

## RECONCILING DIVERGENT INTERPRETATIONS OF QUAKING ASPEN DECLINE ON THE NORTHERN COLORADO FRONT RANGE

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**Abstract.** Ecologists have debated over the past 65 years whether quaking aspen (*Populus tremuloides* Michx.) has or has not declined in abundance, vigor, or regeneration in western North America. Many studies have provided divergent interpretations of the condition of aspen forests, leading to difficulty in translating this ecological information into management recommendations. To reconcile these contrasting conclusions and to test the hypothesis that multiple types of aspen decline and persistence occur simultaneously on heterogeneous landscapes, we assessed 91 aspen stands across the northern Colorado Front Range to determine the range of ecological conditions that underlie aspen decline or persistence.

Approximately 15% of aspen forest area in our sample exhibited dieback of mature stems coupled with a lack of young trees indicative of declining stands, most often at lower elevations where elk browsing is heavy and chronic, and where effects of fire exclusion have been most significant. However, 52% of the area sampled had multiple cohorts indicative of self-replacing or persistent stands. Conifer dominance was increasing in over 33% of all aspen forest area sampled, most often at high elevations among lodgepole pine (*Pinus contorta* var. *latifolia* Englem. ex Wats.) forests. Reconstructions of relative basal area and density of aspen and lodgepole pine in these stands suggest cyclical dominance of these species, where conifers gradually replace aspen over long fire intervals, and aspen vigorously re-establish following stand-replacing fires. The diversity of ecological contexts across the northern Colorado Front Range creates a variety of aspen dynamics leading to decline or persistence, and no single trend describes the general condition of aspen forests in appropriate detail for managers. Active management may be useful in preserving individual stands at fine scales, but management prescriptions should reflect specific drivers of decline in these stands.

**Key words:** aspen decline; aspen dynamics; Colorado Front Range; *Populus tremuloides*; quaking aspen; Rocky Mountains.

### INTRODUCTION

A major land management controversy in western North America revolves around the extent to which quaking aspen (*Populus tremuloides* Michx.) has or has not declined in abundance, vigor, or regeneration over the past century. Beginning as early as the 1940s, ecologists such as Packard (1942), Krebill (1972), Olmstead (1979), and most recently Kay (1997a) have presented evidence suggesting that aspen forests across much of the western United States are on a trajectory leading to near disappearance within a few decades without active management to reverse the trend. Other studies, however, have documented “persistent” aspen stands across the West (e.g., Romme et al. 2001, Kurzle 2004), and aspen actually has increased in abundance in some areas during the past century (Manier and Laven 2002, Elliott and Baker 2004, Kulakowski et al. 2004).

Moreover, studies based on random sampling across a landscape often conclude that aspen is persistent at broad spatial scales, although it may be declining at local scales (Suzuki et al. 1999, Barnett and Stohlgren 2001).

Divergent interpretations of the status and trajectory of aspen forests make it difficult for land managers to develop general management guidelines that will maintain aspen on the landscape. Aspen forests are complex, variable, and may be declining in some areas and not others, but managers require ecological studies reconciling the many different perspectives of aspen dynamics in the western United States if they are to develop applicable protocols for management. This study describes a broad assessment of aspen forest dynamics in the northern Front Range of the Colorado Rocky Mountains, where considerable previous research has reported both decline (e.g., Packard 1942, Baker et al. 1997) and persistence (e.g., Suzuki et al. 1999, Kaye et al. 2003) of aspen. We located and documented the range of ecological contexts—the spatially and temporally heterogeneous drivers of aspen vigor and regeneration—for aspen dynamics in which contrasting interpretations have been made, as well as ecological

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contexts not previously described. Most importantly for managers, we explicitly define the spatial and temporal scales at which various concepts of aspen “decline” may or may not apply to any particular aspen stand in a given ecological context. This comprehensive approach is critical to effective, long-term aspen management (Holling and Meffe 1996).

