in the chronosequence (Figure 5). Production in spruce appeared to decline with stand age for both sampling periods, but fir production and total stand production showed no trend across stand ages. High mortality in combination with low recruitment (Appendix C) contributed to a 36% decrease in average spruce production ($t = 11.97$, $df = 4$, p-value < 0.001) across the chronosequence (Figure 5B). Fir's 87% increase in average production was non-significant (Table 2). Trends in total production across stands, driven by fir, also showed a rise by stand

age. The average production of individual surviving spruce trees increased 46%, but the average production of an individual fir was greater with an increase of 69% over the 29-year period of mortality.

Recent mortality did not correlate with stand age in spruce, fir, or total. Mortality between 1955 and 1984 was not determined, but a standing dead biomass analysis did show significant change from 1984 to 2013 in spruce and total. Net 29-year biomass increment (Figure 8) was calculated from the average production (Figure 5) and the average mortality (Figure 7). Fir showed a primarily neutral net increment. Spruce net increment across the chronosequence was negative, averaging -2,775 kg ha^{-1} $year^{-1}$. Net increment did not show correlation with age for either species.

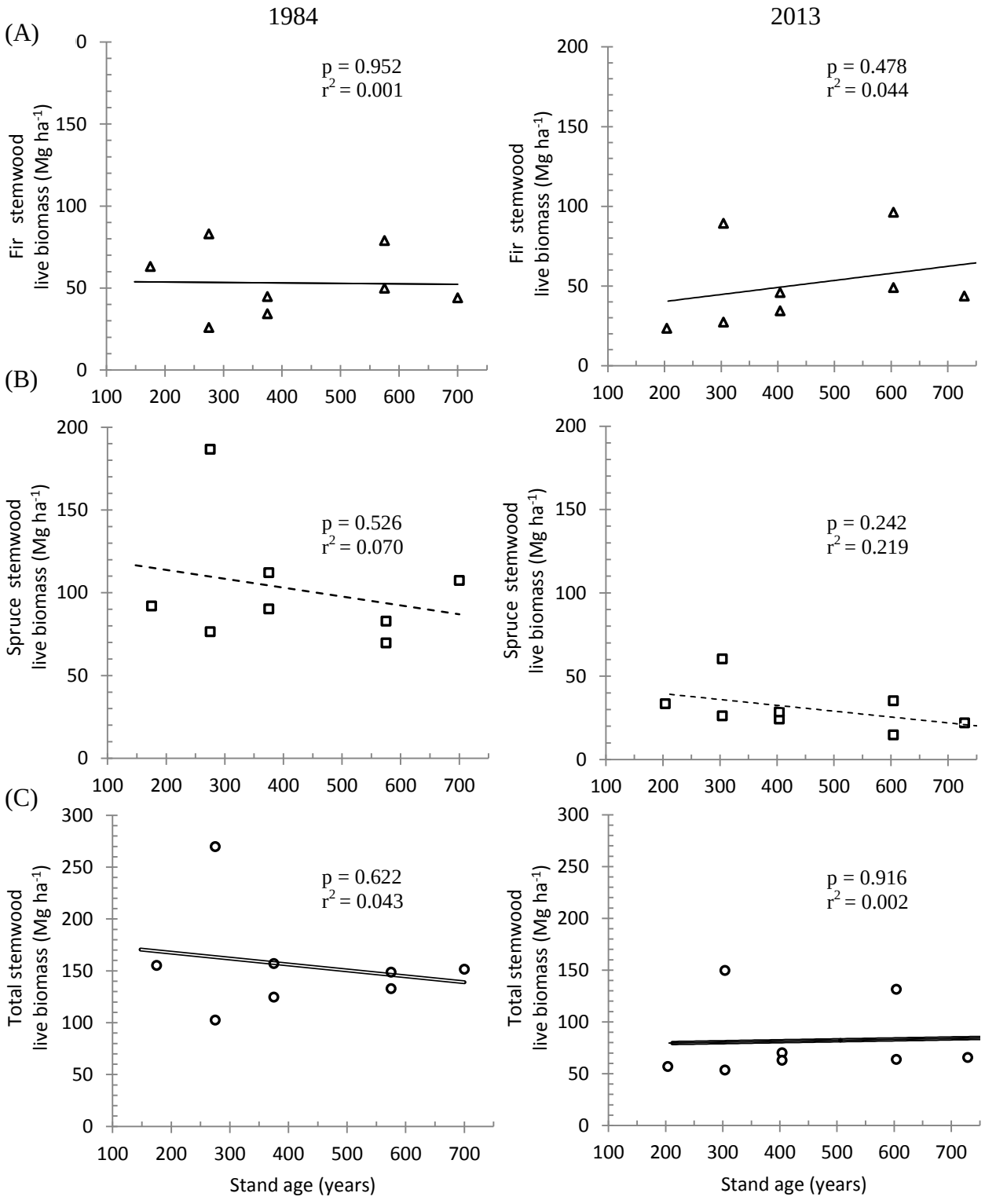


Figure 3: A comparison of the observed trends in live stemwood biomass in 8 stands (#2-#9) in 1984 and 2013: (A) fir, (B) spruce and (C) total. No trends in stemwood biomass were significant in either species for either sampling period. However, linear regression lines suggest decreases in (B) spruce and (C) total live biomass between sampling periods.

