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Shifting ecological filters mediate postfire expansion of seedling aspen (*Populus tremuloides*) in Yellowstone

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ABSTRACT

Determining how ecological filters (e.g., climate, soils, biotic interactions) influence where species succeed in heterogeneous landscapes is challenging for long-lived species (e.g., trees), because filters can vary over space and change slowly through time. Stand-replacing wildfires create opportunities for establishment of tree-species cohorts and can catalyze rapid shifts in where species occur, facilitating unique opportunities for long-term study. We quantified effects of multiple ecological filters on a colonizing cohort of aspen (*Populus tremuloides*) that established from seed throughout burned lodgepole pine (*Pinus contorta* var. *latifolia*) forests after the 1988 fires in Yellowstone National Park (Wyoming, USA) to ask: (1) How have aspen presence, density, and size varied across the postfire landscape, and what filters explain these spatial and temporal patterns? (2) How does aspen above-and belowground biomass vary with postfire lodgepole-pine density? Aspen persisted to postfire year 25 in 58% of the plots in which aspen were present in postfire year 11 ($n = 45$), and mean stem density declined from 522 to 310 stems ha^{-1}. Mean aspen height doubled (from 29 to 59 cm) over this period. Ecological filters related to climate, competition, herbivory, and soils all differentially affected aspen presence, persistence, and size. Growing season temperature, inter-specific competition, and herbivory also changed through time, altering their effects on the colonizing cohort, and shifting where on the landscape aspen persistence and growth were ultimately favored. Eleven years postfire, aspen were favored at warmer, low elevations; ungulate browsing strongly constrained aspen heights; and competition was unimportant. By 25-years postfire, temperatures warmed nearly 1 °C, and aspen were more likely to persist at cooler, high elevations. Browsing pressure declined, as ungulate populations decreased during this time, but aspen height and basal diameters were constrained by dense, rapidly growing postfire conifers. Landscape mosaics of ecological filters shift over space and time and can facilitate or constrain the persistence and growth of colonizing species. Long-term study of post-disturbance colonizing cohorts uniquely reveal how species are responding to real-time environmental change in heterogeneous landscapes, which will help us better anticipate 21st century species distributions and abundances.

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1. Introduction

As environmental change accelerates, it is critical to determine how multiple ecological filters (e.g., climate, topography, soils, disturbance, competition, and herbivory) determine where species establish and thrive in landscapes (Walther et al., 2002; Thomas et al., 2004; Bellard et al., 2013). However, identifying the influence of ecological filters on species' success is challenging because filters often vary spatially and may change over time (Venn et al., 2011; Lawler et al., 2015). Particular ecological filters (e.g., disturbance, climate, competition, and herbivory) can also differentially affect establishment, persistence, or performance of a species (Bunker and Carson, 2005), and thus, relative strengths of ecological filters will vary across the life history stages of an organism (Keeley et al., 2005; Masaki et al., 2005; Nogueira et al., 2011; Lasky et al., 2013). For example, landscape heterogeneity may govern propagule supply and affect initial species presence and density, but local topoedaphic conditions might drive subsequent persistence and growth (Neilson et al., 2005). Due to these complexities, tracking the fate of colonizing cohorts in heterogeneous landscapes could yield powerful insights into how species distributions are shaped over space and time.

In forests, opportunities for cohort studies are rare because trees can establish at different times during succession and persist

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for decades (Whitlock, 1993; Hughes et al., 2013). However, stand-replacing disturbances allow for establishment of species cohorts, and disturbances may also facilitate expansion beyond previous patterns of occurrence if environmental conditions have been changing (Johnstone et al., 2010; Turner, 2010; Ettinger et al., 2011; Mann et al., 2012). In subalpine and boreal conifer forests, high-severity wildfires initiate a pulse of postfire tree regeneration, and resulting tree cohorts offer opportunities to evaluate filters that influence their success over time (Romme, 1982; Turner et al., 1997, 2004; Johnstone and Chapin, 2006a). Following the extensive 1988 fires in Yellowstone National Park (Wyoming, USA), a cohort of trembling aspen (*Populus tremuloides*) seedlings established in burned lodgepole pine (*Pinus contorta* var. *latifolia*) forests. These colonizing aspen were found far from (>15 km) and at higher elevations (>500 m) than prefire aspen stands (Turner et al., 2003a; Romme et al., 2005). Excavation and genetic analyses confirmed aspen were seedlings (not resprouts), and 92% of stems were genetically distinct (Stevens et al., 1999; Romme et al., 2005). This widespread recruitment event provided an exceptional opportunity to investigate 25 years of development in a colonizing tree cohort.

Aspen is the most widespread native tree species in North America (Fowells, 1965), ranging from northern Mexico to northern Alaska, and has a flexible life-history strategy (Barnes, 1975; Jones, 1985; Rogers et al., 2013). Aspen are often long-lived because individuals (genets) can produce multiple generations of genetically identical stems (ramets) from a common root system (Day, 1944). Aspen also reproduce sexually, and seed dispersal followed by recruitment is necessary for distribution shifts. Aspen seedling recruitment had been considered rare in the Rocky Mountains because a narrow range of conditions are required for germination and establishment. Yet, a growing number of studies report establishment following stand-replacing fires (Kay, 1993; Quinn and Wu, 2001; Turner et al., 2003a; Landhäusser et al., 2010; Fairweather et al., 2014; Krasnow and Stephens, 2015). Aspen seedling recruitment events appear to be occurring more frequently at higher elevations, facilitating their upslope expansion as climate warms (Turner et al., 2003a; Kashian et al., 2007; Landhäusser et al., 2010). Concomitantly, recent widespread mortality of mature aspen, particularly at southern latitudes and low elevations (Worrall et al., 2013), has heightened interest in understanding shifting distributions (Frey et al., 2004; Hogg et al., 2008; Hanna and Kulakowski, 2012; Bell et al., 2014; Yang et al., 2015). Thus, identifying ecological filters that facilitate or constrain aspen establishment is critical for anticipating shifts in their presence and abundance (Krasnow and Stephens, 2015). Long-term study of a postfire seedling aspen cohort could also strengthen our understanding of how spatially and temporally shifting ecological filters dictate where colonizing species successfully establish and grow.

During early postfire years (i.e., within the first decade), ecological filters affecting initial presence and density of colonizing tree species are related to fire severity and propagule pressure. In Yellowstone, postfire aspen establishment depended on occurrence of fire and proximity to seed source, though seedlings were found as far as 15 km from mature aspen. Fine-scale (<200 m) variation in aspen density was primarily related to elevation, with greater densities at lower elevations, while across broad scales (>1000 m), initial aspen densities increased with burn severity (Turner et al., 2003a). Establishment, density, and growth of colonizers will also be affected by climate, particularly for trees that have not developed sufficient root systems to survive inhospitable conditions. However, early postfire competition is likely minimal, as wildfires release previously unavailable resources and reduce plant uptake (Smithwick et al., 2005a).

