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Bark beetle effects on a seven-century chronosequence of Engelmann spruce and subalpine fir in Colorado, USA

Drew P. Derderian[a], Haishan Dang[b], Gregory H. Aplet[c], Dan Binkley[d,e,*]

[a] Department of Forest and Rangeland Stewardship, Colorado State University, Fort Collins, CO 80521, USA
[b] Key Laboratory of Aquatic Botany and Watershed Ecology, Wuhan Botanical Garden, Chinese Academy of Sciences, Wuhan 430074, PR China
[c] The Wilderness Society, 1660 Wynkoop St., Suite 850, Denver, CO 80202, USA
[d] Department of Ecosystem Science and Sustainability, Colorado State University, Fort Collins, CO 80521, USA
[e] Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, S-901 83 Umeå, Sweden

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ABSTRACT

Many important trends in forest development across landscapes and centuries are difficult to measure directly, and a space-for-time substitution in a chronosequence may provide useful insight at these scales. The value of chronosequences for forest ecology and management depends on a number of sources of variation, including geographic differences in site productivity, differences in climate over long periods, and the presence or absence of rapid events such as fire, windthrow, and insect outbreaks. Confidence in the value of a chronosequence may be increased if later resampling shows that each site followed the predominant trajectory expected from the chronosequence pattern. We resampled a 700-year chronosequence of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) three decades after the initial sampling. The original chronosequence suggested long-term stasis in both biomass and production after about 200 years of stand developments in the absence of major fire, beetle outbreaks, and windstorms. Three decades later, a spruce beetle (*Dendroctonus rufipennis*) outbreak had reduced spruce biomass by 68% and total stand biomass by 44% across the chronosequence (to an average of 7.8 kg m^{-2}). There remained no trend in total stem biomass with stand age, averaging 13.9 kg m^{-2} of stemwood across all ages. Stem production averaged 0.15 kg m^{-2} yr^{-1} between 1984 and 2013, higher than the 0.09 kg m^{-2} yr^{-1} estimated in 1984. Over the three decades, stand biomass shifted from about 2/3 spruce to 2/3 fir. Stands may be selected for chronosequences based on an absence of rapid events that substantially change stand structure, but this may limit the ability of a chronosequence to represent real long-term patterns across landscapes.

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1. Introduction

Forests of spruce (*Picea*) and fir (*Abies*) cover vast portions of the northern hemisphere. A variety of ecological factors appear to sustain the codominance of trees in these forests, including shared abilities to survive for decades and centuries in highly shaded locations, and differential susceptibility to pests (e.g. Peet, 1981; Veblen, 1986a,b; Seymour, 1992; Aplet et al., 1988; Nishimura et al., 2010). Forests dominated by Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) dominate many landscapes from central British Columbia and Alberta in Canada southward to Arizona and New Mexico in the United States (Alexander, 1984). Long-term changes in composition, production, and biomass develop at century time scales in these forests, posing major challenges for testing ideas about the changes in these forests over time.

A chronosequence approach has the potential to identify trends expected through time based on patterns among stands of different ages across landscapes, assuming that a predominant trajectory should be followed within individual stands (Walker et al., 2010). The critical assumption of a chronosequence is that variations in ecological factors across space and time are relatively small compared to the predominant trajectory over time. Differences in site factors may confound any time-related pattern, as would any trends in climate across centuries. The occurrence and legacies of rapid change events such as fires, insect outbreaks, and windstorms could add variance that further limits the utility of chronosequences. These three sources of variation (ecological site factors, climate, and rapid events) may even challenge the idea that a clear predominant trajectory should be expected for forest development across landscapes and centuries.

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* Corresponding author. Department of Ecosystem Science and Sustainability, Colorado State University, Fort Collins, CO 80521, USA.
E-mail address: dan.binkley@alumni.ubc.ca (D. Binkley).

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Aplet et al. (1988, 1989) used a chronosequence approach to determine the likely changes in forest composition, stemwood biomass, and stemwood production across seven centuries of change in forests of Engelmann spruce and subalpine fir in northern Colorado. They chose nine stands representing different ages since stand-initiating disturbance (likely severe fire) and used tree ages, diameters, growth, recruitment, and coarse woody debris to examine stand development in response to chronic factors (competition, minor windthrow, endemic bark beetle activity, root diseases) in the absence of major mortality events. Later, Rebertus et al. (1992) presented a general course of forest development (citing Whipple and Dix, 1979; Peet, 1981; Veblen, 1986a, and Aplet et al., 1988) that, in the absence of broad-scale disturbance, follows a continuum that can be divided into four broad phases: colonization, spruce exclusion, spruce reinitiation, and second-generation spruce–fir ”old growth.” Colonization follows a major disturbance and consists of recruitment of both spruce and fir under conditions of available resources. As the canopy closes, conditions become inhospitable for spruce regeneration, and the stand enters the spruce exclusion period, while fir continues to recruit. Eventually, mortality of large trees, either through competition-induced mortality or as fir reaches the end of its lifespan, opens the canopy and spruce recruitment reinitiates. With time, this spruce recruitment joins the fir as an all-aged forest or forms a second cohort in a long-period cycle of recruitment and exclusion. Various authors (Rebertus et al., 1992; Aplet et al., 1988; Peet, 1981) noted that existence of second-generation forest is unlikely to persist for long, if it is indeed ever reached, as virtually all stand age class structures show evidence of stand initiating disturbance events, and stands containing trees >500 years old are rare.