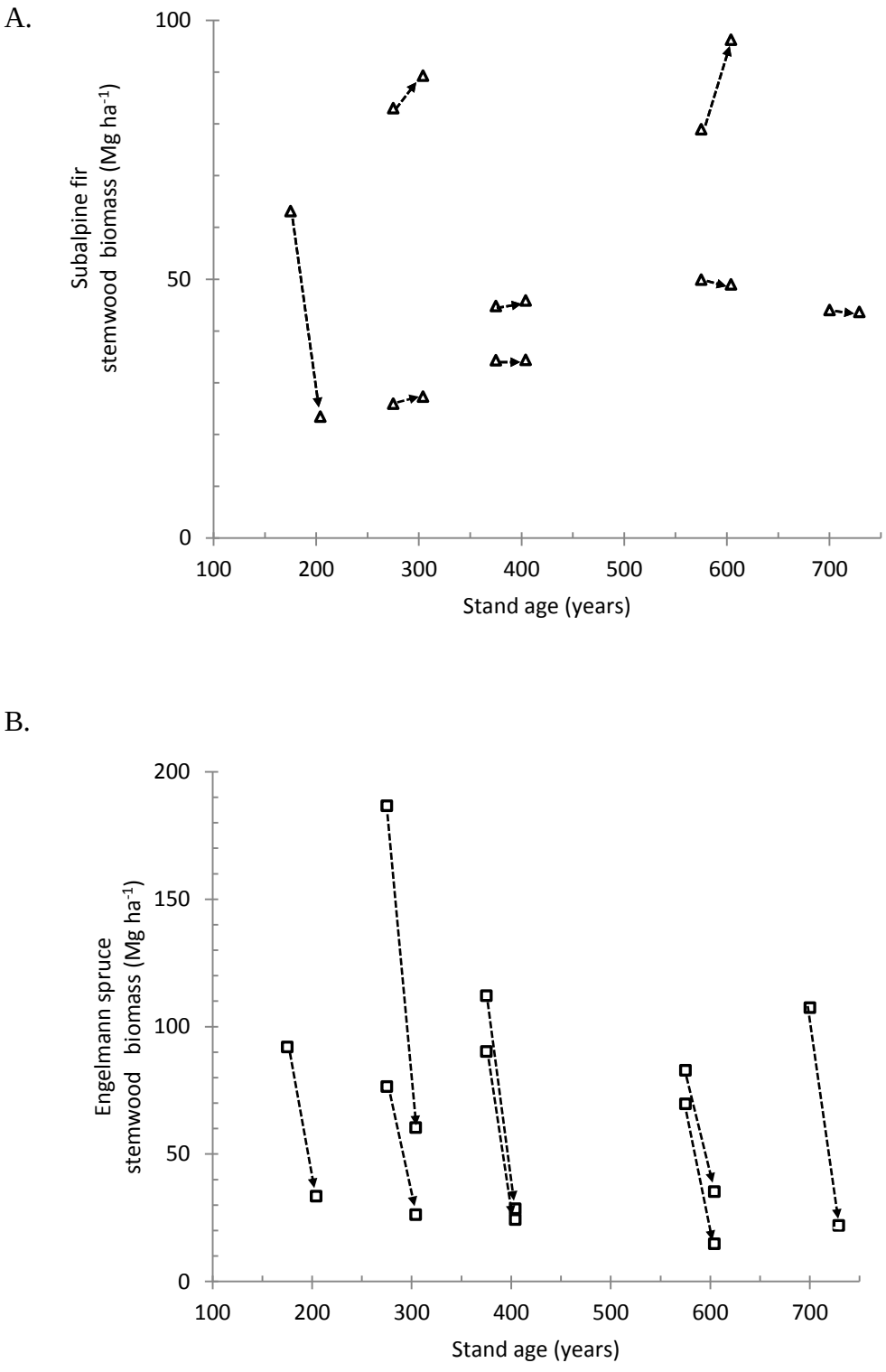


Figure 4: The dotted arrow lines represent the 29-year trajectory of stand stemwood biomass from 1984 to 2013. A paired t-test shows a landscape-scale significant decrease in average (B) spruce (t = 7.18; df = 7; p-value < .0001) and total biomass (t = -6.549; df = 7; p-value < 0.0002) over 30 years suggesting disturbance and greater frequency of biomass oscillations than initially expected. No significant decrease was found in (A) fir between sampling points (t = -0.3206; df = 7; p-value < 0.38).

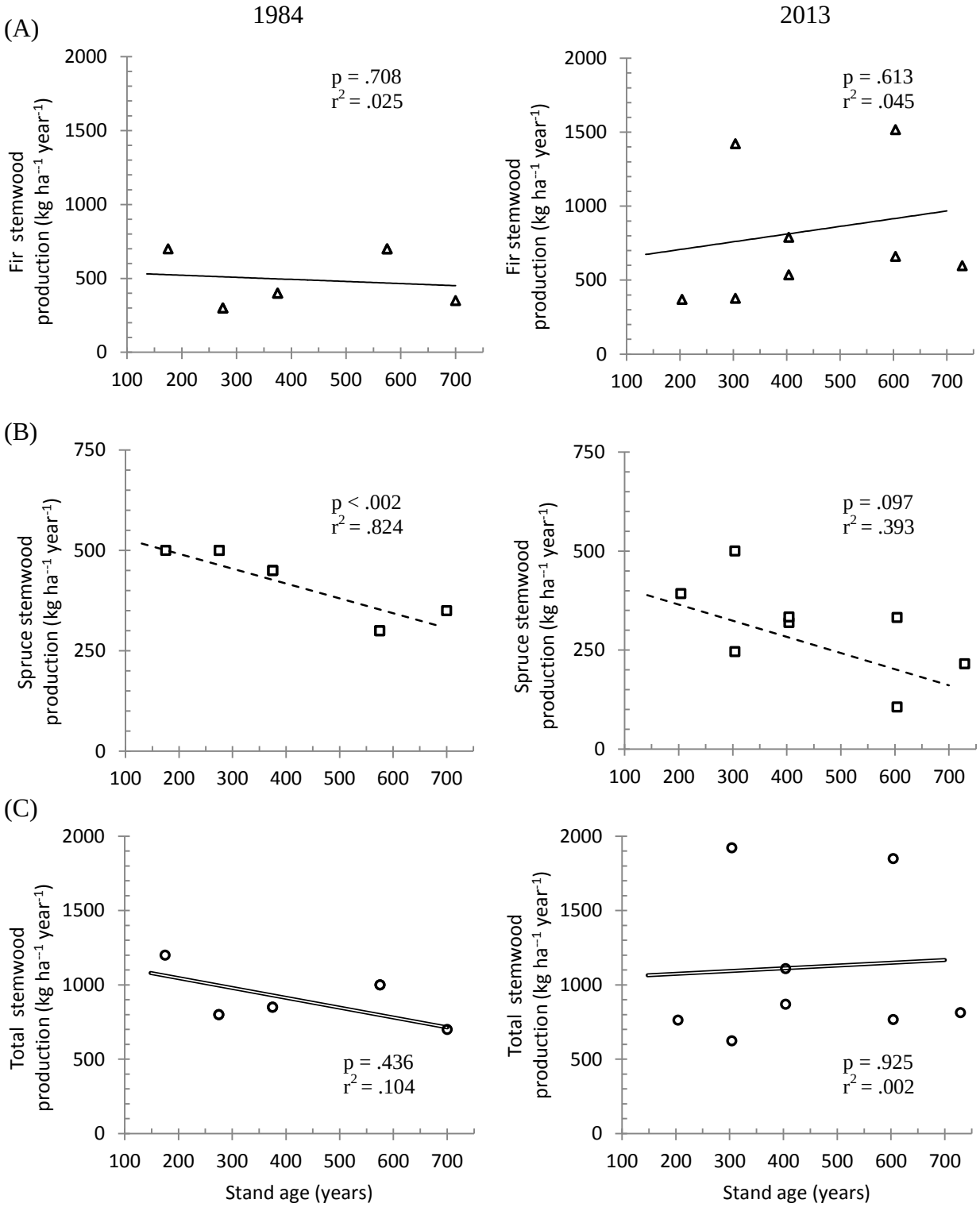
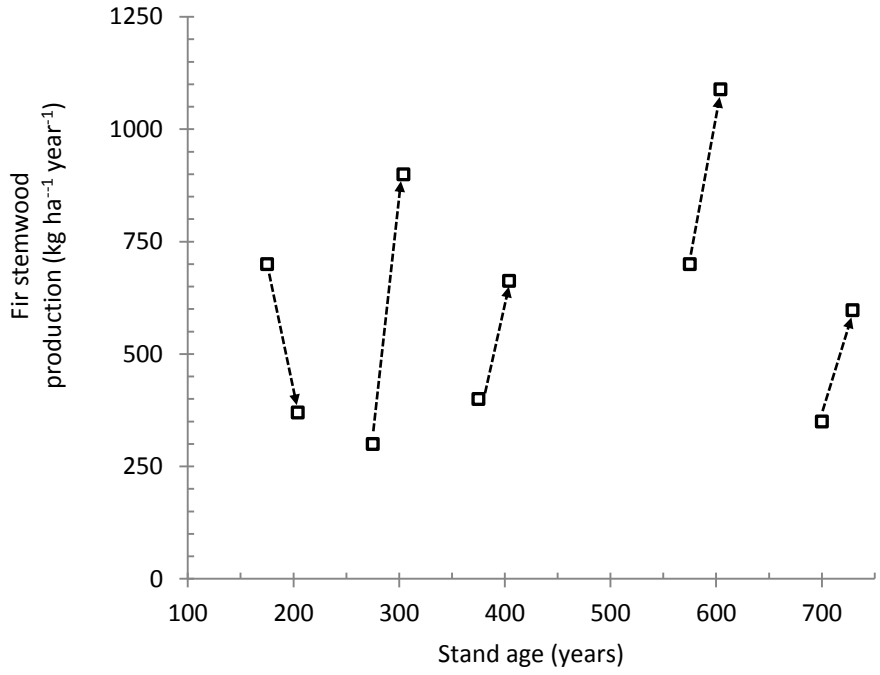