Once colonizers establish, other filters, such as soil conditions and biotic interactions (including inter-specific competition and herbivory) are likely to become increasingly important determinants of persistence and growth (Kaye et al., 2005; Cavard et al., 2011; Seager et al., 2013). Benefits of soil fertility for aspen growth are well documented (Hobbie and Chapin, 1998; Smith et al., 2011) and, in Yellowstone, postfire colonizing aspen grow very slowly because soils are highly infertile (Romme et al., 2005). As growth of postfire conifers accelerates, competition with aspen for water, nutrients, and light may intensify (Romme et al., 2005), altering aspen stem and root growth and increasing aspen mortality (Casper and Jackson, 1997). Aspen are a nutrient-rich resource for herbivores (DeByle, 1985), and browsing by ungulates such as elk (*Cervus elaphus*) can limit ramet (Romme et al., 1995; Rogers and Mittanck, 2014) or seedling heights (Romme et al., 2005). Browsing effects depend on ungulate behavior and population size, which varies over time; a substantial decline in Yellowstone elk numbers between 1997 and 2014 (Smith et al., 2015) has been linked to increased aspen-ramet heights in mature stands (Painter et al., 2014).

We quantified how multiple ecological filters have affected the success of a colonizing seedling-aspen cohort that established after the 1988 Yellowstone fires. We asked: (1) How have aspen presence, density, and size varied across the postfire landscape, and what ecological filters explain these spatial and temporal patterns? We hypothesized climate and elevation would serve as primary filters of aspen presence and density, and soil fertility, competition with conifers, and ungulate browsing would influence aspen size. We also hypothesized climate and elevation would become less important for predicting aspen presence over time, and that declining numbers of Yellowstone elk would correlate with aspen release, but competition with conifers would increasingly constrain aspen size. To further characterize how competition with conifers might influence aspen stem and root growth, we excavated colonizing aspen 26 years postfire to ask: (2) How does aspen above- and belowground biomass vary with lodgepole pine density? We hypothesized that 26 years postfire, aspen would have begun developing clonal structure, thus allocating more biomass to lateral roots than stems. We also expected biomass allocation to vary with lodgepole pine density, but with two alternative patterns possible. If nutrients or water limit growth, aspen would allocate relatively more biomass to roots than stems in high-density lodgepole pine stands. If light limits growth, aspen would allocate relatively more biomass to stems than roots.

2. Materials and methods

2.1. Study area

Located in northwestern WY, USA, Yellowstone National Park is approximately 9000 km^2 (Fig. 1). Our study focused on the subalpine central plateau that covers most of the park and is dominated by coniferous forest, primarily lodgepole pine (Despain, 1991). Climate is cool with mean temperatures of −9 °C in the winter and 12 °C in the summer (Western Regional Climate Center, 2014). An extensive winter snow pack develops at high elevations, increasing growing-season moisture availability. Soils include highly infertile, rhyolite derived substrates, slightly less infertile andesite substrates, and pockets of glacial/lake detrital deposits. In 1988, approximately 174,000 ha of forest burned as stand-replacing fire on the central plateau (Turner et al., 2003b, 2004). Before the 1988 wildfires, aspen occupied 1.4% of Greater Yellowstone (Brown et al., 2006) and were primarily present in low-elevation montane forests (Despain, 1991). Aspen were

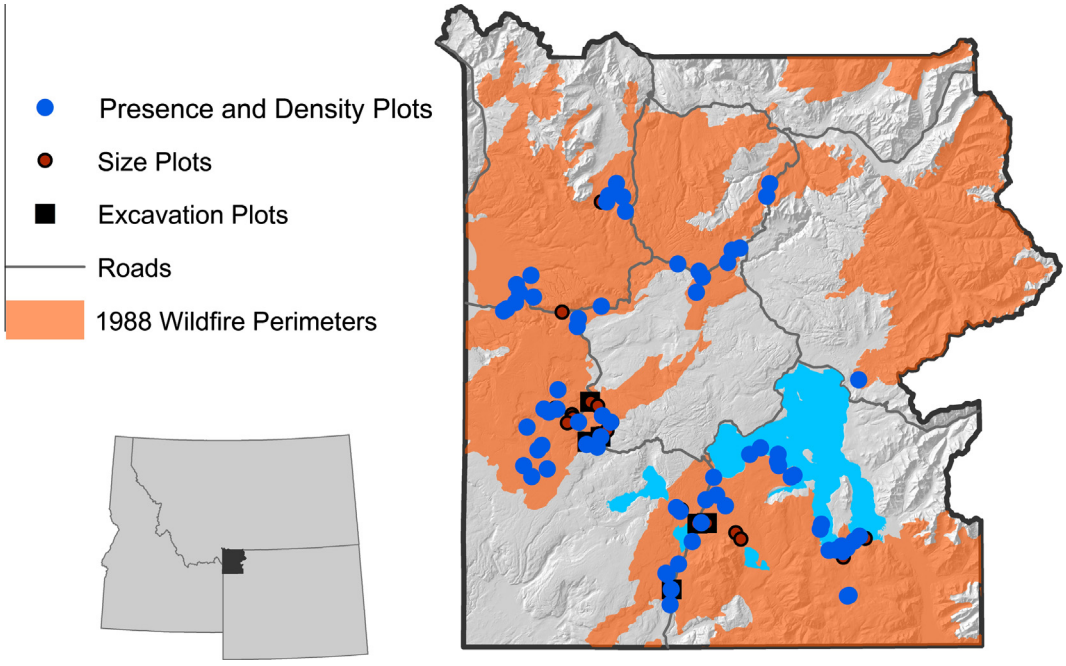

Fig. 1. Map of the study plots across the central plateau, Yellowstone National Park, WY, USA. Blue circles are 72 aspen presence and density plots sampled in 1999 (11 years postfire) and 2012 (24 years postfire). Red dots are 21 aspen size plots sampled in 1996 (8 years postfire), 2000 (12 years postfire), and 2013 (25 years postfire). Black squares are six aspen excavation plots sampled in 2014 (26 years postfire). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

present only occasionally on the central plateau, restricted to talus slopes, where conifer forests were not present (Turner et al., 2003a).

2.2. Field sampling

2.2.1. Aspen presence and density

During summer 2012, we resampled 72 widely distributed 0.25-ha permanent plots (Fig. 1) in lodgepole pine forests that burned in 1988 as stand-replacing fire. These plots were established and sampled in 1999 (Turner et al., 2004), and we followed the same sampling protocols. Briefly, we tallied the number of postfire aspen and conifers by species in three parallel 50-m × 2-m belt transects oriented due north and separated by 25 m. Additionally, we recorded the basal diameter of 25 lodgepole pines.

2.2.2. Aspen size

During summer 2013, we resampled 21 smaller permanent plots (Romme et al., 2005) (Fig. 1). Plots were established in 1996 and were of variable size to encompass at least 10 aspen seedlings. Aspen height and basal diameter, evidence of ungulate browsing, and local lodgepole pine density had previously been measured in 1996, 1997, 1998, and 2000 (see Romme et al., 2005), and we followed the same protocols. Briefly, we sampled along a transect of 10–20 m in length, measuring aspen size on both sides and counting lodgepole pines within a 2–4-m belt (depending on stand density). We examined leaders and branches for browsed buds and twigs to determine percent of individuals browsed. Three mineral soil samples were collected using a 15-cm long PVC corer. Soils were sieved, composited by site, and oven dried at 60 °C to constant mass. Soils were analyzed for % total soil nitrogen (N) (micro Kjeldhal procedure), soil pH (measured in water), % organic matter (determined using dry combustion), and available phosphorous (Bray P1 extract) by the University of Wisconsin Soil and Plant Analysis Laboratory, Madison, WI, USA (UW SPAL, 2013).