Quaking aspen is the most widely distributed native tree species in North America (Little 1971, Perala 1990), but it occupies <2% of the North American Rocky Mountains (Krebill 1972). As the principal upland deciduous forest type on this landscape, aspen forests are “biodiversity hotspots” for native plants (Chong et al. 2001), insects, birds, and mammals (DeByle and Winokur 1985), and some would regard aspen as a foundational species in parts of the Rocky Mountains (Ellison et al. 2005). Aspen is also an economically important species both for timber and wood fiber, and is an important driver of tourism and recreation in western North America (Shepperd et al. 2001).

Aspen primarily regenerates asexually through root suckering, making its ecology and management unique among temperate forest types. An aspen “stand” is often one or more clones composed of genetically identical stems (ramets) arising from common, often extensive root systems (Barnes 1966). Removal or damage to the dominant trees by disturbances such as fire (Brown and DeByle 1987, Bartos et al. 1991) or logging (Jones 1975, Crouch 1983, Shepperd 1996) is a primary means of aspen forest regeneration. Left undisturbed, mature stems experience mortality as they approach about 120 years, and only a small proportion of ramets live beyond 200 years in this region (Krebill 1972, Mueggler 1989a). Aspen does reproduce sexually from seed following disturbances (Barnes 1966, Kay 1993, Romme et al. 1997), but broad-scale regeneration is uncommon because seeds will not germinate and survive without sustained moist weather conditions immediately following the disturbance (DeByle 1978, Romme et al. 1997).

Aspen decline has been defined as extensive dieback of existing aspen stems (Schier 1975), but more often it is described as a lack of ramet regeneration and recruitment. The failure of aspen clones (hereafter termed “stands” to describe the sampling unit) to regenerate has often been attributed to excessive ungulate herbivory, particularly by elk (*Cervus elaphus* Erxleben; Kay 1993, Baker et al. 1997, Kaye et al. 2005), due in part to removal of natural ungulate predators (particularly gray wolves, *Canis lupus* L.; White et al. 1998, Ripple and Larsen 2000, Ripple et al. 2001). Reduced aspen regeneration is also attributed to fire suppression, because wildfires have historically stimulated vegetative reproduction in aspen stands across the Rockies (Brown and DeByle 1987, Bartos et al. 1991). Increased fire intervals across western North America may or may not have also favored the encroachment of shade-tolerant conifers into many aspen stands (Harniss and Harper 1982, Crawford et al. 1998, Shepperd et al. 2001, Kaye et

al. 2005). Kay (1994, 1997a, b) has suggested that the elimination of frequent burning and elk hunting by Native Americans is the primary factor underlying aspen decline across most of western North America. The near extirpation of beaver (*Castor canadensis* Kuhl) cutting and foraging on aspen stems may have contributed to aspen decline, although beaver effects on aspen regeneration are likely to be minor (Baker et al. 1997). Climatic fluctuations may also affect establishment and/or regeneration in aspen stands (Romme et al. 1995, Elliot and Baker 2004).

Our main objective was to integrate differing interpretations of aspen trajectories for the northern Colorado Front Range by developing a comprehensive understanding of the ecological factors driving aspen dynamics across a heterogeneous landscape. Studies concluding that aspen are declining in this region (Packard 1942, Olmstead 1979, Baker et al. 1997) contrast with those documenting high variability in aspen stand structure and regeneration (Suzuki et al. 1999, Kaye et al. 2003, 2005). However, the spatial and temporal variability of the drivers of aspen decline or persistence in this region has not been explored despite the importance of this information for forest management prescriptions. We undertook a broad assessment of aspen stands on the Arapaho-Roosevelt National Forest (ARNF); previous studies were conducted mainly within protected wilderness areas with limited recent human impact, which may not represent aspen dynamics on other public lands where human land use is more intensive (Hessl and Graumlich 2002). Many of the aspen forests in the western United States are located on public land characterized by forest and wildlife management, and thus we found it most appropriate to examine aspen dynamics within a National Forest. We hypothesized that multiple threats to aspen persistence occur simultaneously on a single landscape, but the magnitude of each threat varies spatially. Therefore, understanding the relative proportion of each threat and the ecological context in which it occurs is critical if managers are to sustain aspen forests across the western United States. The ARNF represents only a subset of the ecological conditions present across the western United States, but reconciling very different interpretations of aspen decline within a single landscape would be an important advance in understanding aspen dynamics across the range of this broadly distributed forest type.