Figure 5: A comparison of the observed production trends of 1984 and 2013 across the chronosequence in: (A) fir, (B) spruce and (C) total. Five production values for 1984 are extrapolated from Aplet et al. 1989, in which production values had been averaged at the stand ages of 275, 375, and 575. Only 1984 spruce production showed a significant correlation with stand age from either sampling period. In 2013, (B) spruce production was no longer correlated with stand age ($p < 0.097$) A paired t-test shows significant expected decrease in spruce mean productivity ($t = -3.42$; $df = 7$; p-value < 0.006). The increase in average (C) total production was less certain ($t = 0.99$; $df = 7$; p-value < 0.18).

A.



B.

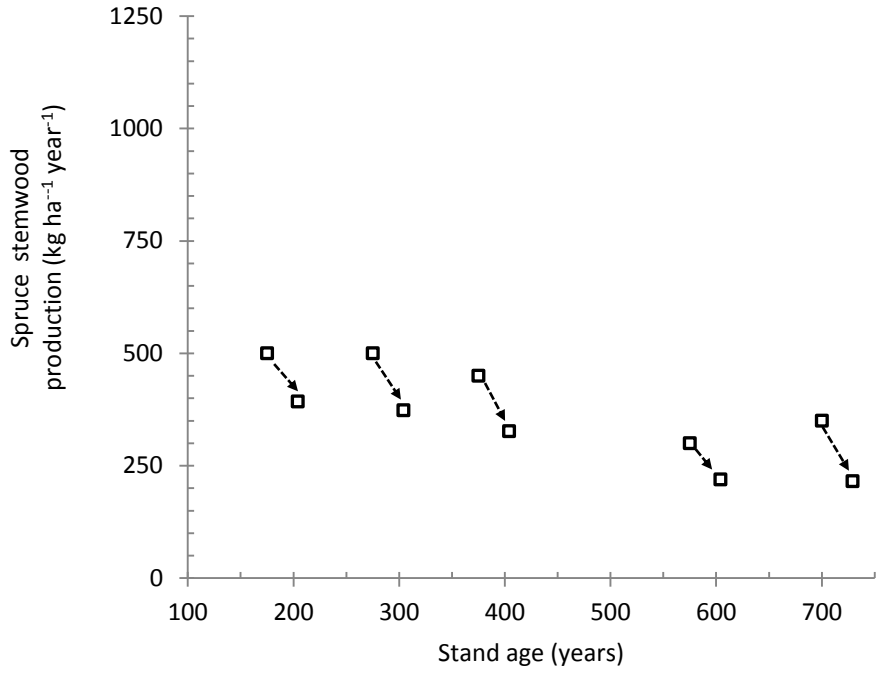


Figure 6: Here the dotted arrow lines represent the 29-year trajectory of stand stemwood production from 1984 to 2013. Average (A) fir stemwood production in 2013, against 1984 expectations, showed a nearly significant increase ($t = 1.82$; $df = 7$; p-value < 0.06). While spruce incurred an expected decline in mean production across stands ($t = -3.42$; $df = 7$; p-value < 0.006).

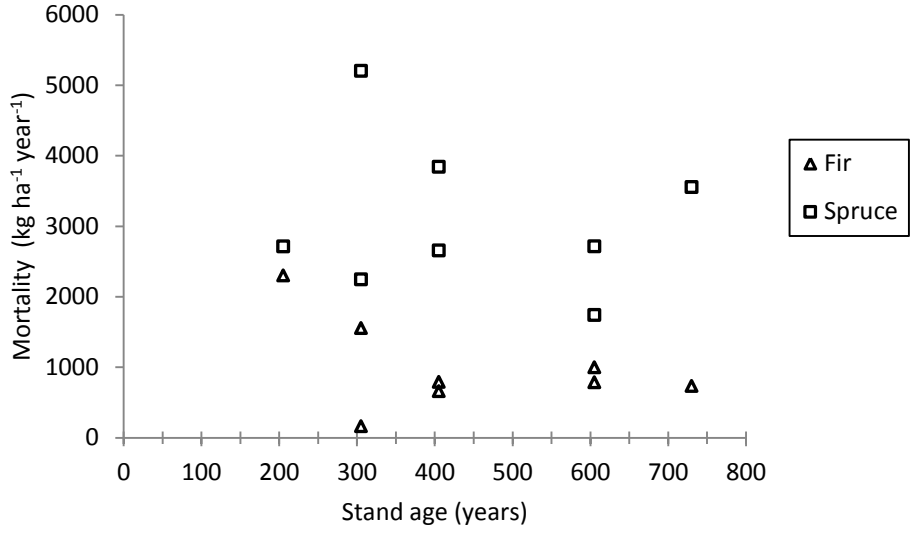


Figure 7: The average mortality over the last 29 years showed no significant relationship with stand age in spruce (p-value < 0.68 r^2 = -0.13), fir (p-value < 0.29 r^2 = 0.05), or total (p-value < 0.42 r^2 = -0.03). Spruce mortality was consistently greater than fir in all of the stands.

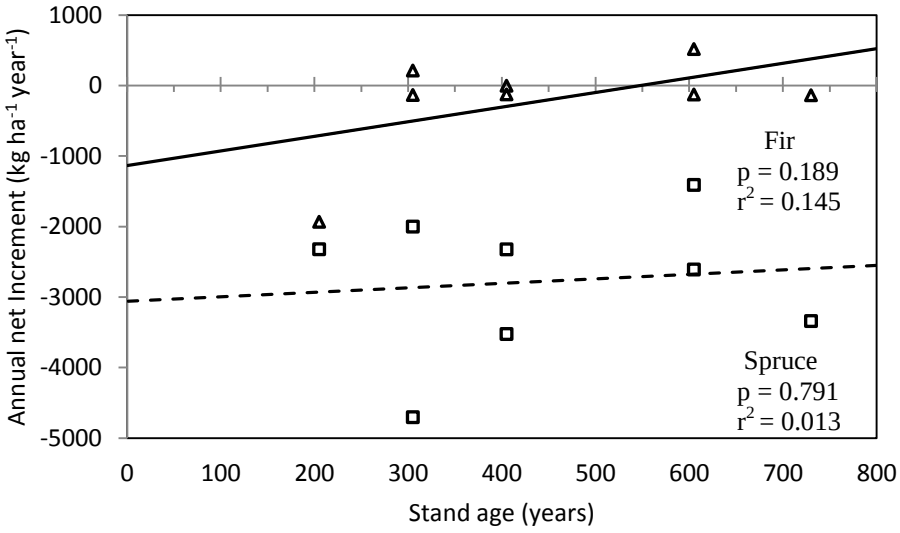


Figure 8: The annual change in live stem biomass for spruce and fir over the last 29 years in relation to stand age showed no significant correlation. Spruce's net increment was negative for all ages. Fir's average net increment averaged around zero.