2.2.3. Aspen above- and belowground biomass

Eighty individual aspen had been excavated in 1996 to document clonal structure and to calculate above- and belowground biomass ratios (see Romme et al., 2005). To estimate current above- and belowground biomass ratios, in summer 2014, we excavated 10 aspen at six plots (approximately two aspen per plot) using hand tools (Fig. 1). Although a sample size of 10 is small, it was logistically infeasible to harvest additional trees. Plots spanned a range of lodgepole pine densities (500–33,000 lodgepole pine ha^{-1}) tallied along a 20-m × 4-m belt transect. At each site, we selected one or two of the largest aspen individuals, separated by at least 15 m. We first measured height and basal diameter of the dominant stem. We then excavated all lateral and sinker roots until they were too small to follow (≤2 mm diameter). We measured the length of each lateral root, counted all ramets that emerged from each lateral root, and recorded their height and basal diameter. All biomass was harvested and separated into three components: aboveground woody biomass, leaves, and belowground biomass. Biomass was dried at 70 °C to constant mass and dry mass was recorded. Cross sections from each dominant stem were collected to determine stem ages. Stem cross sections were finely sanded (400 grit) and tree rings were counted with an Olympus SZ-61 6.7x–45x stereo microscope (Stokes and Smiley, 1996).

2.3. Ecological filters

Covariates related to climate, topoedaphic conditions, and competition with lodgepole pine were obtained for each plot (Appendices A and B). Gridded temperature and precipitation PRISM data (4-km resolution) were used to characterize climate for the 72 aspen presence-density plots and the 21 aspen size plots (PRISM Climate Group, 2014). Mean growing season (April–September) temperature and mean annual precipitation were calculated for the decade prior to each sampling year. Topoedaphic variables included elevation and substrate, which was grouped

into four categories, according to physical characteristics of the soil and their expected effect on vegetation (Turner et al., 2004). Ordered from least to most fertile, based on nutrient status and water-holding capacity (Turner et al., 2004), substrate categories included rhyolite till, which occurs on uplands and is derived from rhyolite-based glacial till; rhyolite glacial, located on glacial outwash plains; rhyolite low-base saturation, occurring on lake plains and derived from rhyolite-based glacial rubble; and andesite, located in glacial valleys and alluvial fans. The andesite category includes soils derived from andesite, as well as alluvial, lake-based, and organic deposits. As an indicator of competition with lodgepole pine, annual aboveground net primary production (ANPP) was calculated for each of the 25 trees using allometric equations specific to the region and tree age (Turner et al., 2004; Copenhaver and Tinker, 2014). Annual stand-level ANPP was then determined by multiplying mean tree ANPP by tree density and reported as Mg ha^{-1} yr^{-1} (Turner et al., 2004).

2.4. Data analysis

2.4.1. Aspen presence and density

Presence of aspen seedlings in 1999 and persistence to 2012, given aspen presence in 1999, were analyzed using logistic regression. We also used multiple linear regressions to analyze aspen seedling density when they were present in 1999 and when aspen persisted from 1999 to 2012. For all regressions, variables were log transformed as necessary and multicollinearity was evaluated using variance inflation factor cutoff of less than five. Aspen seedling presence and density were modeled as a function of climate (mean growing season temperature and mean annual precipitation), topo-edaphic conditions (elevation and substrate), and conifer competition (lodgepole pine ANPP) (Appendix A). Exhaustive model selection (Burnham and Anderson, 2002) was conducted using the R package MuMIn (Bartón, 2015). Coefficients from all top models (ΔAICc < 2) are presented. All analyses were conducted in R statistical software (R Core Development Team, 2010).

2.4.2. Aspen size

Aspen height and basal diameter in 1996, 2000, and 2013 were modeled using multiple linear regressions, as for aspen density. Soil organic matter, total soil N, and available phosphorous were highly correlated. To avoid collinearity, we conducted a factor analysis on the 1996 soil data with varimax rotation (Revelle, 2015). Total N loaded most strongly on factor one. Soil pH loaded most strongly on factor two (Appendix C). Thus, total N and soil pH were retained in analyses. Additional independent variables included climate variables (average growing season temperature and average annual precipitation), and conifer competition (lodgepole pine density) (Appendix B). We used lodgepole pine density instead of ANPP, because lodgepole pine basal diameters necessary for applying allometric equations were not measured in 1996 or 2000, but lodgepole pine density is positively correlated with stand-level ANPP (Turner et al., 2004). Ungulate browsing could not be included in regressions because browsing was uniformly high in 1996 and uniformly low in 2013, providing little variation among sites for regression.

2.4.3. Aspen above- and belowground biomass

Aspen biomass allocation was quantified by calculating two ratios: (1) aboveground woody biomass to belowground biomass,

Table 1
(A) Logistic regression results from top models (AICc < 2) predicting aspen presence in 1999 and persistence to 2012 if aspen were present in 1999. Coefficients (SE) are presented. (B) Linear regression results from top models (AICc < 2) predicting aspen density in 1999 and if aspen persisted from 1999 to 2012. Coefficients (SE) are presented. Model fit includes likelihood ratio tests for logistic regressions and Adj. R^2 for linear models.

		Climate		*Topo-edaphic conditions*				*Conifer competition*	
	Intercept	Log Growing season temperature	Log Annual precipitation	Elevation	Rhyolite till	Rhyolite glacial	Rhyolite low base	Log Lodgepole pine ANPP	Model Fit
A									
1999 aspen presence									
Model 1	−25.98**	30.04 (14.86)**			−0.34 (1.36)	−3.96 (1.46)***	−0.65 (0.78)	5.33 (1.97)***	32.0***
Model 2	−2.75		8.74 (4.37)**	−0.01 (0.004) **	−0.67 (1.39)	−4.66 (1.63)***	−0.90 (0.78)	6.40 (2.26)***	33.8***
Model 3	−35.28**	28.44 (15.19)*	3.59 (3.65)		−0.39 (1.36)	−4.09 (1.52)***	−0.65 (0.77)	6.13 (2.19)***	33.0***
2012 aspen persistence									
Model 1	−8.61*			0.004 (0.002)*					3.2*
Model 2	18.71*	−19.64 (12.04)*							2.8*
Model 3	0.31								–
Model 4	7.64	−20.62 (12.27)*	4.13 (4.55)						3.7
Model 5	3.15	−9.53 (16.8)		0.003 (0.003)					3.54
B									
1999 aspen density									
Model 1	−5.02*	8.17 (2.89)***							0.14
2012 aspen density									
Model 1	2.17***								–
Model 2	2.66	5.19 (3.45)							0.05
Model 3	2.42***							−0.35 (0.26)	0.03
Model 4	−1.55		1.27 (0.98)						0.03
Model 5	−9.12	8.84 (4.23)**		0.001 (0.001)					0.08
Model 6	−2.29	5.05 (3.39)						−0.34 (0.26)	0.08

* $P \leq 0.1$.
** $P < 0.05$.
*** $P < 0.01$.