Chronosequence studies depend on the assumption that the only significant difference between sites is time, and Aplet et al. (1989) cautioned that “[i]n spite of restricting slope, aspect, parent material and climate in this study, other unknown plot-to-plot variation (e.g. initial density and species composition, site quality, stand history) may exist.” Rebertus et al. (1992) noted that various authors concluded that differences in site quality among stands affect developmental dynamics such that a variety of stand structures may result: actual trajectories may vary substantially in a population of stands around any central tendency. On especially dry and wet sites, slow recruitment may prevent the onset of a spruce exclusion phase, and Aplet et al. (1989) suggested that, on relatively high-quality sites, overstory mortality early in stand development keeps the canopy open and allows for continuous spruce recruitment. Other authors have reported similar differences in stand trajectory depending on site quality (Whipple and Dix, 1979; Peet, 1981).

Despite apparent differences among sites, Aplet et al. (1989) reported generally stable stand-level biomass from 125 through 700 years of stand development. Stemwood production peaked early in stand development, and then dropped by about half from age 250 years onward. The decline in stemwood production mirrored the decline in stand leaf area. Beyond 175 years since stand establishment, spruce comprised about two-thirds of stem biomass and half of stem production. The distribution of sizes and ages of fir was relatively constant after 200 years, though the distributions for spruce continued to change as the initial even-aged cohort progressed through time. Total biomass and production of stems showed no trend after 200 years.

Did the lack of trend result from long-term patterns of consistent production and mortality (leading to no change in biomass), or did the lack of apparent trend reflect confounding variations of ecological site factors, time, and rapid events that obscured the trends actually followed through the history of each stand? Aplet et al. (1988) marked individual trees so these questions could be tested by resampling in future decades. We report on the changes in stem biomass and production over the next three decades, addressing two questions:

1. Did each stand follow the trend in stemwood biomass and production over time that was suggested by the original chronosequence?
2. Would a remeasurement show the same pattern as the original chronosequence?

Two additional questions were developed once it was clear that rapid mortality from spruce beetles (*Dendroctonus rufipennis*; Colorado State Forest Service, 2013) had substantially altered the stands:

3. Did mortality differ with tree size?
4. Did mortality differ with stand age?

2. Methods

The methods of the original sampling of the chronosequence were described in detail by Aplet et al. (1988, 1989). The stands are located in the upper watersheds of the Cache La Poudre River and Laramie River in Larimer County, Colorado, USA, between 3000 m and 3200 m, most on north-facing aspects (Fig. 1; see Table 1 of Aplet et al. (1989) for details on location and site, where Stand 1 in the present study corresponds to Stand 2 in the 1989 paper, etc.). Spruce and fir comprised >97% of overstory trees and biomass, with minor amounts of lodgepole pine (*Pinus contorta*). Tress of all sizes were cored as close to the base as possible, and stand ages were determined from the oldest, largest trees, all of which displayed ring patters indicative of growth in the open. No stands showed evidence of trees that survived the stand-initiating disturbance.

All of the original plots from 1984 were resampled in 2013 except for the youngest stand (about 125 years old in 1984), which had not been permanently marked for resampling. Each stand was sampled with three plots, either 0.05 ha plots (the youngest resampled stand) or 0.10 ha plots (all others). The resampling entailed locating each original tree and measuring current diameter at breast height (1.4 m), and tallying tree condition (live, dead standing, or dead fallen), but we made no attempt to assess cause of death. A few trees were missing tags, but they were identified reliably based on species, size and location within plots. The diameter cut-off for measurement in 1984 was 5 cm, and new recruits that passed this threshold were tallied by diameter and species (Table 1).

The biomass of stems was estimated using allometric equations for volume, based on diameter and height, and wood density (see methods in Aplet et al., 1989). The diameters were measured directly, and heights were estimated based on locally derived linear relationships between diameter and height in 1984 (measured with a clinometer: spruce, $n = 390$ $r^2 = 0.86$; fir, $n = 307$ $r^2 = 0.88$). Stemwood volume was calculated with equations from Myers and Edminster (1972), and volume was converted to mass based on typical densities (368 kg m^{-3} for spruce, and 433 kg m^{-3} for fir, Wenger, 1984). The values for fir and spruce are given separately, and the total stand values are slightly higher than the sum of the two species owing to inclusion of minor contributions of lodgepole pine.

Stemwood in the first sampling was determined from 10-year growth increments on cores. For the resampling, productivity was calculated from gross stem increments between 1984 and 2013. The production estimates for the 1984 sampling would be somewhat low, as the growth of any tree that occurred between 1975 and 1984 was included only if the tree was alive in 1984. The production estimates for the 2013 sampling did include any

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