Table 2: Means of various stand attributes across all stands

Stand attributes	Fir	Spruce	Total
1984 live stem biomass (Mg/ha^{-1})	53	102	155
2013 live stem biomass (Mg/ha^{-1})	51	31	82
Percent change in live stem biomass	-4%	-70%***	-47%***
1984 stem production (kg/ha-1/year-1)	419	481	900
2013 stem production (kg/ha^{-1}/year^{-1})	784	306	1090
Percent change in stem production	87%	-36%***	21%
Mortality from 1984 to 2014 (kg/ha^{-1}/year^{-1})	998	3083	4082
Net Increment 1984 to 2014 (kg/ha^{-1}/year^{-1})	-214	-2777	-2992

*** significant at $p < 0.001$

DISCUSSION

Patterns

Aplet et al. (1989) reported that the percentage of stem biomass contribution within stands changed between spruce and fir over time despite nearly constant total biomass levels across all stand ages. Whereas growth in the largest spruce once compensated for a decrease in fir biomass with increasing stand age, by 2013 live stem biomass across the entire chronosequence declined, primarily due to spruce mortality (Figure 4B). In 1984, spruce had double the stand stemwood biomass of fir across stand ages compared to 2013 chronosequence fir biomass data. Aplet et al. (1989), citing Peet's first model of biomass accretion and production change (Peet, 1981), expected that spruce biomass would continue in a steady state with recurrent regeneration and mortality. The 2013 chronosequence did not follow this pattern. Instead, the sharp decrease in spruce biomass aligned more closely with an ecological alternative allowed by Aplet et al. that spruce may follow Peet's third model whereby biomass falls after overstory mortality, then achieves a lower than expected equilibrium with oscillating development. The latter model depends on abrupt mortality and a period of exclusion.

Many factors, including sudden or gradual changes in the forest ecosystem, can be involved in tree mortality for a given species. Severe disturbances, such as fire, blowdown or insect outbreak, can coincide with more long-term climatic changes, for example an increase in average temperatures and associated drought (Hansen and Bentz, 2003). In the Front Range, the likely cause for much of the increase in mortality is spruce beetle (*Dendroctonus rufipennis*) infestation, its impact effectively subverting the long-term trend that was evident in the chronosequence of Aplet et al. in 1984.

The spruce beetle is an indigenous insect species of Colorado, primarily infesting Engelmann spruce. Under normal conditions they feed on stressed or downed trees, but when conditions are ideal, windthrown stands can cause spruce beetle populations to erupt allowing the species and associated fungi to cause mortality in even the healthiest of trees (Cardoza et al., 2008). Spruce < 10 cm generally are not attacked as spruce beetles succeed more with larger trees and stands in more advanced stages of development (Veblen et al., 1991). In the 2013 chronosequence, mortality was not correlated with stand age although greater mortality probability of trees in certain age ranges could exist (Figure 7). Additional conditions that promote spruce beetle outbreaks in Colorado are an accumulation of fallen trees, more than 65% of spruce in the canopy (Schmid and Frye, 1977; Schmid and Hinds, 1974), and, likely, a prolonged period of a below normal precipitation and warm fall and winter temperatures (DeRose and Long, 2012). A 2013 USDA Colorado Aerial Detection Survey showed a rapidly expanding spruce infestation over the last decade, active on over 16,000 hectares in northern Colorado, a large percentage of these in Larimer County (Colorado State Forest Service, 2013).

Spruce production over the last 29 years has decreased across all stands by an average of 36% (Figure 6B). In contrast, 1984 measurements indicated stability in biomass suggesting stable spruce production with continuous growth and some possibility of fluctuation due to episodic or chronic mortality (Aplet et al., 1989). Reduction in spruce productivity shown by the latter chronosequence is expected as a result of the loss of over half of spruce stems over all age stands. Interestingly, spruce stem growth declined by 36%, despite a 70% reduction in live spruce biomass (Table 2).

Data in 1984 showed that fir biomass and production were higher than spruce in the colonizing cohorts. Second generation fir biomass values decreased to asymptotes with zero net

increment (Aplet et al., 1989). The 87% increase (Table 2) in gross fir production over the last three decades is probably related to mortality of large spruce and accompanying growth improved from an increase in light, nutrients, and water availability. A positive net increment in fir could be expected under these conditions. However, between 1984 and 2013, there was also little net change in fir biomass (Figure 4A) with a marked growth of fir offsetting increases in mortality (Figure 6A). The unexpected high levels of mortality of fir could be the result of a multitude of factors, but similar disturbances on fir in the area have been caused by western balsam bark beetle (*Dryocoetes confusus*) and fungi (*Armillaria spp*. and *Heterobasidion parviporum*) complex (Colorado State Forest Service, 2013), together often referred to as subalpine-fir decline (SFD).

Expectations

An understanding, of how a forest ecosystem develops through time, and of the changes that might occur in the near and long-term, can facilitate management for timber and other resources such as water, wildlife, and for recreational purposes. The chronosequence approach to studying stand development allows researchers to "view" the past or future to track stand development, based on the assumption that stands have the same life history and are ecologically similar (Walker et al, 2010). Spruce-fir stands studied by Aplet et al. (1989) were selected to represent ages since stand-destroying disturbance, without evidence of subsequent major disturbance, whereby the researchers were able to ascertain patterns allowing for predictions in future development. However, trends identified by Aplet et al. in 1984 have been vanquished by a pattern shift in major forest structure change across the entire chronosequence suggesting landscape scale disturbance. No expectation of this loss in biomass was seen in 1984 and, indeed, the uncertainty of timing, type, intensity, and spatial pattern of forthcoming disturbance

events renders plausible trend prediction in development of study stands nearly impossible, especially in the un-even aged subalpine forests of the Colorado Rocky Mountains where there are multiple disturbance regimes having major impacts (Veblen et al., 1994).

Many researchers recognize that, along with variation in numerous climatic and ecosystem factors, interactions with major disturbance agents influence the pathways that a forest site can follow in terms of vegetation responses and occurrence of ensuing disturbances (Rebertus et al., 1991; Veblen et al., 1994; Turner, 2010). However, observations of central tendencies and probable factors associated with divergence can be useful. Studies have given insight into expected vegetative responses, over varying time periods, of spruce-fir stand structure following large-scale spruce beetle infestation. There is consensus that the growth of established survivors of both species accelerates rapidly over decades, with subalpine fir dominating the overstory. Schmid and Hinds (1974) predicted a fluctuating pattern of alternating dominance by spruce and fir over the following centuries as fir dies out and then dominant spruce succumbs again to episodic spruce beetle outbreak. In contrast, there is speculation in later studies (Schmid and Hinds, 1974; DeRose and Long, 2007; Veblen et al., 1991; Veblen et al. 1994) that a combination of limited spruce recruitment and a higher mortality rate for fir results in long-term co-dominance of the two species. It is difficult to speculate on expected long-term trends in spruce-fir forest biomass and production in stands in which live tree biomass has been affected by major disturbance (Veblen et al., 1991; DeRose and Long, 2012), such as seen in the stands studied here.