## METHODS

### *Study area*

We examined aspen stands across the 260 000 ha of the Canyon Lakes District (CLD) of the ARNF located within Larimer County, Colorado, adjacent to Rocky Mountain National Park (Fig. 1). Our study area was limited to forests in the CLD because it lies exclusively on the eastern slope of the Continental Divide, and is inherently different from forests on the western slope in terms of climate and soils. Elevations on the CLD range

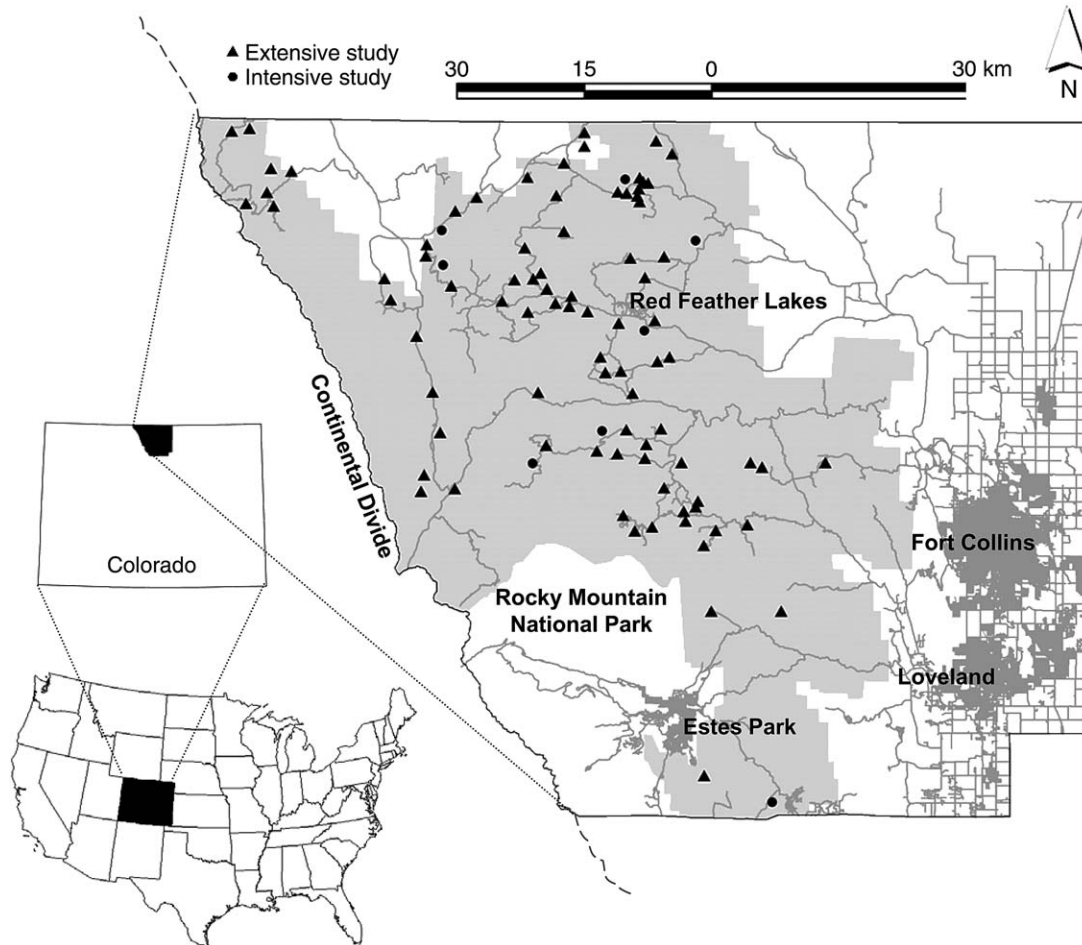


FIG. 1. Locations of 91 aspen stands sampled within the Canyon Lakes District of the Arapaho-Roosevelt National Forest (shaded) in Larimer County, Colorado, USA. Gray lines represent roads within the county; triangles represent stands sampled for the extensive survey; circles represent stands sampled intensively.