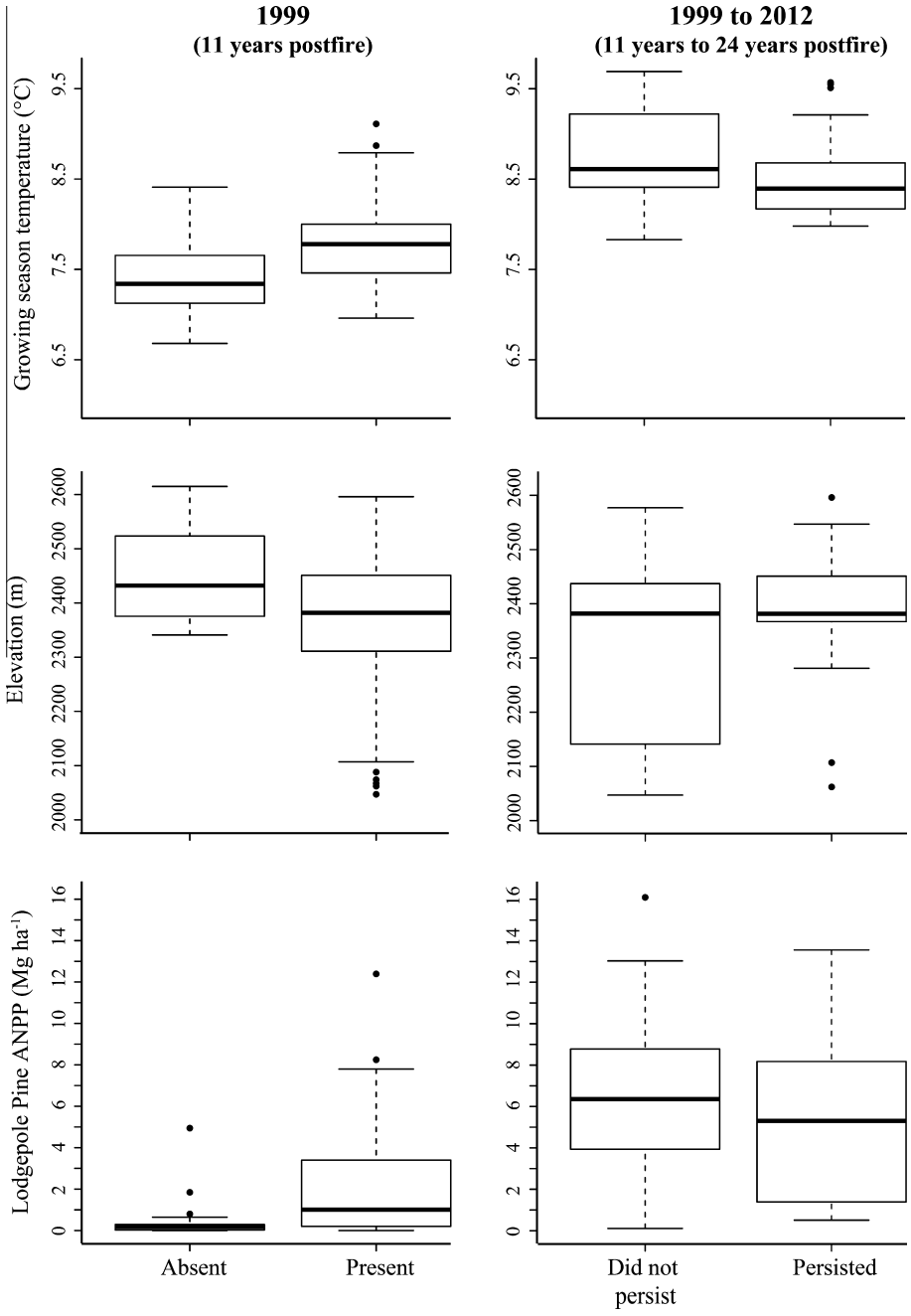

Fig. 2. Aspen seedling presence in 1999 and persistence from 1999 to 2012 vs. growing season temperature (°C), elevation (m), and lodgepole pine ANPP (Mg ha^{-1} yr^{-1}).

and (2) belowground biomass to whole plant biomass (belowground + aboveground woody + leaf biomass). One plot was excluded from biomass ratios as we were unable to harvest the entire taproot that extended below an immoveable rock. Because root length may be a good indicator of nutrient and water acquisition capabilities (Chapin et al., 2012), we calculated four other ratios: dominant stem height to median lateral root length, mean lateral root length, and max lateral root length, and sum of stem heights (dominant stem + ramets) to sum of lateral root lengths. The site excluded from biomass ratios was included in length ratios because we were able to collect all lateral roots of that individual, allowing for rigorous comparison. Relationships between all ratios and lodgepole pine density were evaluated using Kendall's Tau, which is a correlation coefficient appropriate for data with tied ranks.

3. Results

3.1. Aspen presence and density

In 1999, aspen were present at 45 of 72 plots (62.5%). Probability of aspen presence in 1999 increased strongly with growing season temperature (Table 1A and Fig. 2). Aspen were also more likely to be present in plots where annual precipitation and lodgepole pine ANPP were higher (Fig. 2). Aspen were less likely to occur at high elevations (Fig. 2) and on infertile rhyolite-glacial soil, as compared to andesite soils. Aspen seedlings persisted from 1999 to 2012 at 26 of the 45 plots (58%). Effects of growing-season temperature and elevation switched directions from 1999 (Table 1A and Fig. 2). Aspen were more likely to persist from 1999 to 2012 at *higher* elevations and *cooler* temperatures.

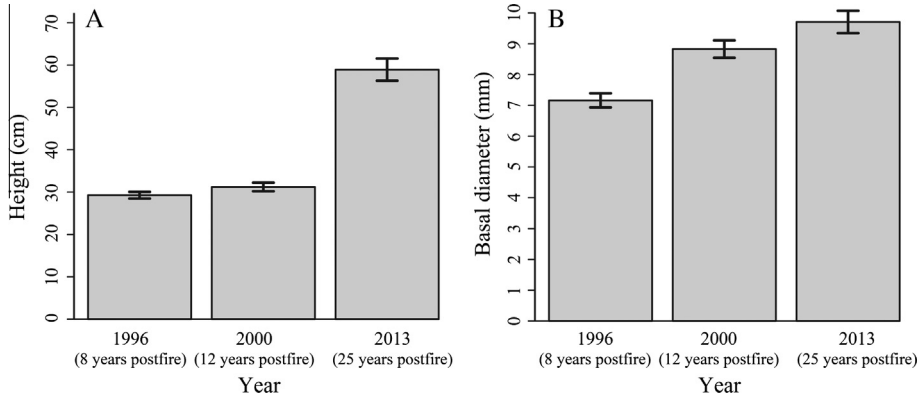

Fig. 3. Mean aspen (A) height (cm) and (B) basal diameter (mm) in 1996 (n = 392), 2000 (n = 392), and 2013 (n = 381) at 21 aspen size plots. Values are mean ± one standard error. Data from 1996 and 2000 have been previously published in Romme et al. (2005).