A chronosequence of biomass dynamics in similar old-growth forests has recently found, with high heterogeneity after long periods of growth, sudden mortalities can occur across stand ages (Harmon and Pabst, 2015). Given the slow rates of tree growth, and despite expected

acceleration, lost biomass presumably cannot be recovered for at least decade, but high resilience may be a long-term trait of spruce-fir forests (Minckley, Shriver, and Shuman, 2012). In our stands increased uncertainty in significant disturbances will make future small-scale gap dynamics much more difficult to predict. It is foreseeable that there will be more significant disturbance in these spruce-fir stands than initially expected, but how much change in climate will increase the size and intensity of these disturbances is inconclusive.

CONCLUSION

Re-measurements of spruce-fir forest stand chronosequence in the Front Range of Colorado provided evidence of recent disturbance resulting in a drastic change in forest structure over the last 29 years. This change is evidenced by data showing a 47% decline in live aboveground biomass since 1984, primarily due to a 70% decrease in spruce aboveground biomass (Table 2) over the same time period. The assumed culprit is the spruce beetle, as this indigenous bark beetle has progressively disturbed a high percentage of the spruce-fir forest of Colorado, including the Front Range, with a sharp increase in landscape area infested over the last decade (Colorado State Forest Service, 2013). There was no correlation in 2013 between stand age and biomass reduction suggesting that the beetle outbreak has high severity across stands from 200 - 700 years of age. In contrast, in 1984 Aplet and colleagues found that both biomass and production were stable during across the chronosequence (Aplet et al., 1989), and expected that spruce would remain dominant, perhaps with ongoing oscillations and replacement through gap phase dynamics (Aplet et al., 1988).

The zero net increment of fir (Figure 8) gives the appearance that the previous trend of consistent fir biomass with stand age trend remains true in 2013, but the increase in production over 29 years is nearly significant. Lack of net increment in 2013, despite many stands showing increased fir production (Figure 6A) across the chronosequence, might indicate fir mortality. As aforementioned, subalpine fir decline could be the source of fir loss. SFD has been active on Colorado's landscape for over a decade, with the Front Range indentified as an area experiencing large swaths of impact in 2013 (Colorado State Forest Service, 2013).

Natural disturbances, and interactions between disturbances, play a major role in shaping the sub-alpine forests of Colorado. Spruce-fir forest development is reflective of disturbances of diverse sources and intensities that, in turn, interact with the life histories of the two species (Aplet et al., 1988). The 1984 chronosequence was valuable in showing the best-guess temporal dynamics of spruce and fir at decadal to century time scales as trends in stemwood biomass and production at sites of different ages appeared to follow similar trends in the "absence" of disturbance offering predictive capabilities towards forest structure in relation to stand age. The value in the current study chronosequence lies in comparative data of a 29-year interval showing earlier trends subverted, giving a picture of progression from relative absence to onset of disturbance, providing further opportunities for studies of stand and disturbance dynamics, and substantiating that the nature and timing of disturbances are not easily predicted. The disturbance of large areas, such as that seen in spruce-fir forests in the Front Range, including the study stands, reduces the value of a subsequent chronosequence approach because the event may not reset the general trends previously seen (Walker, 2010). There may be opportunities to research effects of disturbances, additional responses such as understory recruitment and recovery, and even potential uses of the plots in disturbance mitigation experimentation. Additional analyses of the diameter data and individual tree age relationships may present other interesting findings regarding spruce-fir forests.

Further disturbances as drivers of rapid ecological transformation will continue to present important opportunities for research. Global climate change, shifts in biotic competition, alterations in species composition and land use changes will also influence disturbance dynamics (Turner, 2010). Continued observations and further research using chronosequences and other methods are needed for improved understanding of spruce-fir dynamics, subalpine environments,

and factors that actuate disturbance. Such knowledge will inform decisions regarding potential management of spruce-fir forests, its wildlife, watershed, wood production, and recreational opportunities.

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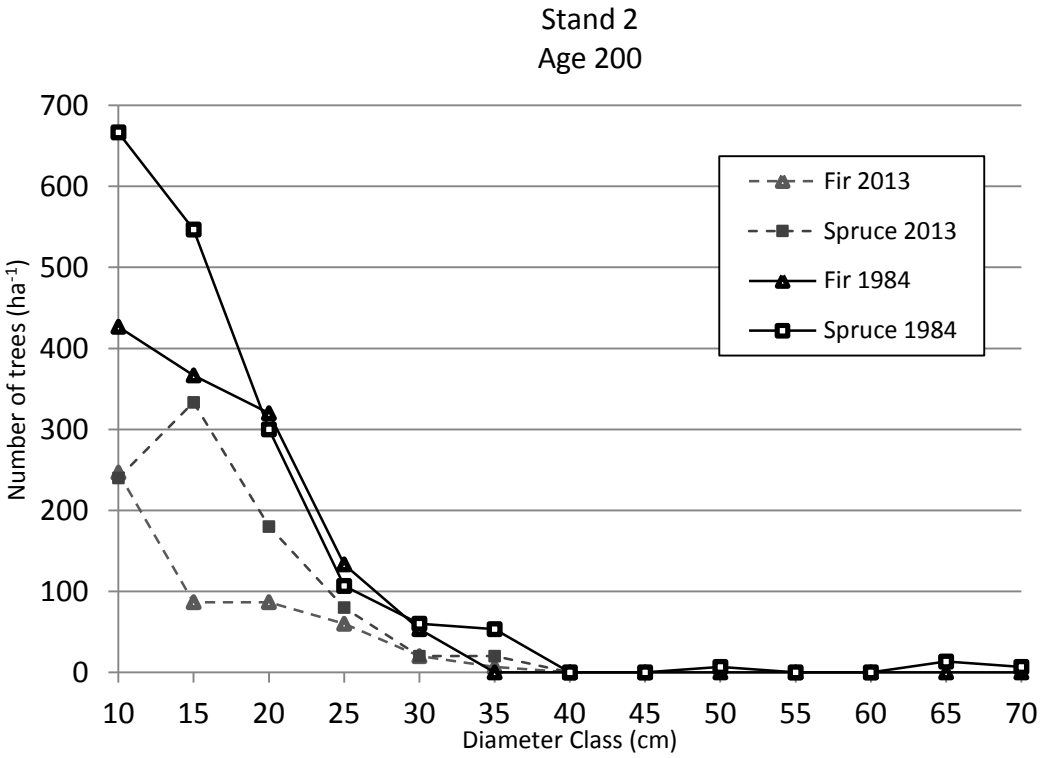
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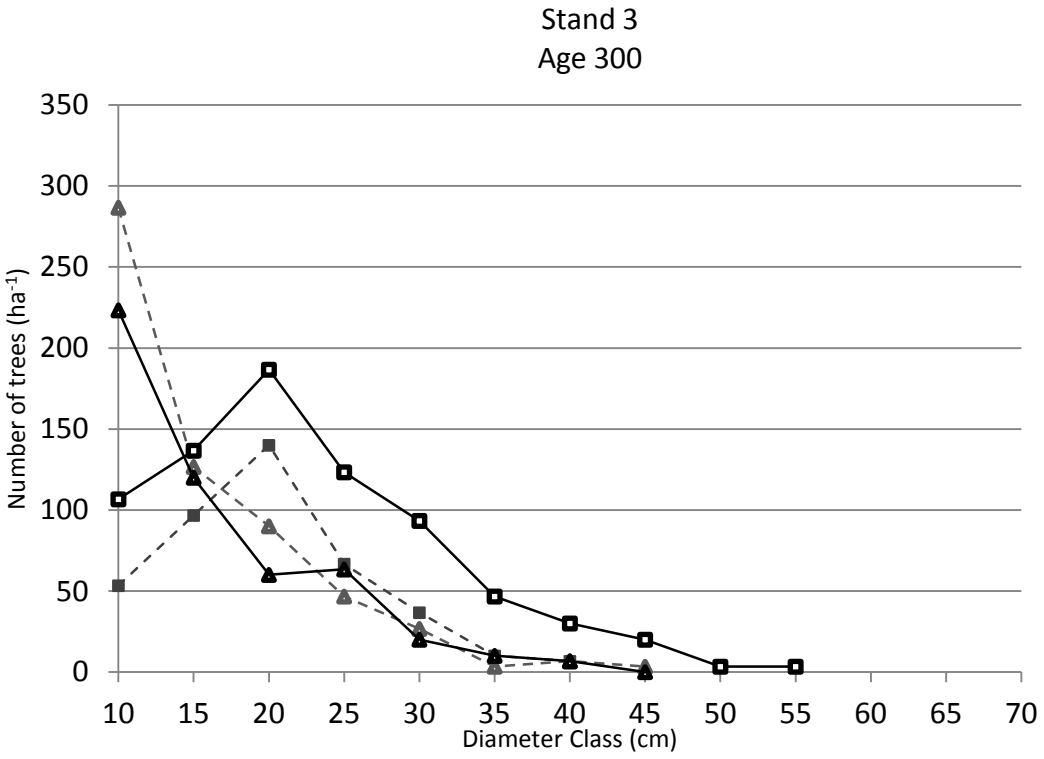
APPENDICES