from about 1825 m near the plains to the east to nearly 3600 m in the mountains to the west. Based on weather averages from Estes Park, Colorado ( $105^{\circ}31'16''$  W,  $40^{\circ}22'37''$  N, at 2300 m elevation), July temperature averages  $17.8^{\circ}\text{C}$ , and January averages  $-2.8^{\circ}\text{C}$ . Total precipitation averages 36.8 cm, with 70% falling as rain between May and October. Soils are generally coarse and rocky (USDA Soil Conservation Service 1994), and about 56% of aspen forests on the CLD are found on coarse-textured soils that consist mainly of stone fragments, sand, and gravel. Approximately 20% of aspen forests are located on loamy soils; the remaining 24% of aspen forest is found on soils composed of silt and clay materials (USDA Soil Conservation Service 1994).

At the lowest elevations (1600–2000 m) in the CLD, ponderosa pine (*Pinus ponderosa* Douglas ex Lawson) forests dominate and were historically characterized by frequent, low-severity surface fires (Veblen et al. 2000, Sherriff 2005). Mixed conifer forests of ponderosa pine, Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.)

Franco), and lodgepole pine (*Pinus contorta* var. *latifolia* Englem. ex Wats.) dominate at middle elevations (2000–2800 m) and are characterized by fires of mixed severity and frequency (Brown et al. 1999, Veblen 2000, Ehle and Baker 2003). Lodgepole pine and Engelmann spruce–(*Picea engelmannii* Parry ex Engelm.) subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) forests dominate at high elevations (2800–3350 m) with infrequent, stand-replacing fires (Aplet et al. 1988, Veblen 2000). Aspen forests, which occupy approximately 9800 ha in the CLD, are scattered within and among all forest types and elevations.

The historical land use of the CLD includes evidence of Native American hunting for ungulates concentrated mainly along rivers and streams at lower elevations in the eastern portion of the District (Waltrous 1911). Little evidence exists that fire was used by Native Americans to facilitate hunting in forested areas, and most hunting in this area likely focused on grassland-dwelling bison rather than forest-dwelling elk and deer (Waltrous 1911). However, the extent and ecological

significance of Native American burning in this region are simply unknown (Baker 2002).

Permanent Euro-American settlement began in the CLD prior to the 1840s, but the population was estimated to be only about 600 by 1860. The CLD was dominated by the open range cattle industry between the mid 1860s, and the late 1880s (Waltrous 1911). The expansion of open-range grazing may have been intense enough to reduce fuels and decrease the frequency of fires at lower elevations, perhaps favoring aspen establishment if fire was too frequent prior to grazing (Binkley et al. 2005). Railroad tie cutting was probably the dominant human disturbance in forests across the CLD between the late 1860s and 1905, focusing mainly on larger-diameter ponderosa pine and lodgepole pine rather than aspen (USDA Forest Service 1984). Fire suppression activities were probably not effective until at least the 1920s. Currently, timber harvesting and grazing make up only a minor proportion of the management activities on the CLD, which is largely dominated by recreational uses, including hunting. Fire exclusion remains widespread, especially as the wildland–urban interface increases (USDA Forest Service 1984).

Reliable elk herd size estimates are not available prior to 1995 for the CLD, but post-harvest herd estimates have been fewer than 5000 animals since at least 1995 and was approximately 3700 animals in 2003 (M. Vieira, *personal communication*). Hunting occurs between late August and mid-November on the CLD and has averaged about 215 animals harvested each year since 1999. At least half of the total elk herd winters in adjacent Rocky Mountain National Park where hunting is prohibited (Baker et al. 1997). Spatially explicit population estimates for the CLD do not exist, but more elk likely occupy the summer range of the CLD than the winter range due to seasonal migrations (Stevens 1980). Elk populations are ubiquitous on the winter range due to the lack of natural predators.