Table 2
(A) Linear regression results from top models (AICc < 2) predicting mean aspen height in 1996, 2000 and 2013. (B) Linear regression results from top models (AICc < 2) predicting mean aspen basal diameter in 1996, 2000 and 2013 at 21 aspen size plots. Coefficients are presented (SE). Data from 1996 and 2000 have been previously published in Romme et al. (2005).

		Climate		*Topo-edaphic conditions*		*Conifer competition*	
	Intercept	Growing season temp	Annual precipitation	Soil pH	Log total soil N	Log lodgepole pine density	Adj. R^2
A							
1996 height							
Model 1	0.01			0.22 (0.07)***	−0.24 (0.11)**		0.38
2000 height							
Model 1	−0.38			0.33 (0.08)***			0.43
Model 2	−0.01			0.31 (0.08)***		−0.07 (0.05)	0.46
Model 3	−0.80		0.0004 (0.0003)	0.34 (0.08)***			0.44
Model 4	−0.28			0.33 (0.08)***	0.12 (0.12)		0.43
2013 height							
Model 1	−0.16			0.47 (0.12)***	0.62 (0.19)***		0.48
Model 2	0.36			0.44 (0.12)***	0.64 (0.19)***	−0.09 (0.06)	0.52
B							
1996 Basal diameter							
Model 1	−0.08			0.16 (0.09)*			0.10
Model 2	−0.98	0.23 (0.13)*					0.10
Model 3	0.84***						
Model 4	1.34***		−0.001 (0.0004)				0.08
Model 5	0.46		−0.001 (0.0004)	0.15 (0.09)			0.15
Model 6	−0.29	0.10 (0.15)	−0.0004 (0.0005)	0.12 (0.10)			0.12
2000 Basal diameter							
Model 1	−1.40	0.30 (0.11)**					0.24
Model 2	−1.47	0.21 (0.12)*		0.14 (0.09)			0.30
Model 3	−0.23			0.21 (0.08)**			0.23
Model 4	−0.39			0.21 (0.08)**	−0.18 (0.11)		0.28
Model 5	−1.02	0.29 (0.11)**				−0.07 (0.05)	0.28
Model 6	−0.03			0.20 (0.07)**	−0.19 (0.11)*	−0.08 (0.05)	0.33
Model 7	0.10			0.20 (0.08)**		−0.07 (0.05)	0.25
Model 8	−1.12	0.21 (0.12)*		0.13 (0.08)		−0.06 (0.05)	0.33
2013 Basal diameter							
Model 1	−0.23			0.36 (0.10)***	0.32 (0.15)**	−0.10 (0.05)**	0.50
Model 2	−0.39			0.32 (0.10)***		−0.09 (0.05)*	0.40
Model 3	−0.83			0.39 (0.10)***	0.30 (0.16)*		0.39

* $P < 0.1$.
** $P < 0.05$.
*** $P < 0.01$.

In the 45 plots where aspen were present in 1999, mean density was 522 ± 140 stems ha^{-1}. In the 26 plots where aspen persisted to 2012, mean density declined to 310 ± 147 stems ha^{-1}. In 1999 and 2012, aspen density increased with growing season temperature (Table 1B and Appendix D), though models explained little of the variation (adj. $R^2 \leq 0.14$).

3.2. Aspen size

Mean aspen height was similar in 1996 (29.3 ± 0.8 cm) and 2000 (31.2 ± 1.0 cm), then nearly doubled by 2013 (58.9 ± 2.6 cm) (Fig. 3A). The tallest aspen recorded in 1996 was 92.5 cm; in 2013, the tallest aspen was 323 cm. Ungulate browsing declined

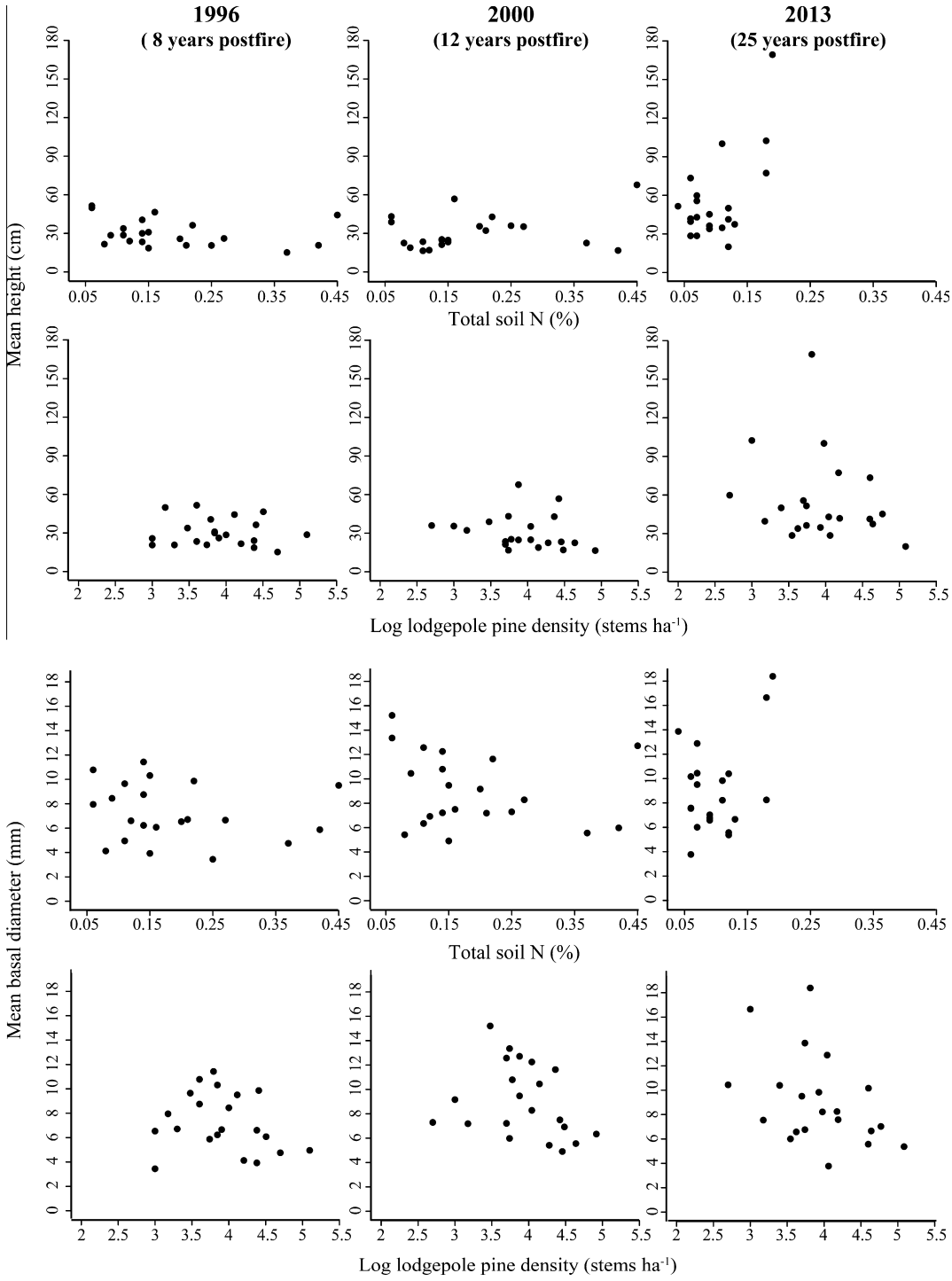

Fig. 4. Mean aspen height (cm) and basal diameter (mm) in 1996, 2000, and 2013 vs. total soil N (%), and log transformed lodgepole pine density (ha^{-1}). Data from 1996 and 2000 have been previously published in Romme et al. (2005).