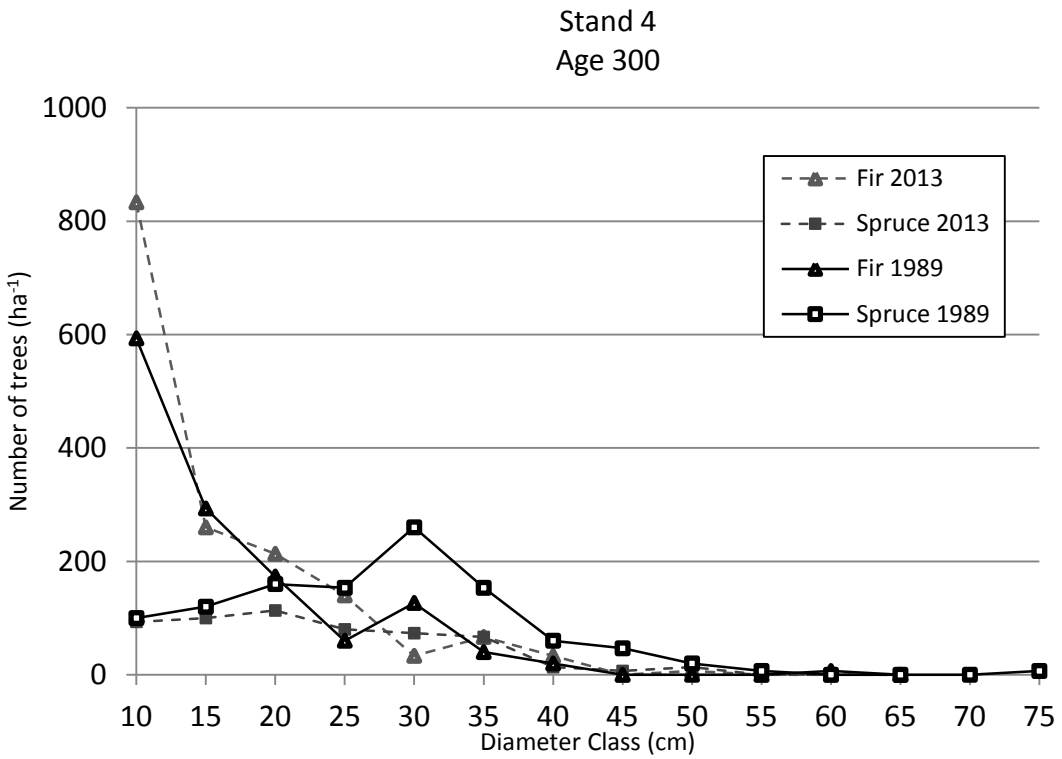
Appendix A: A table of plot labeling and locations around the Cache La Poudre watershed. The 1988 labels show initial plots established and labels associated to the data sheets of the respective stands.

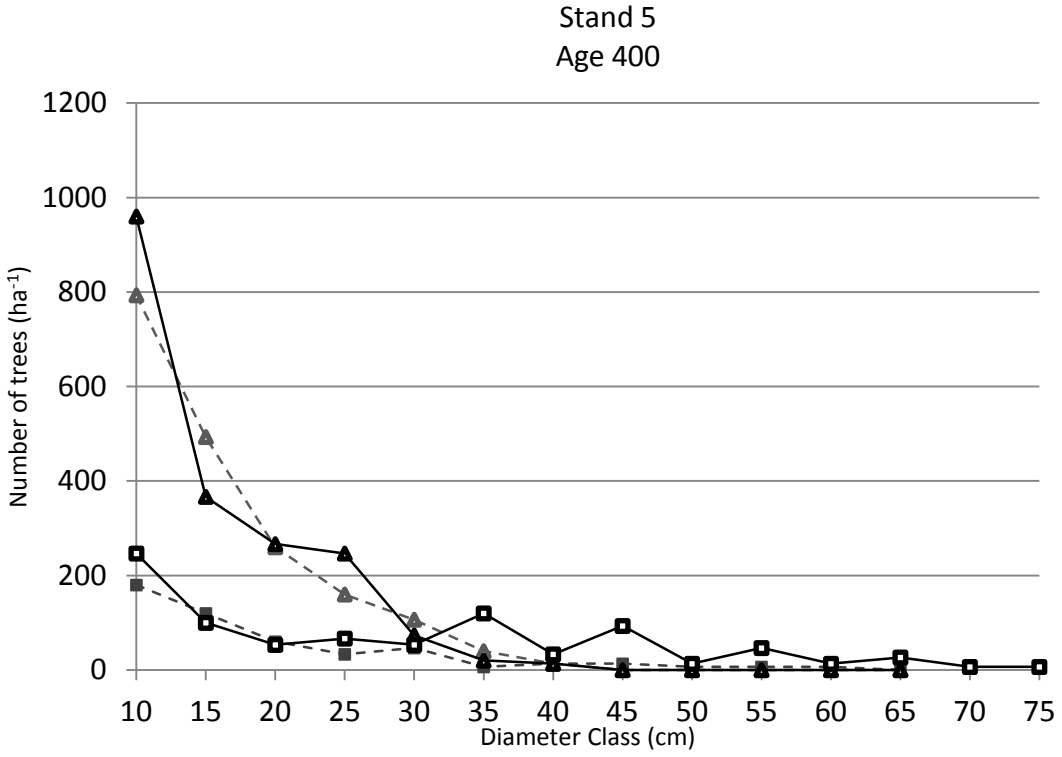
Stands	Age (years)	Aplet '88 labeling	Plot labels	Stand Area (ha)	Locations Latitude and Longitude (North West)
2	205	1	1A	0.15	40.52415 -105.89577
3	305	2	2B	0.3	40.54247 -105.79012
4	305	n/a	2A	0.15	40.55035 -105.80765
5	405	n/a	3C	0.3	40.61800 -105.86104
6	405	3	3A	0.3	40.60958 -105.72737
7	605	4	4A	0.3	40.54754 -105.80492
8	605	5	5A	0.3	40.55136 -105.80714
9	730	n/a	3B	0.3	40.54985 -105.79964