#### *Field methods*

Field sampling consisted of an extensive survey of aspen stands across the CLD. We randomly selected 91 aspen stands (Fig. 1) using a fine-grained (900 m<sup>2</sup> minimum mapping unit) cover-type raster map of Colorado vegetation (Theobald et al. 2004), stratified by elevation and aspect (north and east slopes vs. south and west slopes). We chose 2740 m as the boundary between high- and low elevation forests in the CLD because it represents the boundary between elk summer and winter ranges, the upper limit of the mixed conifer zone, and the division between historical fire regimes characterized by infrequent, high-severity fires or frequent, low-severity fires (Veblen 2000). The sampling effort at high and low elevations was proportional to the area occupied by high- and low-elevation aspen forests in the CLD. Only stands within 2 traversable kilometers of a road or trail were sampled, which represented 89% of the District.

Stand area was calculated as a rectangle and was measured using perpendicular ground measurements along the length and width of the stand. Measurements of stand area included an estimate of “current area” (live aspen) and “former area” (live + dead aspen) when the margins of the stand consisted of dead aspen stems only (see *Results*). We defined the boundaries of a stand using a 20-m buffer of non-aspen vegetation between the live trees of the stand and those of an adjacent stand (Kaye et al. 2003). The distance to the nearest live aspen stand was measured on the ground if the stand was within 200 m, and from a 1:24 000 scale USGS topographic map if the distance was >200 m. In each stand, we made ocular estimates of the percentage of aspen regeneration browsed, the percentage of aspen stems with bark scars, and the percentage of trees with obvious fungal infections (indicated by the presence of fruiting bodies or liquid discharge). Precision of ocular estimates was estimated early in the field season using five stands ranging in browse intensity and fungal infection and was found to be within 5% of actual plot measurements. Increment cores were extracted approximately 30 cm from ground level from five dominant aspen and three dominant trees of each other tree species present in the stand for age estimation.

Variable-radius plots located 50 m apart on a transect placed along the length of the stand were sampled with a 10- or 20-BAF prism to estimate the basal area and density of live and standing dead trees by species in each stand. The diameter at breast height (dbh) of all trees  $\geq 3$  cm dbh and tallied as “in” with the prism was measured and recorded by species. Fallen dead trees and tree regeneration were measured along 4  $\times$  50 m belt transects placed between each pair of variable-radius plots. The dbh of trees formerly rooted within the belt transect was measured for each fallen tree, and the tree was classified as either “sound” or “rotten.” Regeneration (all stems  $\leq 3$  cm dbh) for each species, usually either a clump of aspen suckers (Romme et al. 1995) or a conifer seedling, was also tallied within the 4  $\times$  50 m transect, in height classes greater or less than 1 m. Height of aspen suckers, rather than age, was considered to be more representative of the likelihood of sucker recruitment into the canopy (Baker et al. 1997).

Preliminary analysis of the 91 stands revealed distinctive aspen trends (see *Results*), and we selected eight stands representative of the range of variation in these trends for intensive sampling. Intensive sampling utilized 10  $\times$  10 m (100-m<sup>2</sup>) plots located 25 m apart along two perpendicular transects spanning the length and width of the stand. The number of plots per stand varied with stand size. In each plot, all live trees  $\geq 3$  cm dbh were measured at breast height and cored at 30 cm above ground level and their canopy position estimated, all dead trees (standing or fallen) were measured at breast height and a cross-section sampled from their base, and all regeneration was tallied. In stands that included a mixture of aspen and lodgepole pine (see

TABLE 1. Structural features of quaking aspen stands at high ( $n = 32$ ) vs. low ( $n = 59$ ) elevations and north and east ( $n = 53$ ) vs. south and west ( $n = 38$ ) aspects in the Canyon Lakes District of the Arapaho-Roosevelt National Forest, Colorado, USA.