across the three study periods. Eighty-six percent of stems showed evidence of browsing in 1996, but only 2.6% of stems were browsed in 2013. Across all three sampling periods, aspen heights were related to soil pH, with taller aspen trees growing in more basic soils (Table 2A). Total soil N declined markedly between 1996 and 2013 (between eight and 25 years postfire, coinciding with rapid growth of lodgepole pine), and total N was important for explaining aspen heights (Fig. 4). In 1996, aspen trees were shorter in plots with the highest total soil N (>0.25%). As total N declined over time, the relationship switched, and aspen height increased with total N in 2013.

Mean aspen basal diameter increased from 7.2 ± 0.2 mm in 1996 to 9.7 ± 0.4 mm in 2013 (Fig. 3B). In 1996, aspen basal diameters were larger in more basic soils and at plots where growing season temperature was warmer (Table 2B) and these same relationships strengthened by 2000 (Table 2B). Aspen basal diameters in 2013 were larger at plots with higher total soil N (Fig. 4) and more basic soils, and smaller at sites with high lodgepole-pine

Table 3
Measurements of 10 excavated aspen and lodgepole-pine stand characteristics at six sites. Height and basal diameter measurements of ramets are calculated only for aspen that produced ramets. Biomass measurements exclude one site because not all belowground biomass could be harvested, due to logistical constraints.

	Mean	SE	Median	Min.	Max.	Obs.
Dominant stem morphology						
Dominant stem height (cm)	117.3	25.0	91.5	40.0	300.0	10
Dominant stem basal diameter (cm)	2.4	0.6	2	1.1	7.6	10
Age in 2014	19.2	1.1	20	12	24	10
Ramet morphology						
Number of ramets	1.6	0.7	1	0	7	10
Ramet height (cm)	49.7	10.8	32.5	7.5	135.0	16
Ramet basal diameter (cm)	1.4	0.4	0.7	0.3	4.5	16
Root morphology						
Number of lateral roots	5.2	0.77	4.5	2	10	10
Lateral root length (cm)	166.1	30.2	101.5	16.5	973.0	10
Live biomass						
Aboveground woody biomass (g)	698.6	625.5	66.9	34.0	5,700.9	9
Leaf biomass (g)	54.3	44.6	6.9	1.63	430.3	9
Belowground biomass (g)	374.0	331.4	35.0	25.0	3,025	9
Ratios						
Above:Belowground biomass ratio	1.7	0.2	1.9	0.8	2.8	9
Root: whole plant biomass ratio	0.4	0.03	0.3	0.2	0.5	9
Dominant stem height: median root length	1.0	0.18	1.0	0.3	2.2	10
Dominant stem height: mean root length	1.0	0.18	1.0	0.3	2.2	10
Dominant stem height: max root length	0.7	0.16	0.6	0.23	1.9	10
Total stem height: total root length	0.33	0.09	0.23	0.13	1.1	10

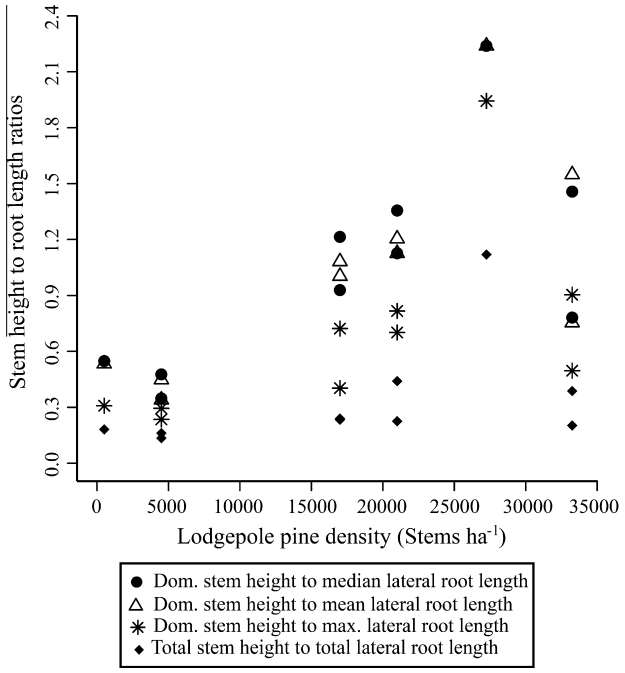

Fig. 5. Stem height to lateral root length ratios vs. lodgepole pine density (ha^{-1}) for 10 excavated aspen in 2014 (26 years postfire) (Kendall's Tau = 0.44–0.58, $P < 0.10$).

densities (Fig. 4). The amount of variance explained in both height and basal diameter models increased substantially in the later sampling periods (Table 2).

3.3. Above- and belowground biomass

All ten excavated aspen had produced lateral roots by 2014, as compared to half of the plants excavated in 1996 (Romme et al., 2005), and seven of the aspen in 2014 supported ramets (Table 3). Forty percent of whole plant biomass was in roots (Table 3), similar to postfire aspen excavated in 1996 (Romme et al., 2005). Lodgepole pine density was uncorrelated with aboveground-to-belowground biomass ratio and belowground-to-whole plant biomass ratio (Kendall's Tau = 0.12 and −0.18, respectively $P > 0.10$). However, lodgepole-pine density was positively correlated with all stem-height to root-length ratios (Kendall's Tau = 0.44–0.58, $P = 0.08$–0.02) (Fig. 5). Height of the dominant stem was greater than length of lateral roots for aspen in high- vs. low-density lodgepole pine stands.

4. Discussion

Our long-term analyses of a colonizing postfire seedling aspen cohort in Yellowstone illustrate how disturbance interacts with shifting ecological filters to influence landscape patterns of species occurrence and performance over time (Table 4). Fire set the stage for aspen seedling establishment; aspen only recruited in areas that burned severely, and initial postfire seedling densities decreased with distance to mature aspen (Turner et al., 2003a; Brown et al., 2015). In subsequent years, aspen grew slowly, with the tallest aspen only reaching 3.2 m after 25 years (Appendix E). Subsequently, ecological filters including climate, competition, herbivory, and soils differentially affected aspen presence, persistence, and size. Several filters (growing season temperature, competition, herbivory) also changed through time, altering their effects, and shifting where on the landscape aspen persistence and growth were favored. Many of these effects would have been missed without long-term study (Table 4) which could lead to misinformed conclusions about shifting aspen distributions in Yellowstone.

Temperature has warmed in Yellowstone since the 1988 fires, and this warming appears to have already affected the geographic distribution of postfire aspen (Table 4). Initially, differences in temperature across elevation gradients favored postfire aspen establishment at lower-elevation sites that aligned more closely to the pre-fire distribution of mature aspen in Yellowstone. This was likely because the colder temperatures and deeper snowpacks at

Table 4
Summary of trends in ecological filters between 1996–2000 and 2013 and their shifting influence on the presence, persistence, and size of a colonizing postfire aspen-seedling cohort in Yellowstone National Park.