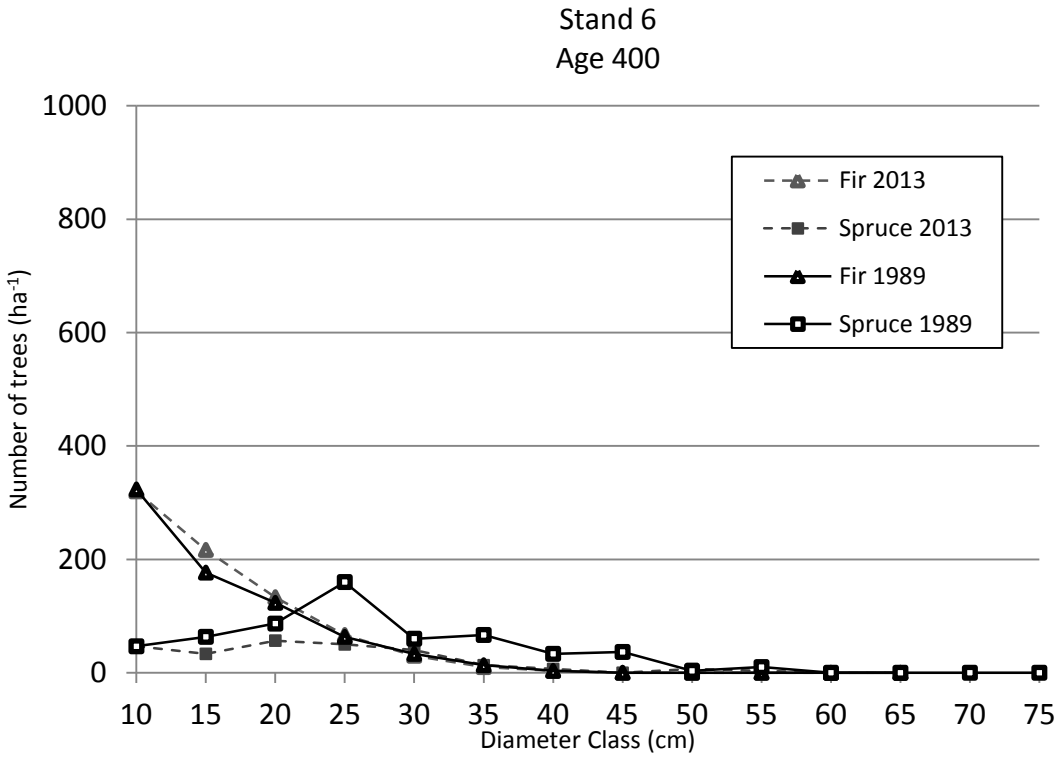
Appendix B: Size class distributions for Stands 2-9 comparing 1984 and 2013 measurements. Spruce showed density decreases in all-sized stems in most stands. Fir showed a decrease in small stems 5-10 cm (x-axis: 10 cm) andincreases in stems sized 15-20 cm (x-axis: 20 cm).