Variable	Elevation		Aspect	
	High	Low	North and east	South and west
Stand age (yr)	127 (22)†	113 (27)†	119 (29.4)	117 (19.7)
Current stand area (m <sup>2</sup> )	6861 (7091)	7644 (11 355)	6090 (6005)	9155 (13 721)
Former stand area (m <sup>2</sup> )	10 525 (11 015)	9525 (11 952)	8270 (8267)	12 120 (14 874)
Aspen density (stems/ha)	2780 (2239)	3020 (3863)	2641 (3533)	3346 (3129)
Aspen basal area (m <sup>2</sup> /ha)	28.0 (14.2)	28.9 (14.5)	29.0 (14.5)	28.1 (14.2)
Snag density (stems/ha)	1300 (1504)	921 (1036)	940 (1130)	1214 (1349)
Snag basal area (m <sup>2</sup> /ha)	9.0 (7.9)	8.2 (5.8)	8.3 (7.1)	8.7 (5.9)
Dead wood density (stems/ha)	801 (549)	720 (543)	618 (532)‡	925 (514)‡
Dead wood basal area (m <sup>2</sup> /ha)	4.3 (4.5)	6.8 (6.7)	4.7 (4.1)§	7.6 (7.8)§
Dead wood rotten (%)	38 (23)	43 (23)	44 (24)	39 (22)
Large (>1 m) aspen suckers (stems/ha)	353 (466)	632 (1128)	610 (1177)	427 (506)
Small (<1 m) aspen suckers (stems/ha)	1338 (1182)	2038 (3123)	2051 (3292)	1431 (1128)

Notes: Values for high and low elevation and north and east and south and west aspects are means, with SD in parentheses.

†  $P = 0.016$ .

‡  $P = 0.008$ .

§  $P = 0.02$ .

Results), plots were located in groups of three, with plots placed in each of pure aspen, mixed aspen and pine, and pine with dead aspen.

#### Analytical methods

For the extensive survey, we compared 20 independent variables (Tables 1 and 2) among the two elevation and aspect classes using univariate analysis of variance (ANOVA). Statistical analyses were performed using the S-PLUS (MathSoft 1998) statistical package using  $\alpha = 0.05$ . Data structure was examined for normality, and equal variances were tested using Bartlett's test. Density and basal area of live and dead trees of each species were calculated from the variable-radius plots and are reported on a per-hectare basis. Stand area, density, and basal area were log-transformed, and proportion variables were transformed using the arcsine square root

transformation, but no serious departures from normality or equal variances were otherwise noted.

Tree ages from the intensive study were used to construct age distributions using 10-yr age classes for each of the eight stands sampled. Increment cores and wedges were mounted and sanded per standard techniques (Stokes and Smiley 1968), and annual rings were counted and measured under a microscope using a sliding bench micrometer. As in other aspen studies from this region (e.g., Romme et al. 1995, Baker et al. 1997), visual crossdating of annual rings was successful only on a limited number of increment cores and wedges because rings were often extremely narrow and generally complacent. Aspen age distributions presented here refer to the minimum time since the last major disturbance rather than true clonal ages, which are difficult to determine. In addition, tree ages reported do not include

TABLE 2. Factors commonly related to quaking aspen decline in stands at high ( $n = 32$ ) vs. low ( $n = 59$ ) elevations and north and east ( $n = 53$ ) vs. south and west ( $n = 38$ ) aspects in the Canyon Lakes District of the Arapaho-Roosevelt National Forest, Colorado, USA.

Variable	Elevation		Aspect	
	High	Low	North and east	South and west
Succession to conifers				
Conifer density (stems/ha)	330 (548)	362 (754)	357 (659)	342 (730)
Conifer basal area (m <sup>2</sup> /ha)	9.0 (9.7)	5.5 (6.5)	7.3 (8.7)	5.9 (6.8)
Age of conifers within aspen stand (yr)	144 (58)	127 (46)	125 (37)	146 (67)
Conifer seedlings (stems/ha)	891 (1088)†	244 (451)†	619 (930)‡	267 (504.7)‡
Conifers in canopy (%)	32 (23)	19 (18)	26 (21)	20 (19)
Elk browsing pressure				
Aspen suckers browsed (%)	46 (27)§	64 (25)§	58 (26)	57 (30)
Aspen with bark browsed (%)	36 (30)†	71 (29)†	63 (33)	53 (34)
Other				
Aspen with fungal infections (%)	25 (21)	38 (18)	35 (22)	31 (18)

Notes: Values for high and low elevation and north and east and south and west aspects are means, with SD in parentheses.