Filter	1996–2000 (8–12 years postfire)	Filter trend 1996–2013	2012–2013 (24–25 years postfire)
Growing season temperature	**Strong filter**: Cold temperatures precluded aspen presence at high elevations but permitted presence at warmer lower elevations	Increase. Substantial warming (7.7–8.5 °C from 1990s to 2000s)	**Strong filter**: Aspen persisted at mid-elevations with cooler temperatures but were eliminated at lower-warmer elevations
Lodgepole pine competition	**No filter**: Lodgepole pine seedlings too small to compete with aspen seedlings	Increase. Rapid growth of lodgepole pine	**Strong filter**: Smaller aspen with high lodgepole pine density
Soil nitrogen	**Weak filter**: Shorter aspen in plots with high total soil N	Decrease. Decline in total soil N, particularly where total soil N had been high in 1996–2000	**Strong filter**: Taller aspen with greater total soil N
Ungulate browsing	**Strong filter**: Uniformly heavy browsing (~90% of stems browsed) kept stems short	Decrease. Substantial decline in elk density and browsing	**No filter**: Aspen size no longer influenced by browsing (<3% of stems browsed)
Soil pH	**Strong filter**: Larger stems in more basic soils	No change	**Strong filter**: Larger stems in more basic soils

higher elevations limited aspen survival and growth (Romme et al., 2005; Krasnow and Stephens, 2015). However, growing season temperatures have since increased nearly 1 °C among our plots. This recent warming appears to have been sufficient for aspen to persist to 2012 at elevations substantially above its prefire distribution, suggesting that temperature limitation has been relaxed at the higher elevations and perhaps as even increased at lower elevations.

Competition with postfire lodgepole pine had little effect on aspen survival and growth during the first decade postfire (Romme et al., 2005), but effects of competition on aspen size were evident after 25 years (Table 4). Competition with conifers is a key driver of aspen recruitment, survival, and growth throughout the Rocky Mountains (Kaye et al., 2003; Calder et al., 2011; Calder and St. Clair, 2012), and our data suggest lodgepole pine contributed to nutrient and light limitations. Young lodgepole pines grow rapidly and are now larger than aspen, reaching heights of 3–4 m, with some >6 m (Copenhaver and Tinker, 2014). Dense young lodgepole pine forests are strong N sinks (Turner et al., 2009), and soil inorganic N declines with lodgepole pine density (Smithwick et al., 2009; Turner et al., 2009). Soil N has declined over time in our plots, and the relationship between aspen size and soil N switched direction. Soil nitrate and ammonium concentrations increase after fire (Smithwick et al., 2005b; Turner et al., 2007), and neither aspen nor lodgepole pine were likely N limited in early postfire years (Romme et al., 2009). Declining soil N availability over time may have contributed to smaller aspen stature in high-density lodgepole pine stands. Additionally, smaller basal diameters of aspen in high-density lodgepole pine stands are consistent with the increased ratio of stem height to root length. Although belowground biomass remained a relatively consistent proportion (~40%) of total plant biomass over time, aspen in dense lodgepole pine stands elongated their dominant ortet stem more than their lateral roots, suggesting competition for light is also important (Frey et al., 2003).

Herbivory on postfire aspen declined drastically over time, and this surely has contributed to aspen height growth (Table 4). Ramet heights in mature aspen stands on Yellowstone's northern winter range have also increased markedly (Painter et al., 2014). Elk seek out aspen, and winter browsing has been high for many years on the northern range (Romme et al., 1995; Ripple and Larson, 2000; Kimble et al., 2011). Although our study area is on elk summer range, we also had observed very high herbivory rates on aspen seedlings during the early 2000s. Nearly 90% of stems were browsed (Romme et al., 2005). Elk habitat selection appears to not be influenced by fire (Wan et al., 2014). Even high-density postfire lodgepole pines and dense coarse down wood did not deter elk from finding and browsing seedling aspen (Forester et al., 2007). Following the 1995 reintroduction of wolves (*Canis lupus*), elk habitat selection shifted to higher elevations and more forested habitat, particularly, burned forest (Mao et al., 2005). Thus, browsing on aspen in postfire lodgepole pine forests was likely at its highest level during the first 15 years after fire. Since, predation on elk by wolves, grizzly bears (*Ursos horribilis*) and cougars (*Puma concolor*); harvest by hunters outside Yellowstone; and environmental change have resulted in fewer elk (Creel et al., 2007; Eberhardt et al., 2007; White et al., 2011; Christianson and Creel, 2014). The Yellowstone elk population declined from approximately 15,000 animals in 1997 to 5000 in 2014 (Smith et al., 2015).

It is notable that the central plateau of Yellowstone is not the most hospitable environment for aspen, and they grow slowly (Appendix E). After 25 years, many aspen were still less than 1 m tall. Given poor soils derived from volcanic substrate (Despain, 1991), it is not surprising that aspen presence and size were related to measures of soil fertility, consistent with other studies (Romme et al., 2005; Smith et al., 2011). Heterogeneity in topoedaphic conditions and microclimate within the landscape will likely continue to provide sites where aspen can survive.

Aspen density was not well explained by predictor variables included in our models. This may be because stem density is the net effect of two opposing processes – mortality and ramet production – that likely respond to different drivers. Following establishment, conceptual models predict strong intraspecific competition will lead to high early mortality in seedling cohorts of predominantly clonal species (Eriksson, 1992). Declining aspen presence and stem density on the central plateau reveals ongoing mortality. However, ramet production by genets that survived in favorable locations or outcompeted other individuals for resources (Frey et al., 2003) may counter mortality-driven declines in stem density.

What do our findings suggest for the future of aspen in the Rocky Mountains? Warming is expected to continue and fire frequency will likely increase during the 21st century (Westerling et al., 2011), which could favor aspen persistence and expansion. In the northern Rocky Mountains, climate suitable for aspen is projected to shift 750 m upward in elevation by the end of the 21st century (Rehfeldt et al., 2009), and drought has already increased mortality and decreased recruitment in marginal portions of the species' current distribution (Worrall et al., 2013). Disturbances that create suitable sites for aspen establishment from seed could play a central role in facilitating upslope expansion of the species (Landhäusser et al., 2010; Kulakowski et al., 2013), although competition could lead to their extirpation in dense conifer stands (Kaye et al., 2003). By resprouting, however, aspen may benefit from a critical a mechanism of persistence, should a fire reburn stands. Our sample size of excavated aspen was small due to logistical constraints, however, root development over the last 25 years suggests that Yellowstone's postfire aspen may have sufficient

lateral roots to resprout after fire. Resprouting aspen can grow faster than seedling conifers and can even dominate early postfire succession (Schier and Campbell, 1978; Bartos et al., 1994; Frey et al., 2003; Johnstone and Chapin, 2006b). In Yellowstone, the 2000 Boundary Fire re-burned 12-year old lodgepole pines and seedling aspen that regenerated after the 1988 fires. Young pines had not developed a seedbank before reburning. Thirteen years after the Boundary Fire, we observed that aspen density was five times greater than lodgepole pine density, and many aspen were more than 2 m tall (Turner et al., Unpublished data).