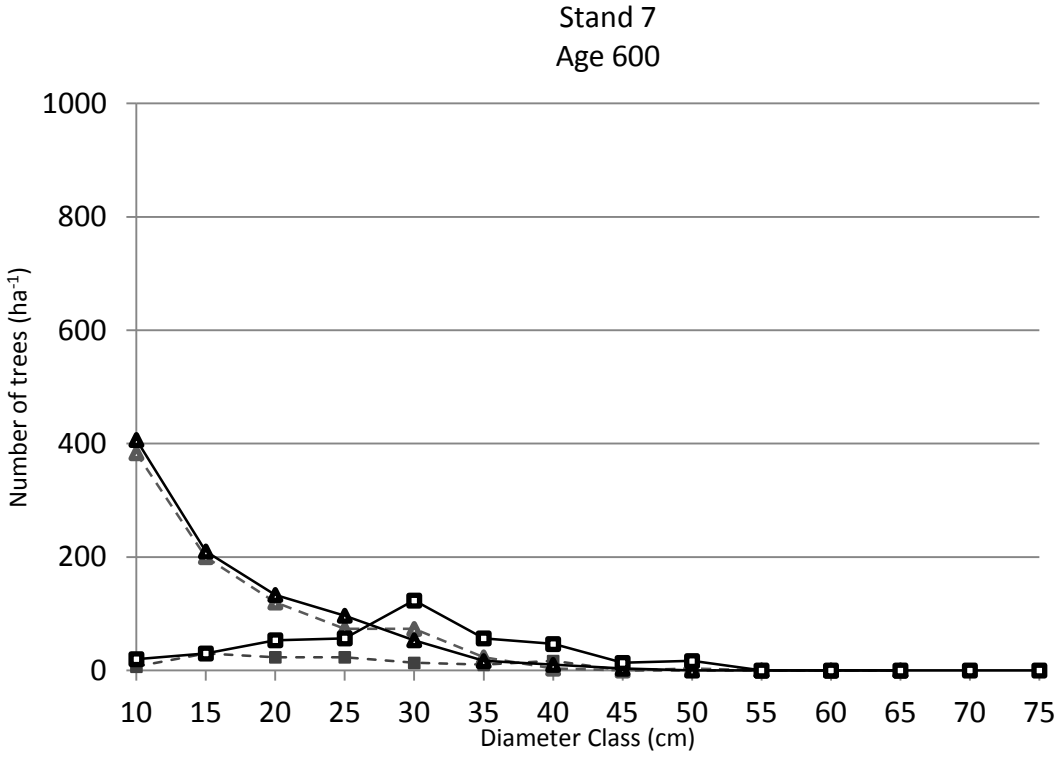


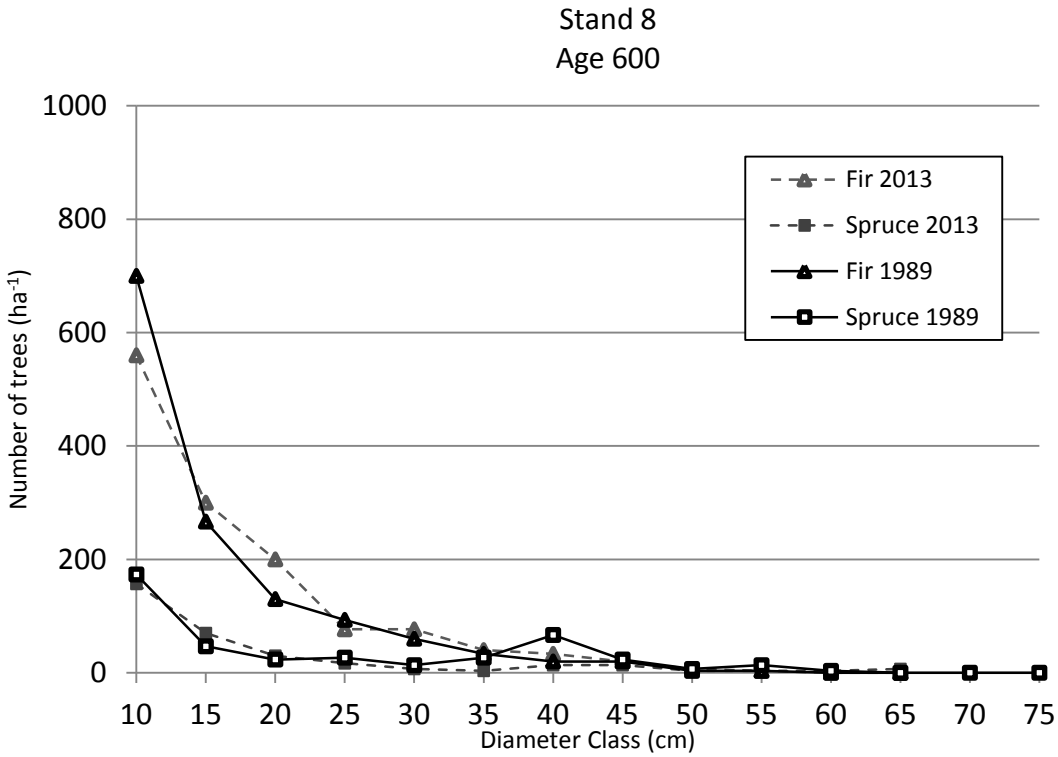


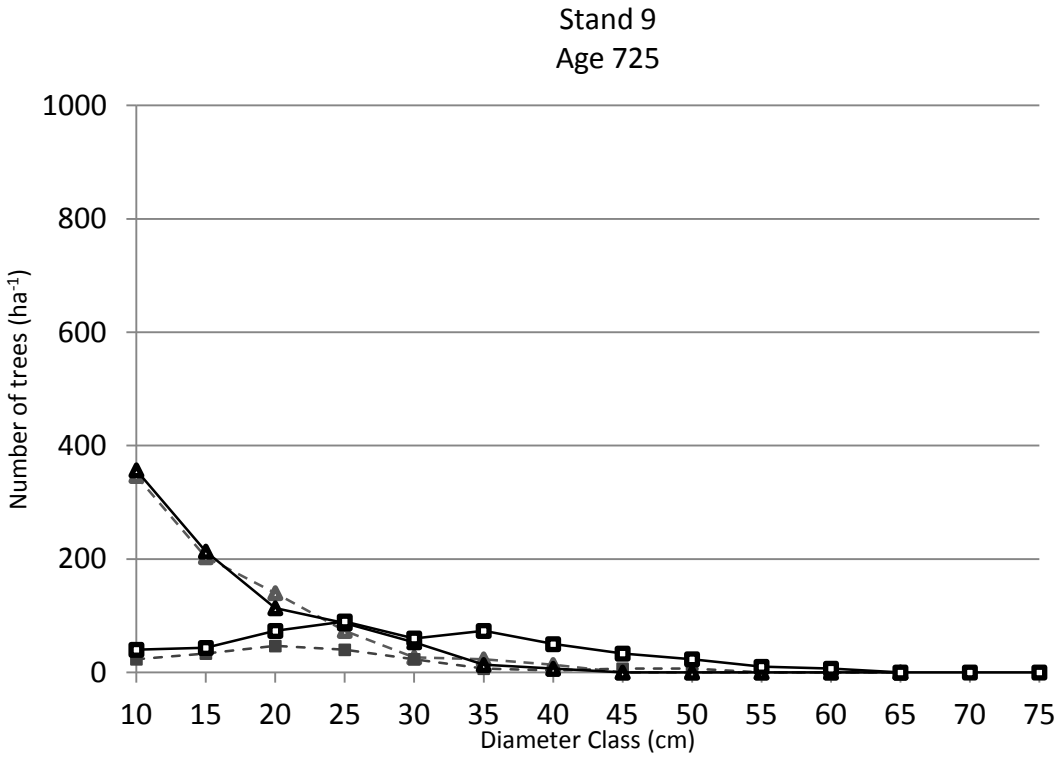

Stand 4
Age 300
Number of trees (ha-1)
Diameter Class (cm)
Fir 2013
Spruce 2013
Fir 1989
Spruce 1989
0
200
400
600
800
1000
10
15
20
25
30
35
40
45
50
55
60
65
70
75


Stand 5
Age 400
Number of trees (ha-1)
Diameter Class (cm)
0
200
400
600
800
1000
1200
10
15
20
25
30
35
40
45
50
55
60
65
70
75


Stand 6
Age 400
Number of trees (ha-1)
1000
800
600
400
200
0
10 15 20 25 30 35 40 45 50 55 60 65 70 75
Diameter Class (cm)
Fir 2013
Spruce 2013
Fir 1989
Spruce 1989

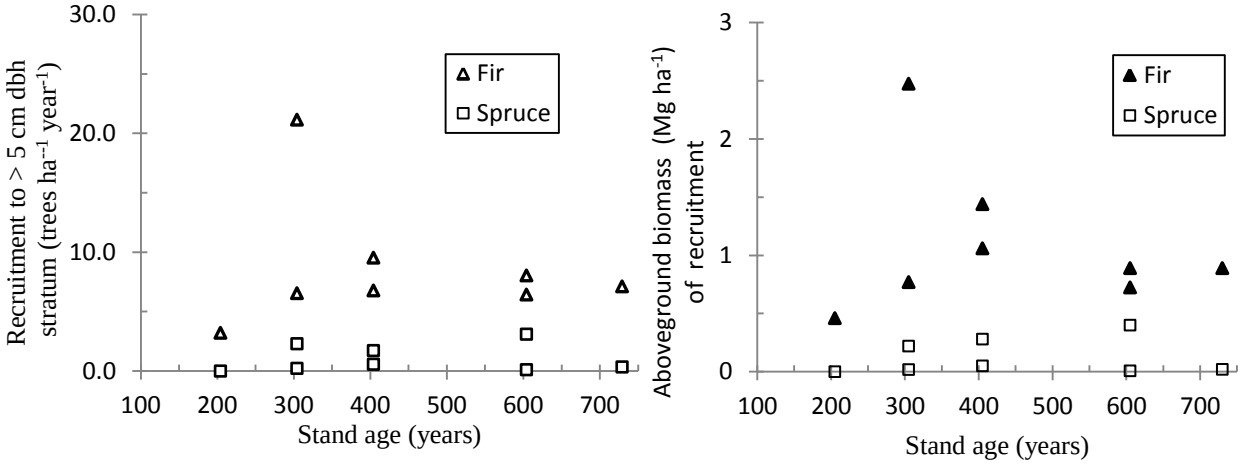

Stand 7
Age 600
Number of trees (ha-1)
1000
800
600
400
200
0
10 15 20 25 30 35 40 45 50 55 60 65 70 75
Diameter Class (cm)


Stand 8
Age 600
1000
800
600
400
200
0
Number of trees (ha-1)
Fir 2013
Spruce 2013
Fir 1989
Spruce 1989
10 15 20 25 30 35 40 45 50 55 60 65 70 75
Diameter Class (cm)


Stand 9
Age 725
1000
800
600
400
200
0
Number of trees (ha-1)
10 15 20 25 30 35 40 45 50 55 60 65 70 75
Diameter Class (cm)

Appendix C: The low recruitment of fir and lower recruitment spruce into the > 5 cm dbh stratum over 3 decades (a) summed to expected unsubstantial yields in stemwood biomass (b).

a. **b.**



Appendix D: A standing dead biomass comparison offers some insight into mortality prior to the 1984 sampling period.