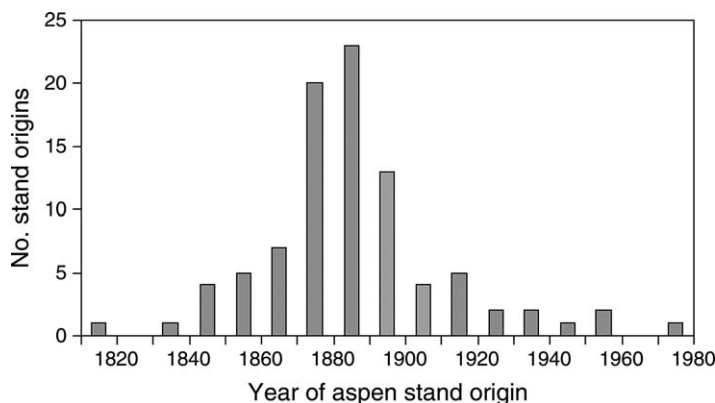
†  $P < 0.001$ .

‡  $P = 0.037$ .

§  $P = 0.002$ .

||  $P = 0.004$ .

FIG. 2. Frequency distribution of aspen stand age classes across the landscape in Larimer County, Colorado, USA. Most stands ages date to the period 1860–1900.



an estimate of the number of years required to reach coring height, because aspen may elongate as much as one meter per year (Romme et al. 1995). Based on cores collected in aspen stands with documented ages of establishment, we estimate dating errors to be  $\leq 5$  yr, which should have only minimal effects on age class distributions for the purposes of this study. For aspen stands among lodgepole pine forests (see *Results*), annual rings of both live and dead aspen and pine were counted and measured to reconstruct past density and basal area, respectively, for each species.

Significant differences in the mean values of the variables described above were also identified with ANOVA at  $\alpha = 0.05$  across the eight stand types. Variables found significant with ANOVA were entered into forward stepwise discriminant analysis using a stopping rule set at a value of  $\alpha = 0.15$  to enter and remove to select the most important discriminatory variables. We selected discriminant analysis because of its value as an a posteriori test to compare the eight stand types that were qualitatively identifiable in the field (Gotelli and Ellison 2004). Potential bias in the a priori assignment of groups was tested using the jackknife method of discriminant analysis (Williams 1983). Because the distributions of the selected variables showed no serious departures from normality or homogeneity, assumptions of discriminant analysis (multivariate normality and equal covariances) were not tested.

## RESULTS

### *Landscape trends in aspen stands*

Aspen stands in the CLD occur mainly as very small patches across the landscape; 58% of the stands we sampled were  $< 0.5$  ha, 90% were  $< 2$  ha, and only 5% were  $> 2$  ha. Based on our sample, aspen stands (by count) in the CLD are nearly equally distributed at high and low elevations (median elevation = 2673 m), such that stands occur within and among ecosystems having very different historical disturbance regimes and browsing intensity. Assuming that the oldest sampled tree represents the date of last significant disturbance, over

69% of all stands we sampled dated to the period 1860–1900 (Fig. 2), which approximates the settlement period in Larimer County. Stands averaged 14 years older at high elevations ( $P = 0.016$ ; Table 1), though elevation explained only about 7% of the variation in stand age.

Dead wood density and basal area were the only variables measured that differed across aspects, with significantly higher density (925 vs. 618 stems/ha;  $P = 0.008$ ) and basal area (7.6 vs. 4.7 m<sup>2</sup>/ha;  $P = 0.02$ ) on south and west aspects (Table 1). Indicators of regeneration in aspen stands were similar between high and low elevations, with aspen suckers present in all 91 stands, although the number of suckers was highly variable. Notably, there was much more regeneration  $< 1$  m tall than  $> 1$  m tall (Table 1), and nearly 28% of all stands had no aspen suckers  $> 1$  m.