Our long-term study of a 25-year old colonizing aspen cohort suggests a shifting landscape mosaic where ecological filters that facilitate or constrain colonizing species vary in space and time. Many of the filters change slowly, and thus, it is difficult to anticipate where on the landscape a colonizing species will succeed without ongoing measurement of the organisms and their local environment. Our findings underscore the need for long-term study and the value of tracking colonizing cohorts for rigorously characterizing population responses to 21st century environmental change.

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Appendix A

Descriptive statistics of predictor variables used in analyses of postfire aspen presence and density in 1999 and 2012 (n = 72 plots). Values are mean (SE) (Min–Max).

Predictor variables	1999	Both years	2012
Climate			
Growing season temp (°C)	7.7 (0.1) (6.7–9.1)		8.5 (0.1) (7.8–9.7)
Annual precip. (mm yr^{-1})	881.6 (23.3) (618.8–1542)		829.7 (22.2) (586–1479.4)
Topo-edaphic			
Elevation (m)		2392.2 (16.4) (2047–2615)	
Rhyolite till (0, 1)		0.08 (0.03) (0–1)	
Rhyolite glacial (0, 1)		0.13 (0.04) (0–1)	
Rhyolite low base sat. (0, 1)		0.61 (0.06) (0–1)	
Andesite (0, 1)		0.18 (0.05) (0–1)	
Conifer competition			
Lodgepole ANPP (Mg ha^{-1} yr^{-1})	1.5 (0.3) (012.4)		5.0 (0.5) (0–16.5)

Appendix B

Descriptive statistics of predictor variables used in analysis of postfire aspen height and basal diameter in 1996, 2000, and 2013 (n = 21 plots). Values are mean (SE) (Min–Max).

Predictor variables	1996	2000	2013
Climate			
Growing season temp (°C)	8.0 (0.06) (7.3–8.2)	7.7 (0.06) (7.2–8.0)	8.4 (0.03) (8.1–8.7)
Annual precip (mm yr^{-1})	750.3 (17.3) (662.6–877.4)	830.0 (19.5) (734.7–977.8)	780.4 (17.4) (694.6–911.1)
Topo-edaphic			
Total soil N (%)	0.2 (0.02) (0.06–0.5)	0.2 (0.02) (0.06–0.5)	0.1 (0.01) (0.04–0.2)
Soil pH	5.6 (0.1) (4.7–6.3)	5.6 (0.1) (4.7–6.3)	5.3 (0.06) (4.9–6.1)
Conifer competition			
Lodgepole pine density (stems ha^{-1})	17,605 (6025) (1000–125,000)	16,071 (4174) (500–82,500)	19,543 (6237) (500–121,500)

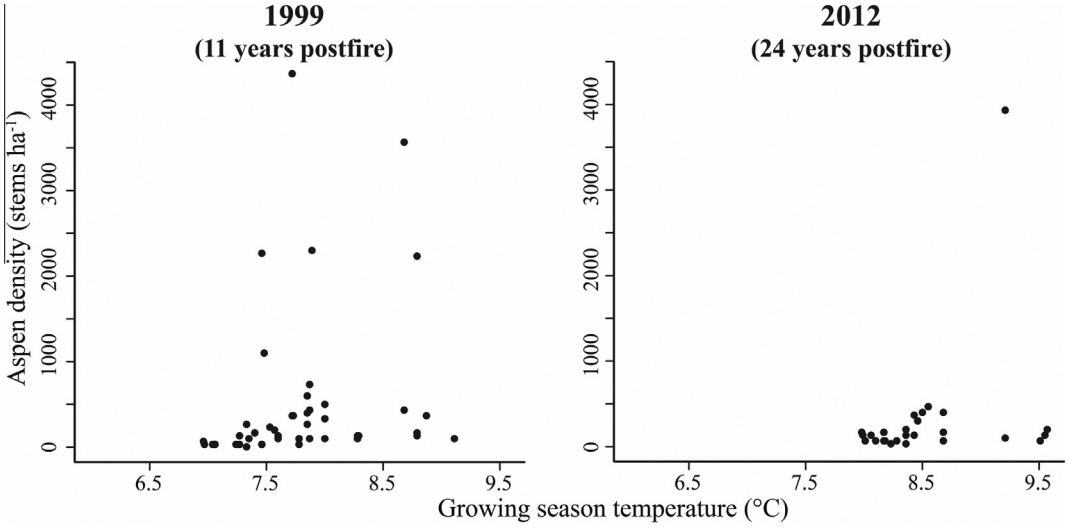
Appendix C

Factor analysis of 1996 soil variables showing rotated factor patterns.

Variables	Factor 1	Factor 2
Total soil nitrogen	0.97	0.24
% Soil organic matter	0.93	0.42
Soil pH	−0.11	0.51
Available soil phosphorous	0.06	0.42

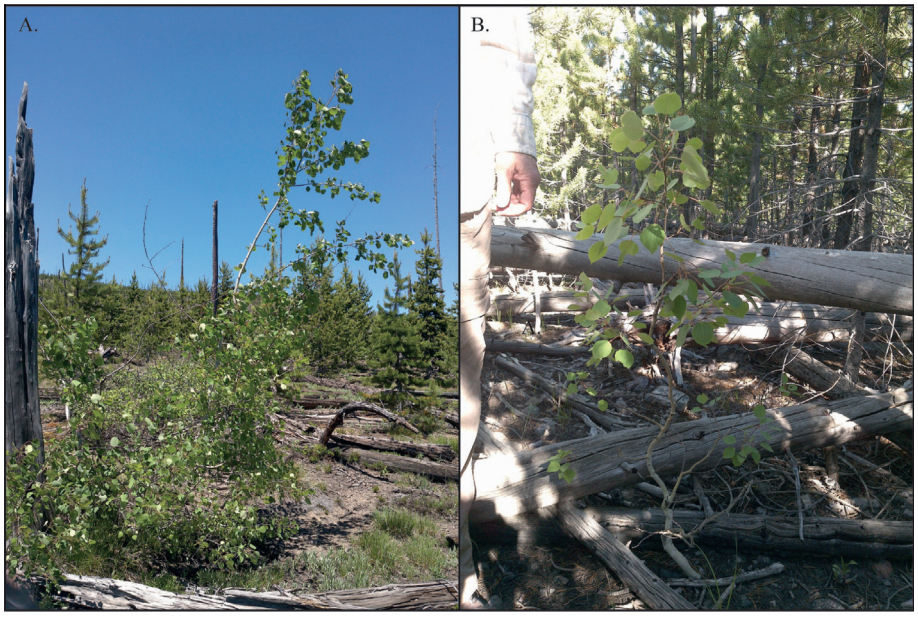
Appendix D

Aspen seedling densities in 1999 and 2012, where aspen were present, vs. growing season temperature (°C).



Appendix E

Postfire aspen grow very slowly on the central plateau of Yellowstone National Park, WY, USA. After 25 years, the tallest surveyed aspen (A) was just over 3 m tall. Mean aspen size was approximately 0.6 m tall (B).



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