Factors identified as threats to aspen persistence in previous studies were also evident in our study. Conifers were evident in many stands, although only 23% of stands had more than 50% conifers in their canopies (Appendix A). Over 67% of all stands had a higher density of aspen regeneration than conifer regeneration (Appendix A). The number of conifer seedlings within aspen stands (range = 0–3400 stems/ha) increased significantly with elevation (891 vs. 244 stems/ha;  $P < 0.001$ ) and on northern and eastern slopes (619 vs. 267 stems/ha;  $P = 0.037$ ; Table 2). Evidence of elk browsing was found in all 91 stands, and almost one-third of stands had browsing damage on every aspen sucker and mature stem in the stand (Appendix A). Browsing pressure appeared to be much stronger at lower elevations, where evidence of browsing was much higher on both aspen regeneration (64% vs. 46%;  $P = 0.002$ ) and mature stems (71% vs. 36%;  $P < 0.001$ ; Table 2). Finally, evidence of fungal infection was significantly higher at lower elevations ( $P = 0.004$ ), with nearly 38% of mature stems exhibiting evidence of infection compared to only 25% at higher elevations.

### *Heterogeneous dynamics in aspen stands*

Our initial analysis and field observations of the 91 aspen stands revealed dominant and distinctive patterns

TABLE 3. Structural characteristics of quaking aspen stands representing eight major stand types in the Canyon Lakes District of the Arapaho-Roosevelt National Forest, Colorado, USA, based on a sample of 91 aspen stands.

Aspen type	Elevation (m)	Live stand area (m <sup>2</sup> )	Basal area (m <sup>2</sup> /ha)	
			Aspen (m <sup>2</sup> /ha)	Conifer (m <sup>2</sup> /ha)
High-elevation aspen/ lodgepole pine	2790 (140)	6371 (7299)	25.5 (13.6)	11.8 (8.0)
High-elevation rocky slopes	3050 (180)	6300 (3243)	25.9 (9.1)	5.2 (5.5)
High-elevation aspen/spruce-fir	2810 (30)	4790 (3390)	33.1 (19.2)	21.5 (11.2)
Low/mid- elevation aspen on silty soils	2640 (90)	35 686 (26012)	40.6 (20.5)	3.8 (7.5)
Low/mid-elevation aspen/mixed conifers	2570 (220)	4136 (3638)	24.1 (3.0)	12.1 (6.0)
Low-elevation aspen/ ponderosa pine	2380 (210)	6392 (4808)	25.8 (8.9)	19.5 (17.9)
Low-elevation self-replacing aspen	2520 (120)	5803 (4760)	27.6 (10.8)	4.5 (4.5)
Low-elevation aspen	2520 (190)	5461 (3755)	29.9 (16.8)	5.0 (5.6)
<i>P</i>	<0.0001	0.001	0.48	0.01

Note: Values are means, with SD in parentheses.

of aspen dynamics. Eight stand types representative of the range of variation in aspen dynamics were quantitatively classified and analyzed to highlight ecological differences in the dominant aspen trends in the CLD. The purpose here is not to catalog all aspen stand types on the landscape, but to illustrate the diversity of aspen dynamics and to differentiate the ecological conditions that drive them. The dominant aspen stand types and trends included the following:

*Low-elevation aspen stands* contain 85% aspen by basal area (Table 3) and are found below 2600 m. These stands are defined by a lack of young trees (aspen < 30 yr old) and suckers (Figs. 3a, b, 4a), coupled with dieback of mature stems and an average of 80% of mature trees having evidence of ungulate browsing (Table 3). Conifer regeneration may equal or exceed that of large aspen suckers, which we consider to be the most important indicator of future aspen recruitment into the canopy (Baker et al. 1997). The location of these stands at low elevations within the elk winter range creates a chronic exposure to heavy elk browsing, as evidenced by a high density of aspen suckers <1 m tall (Table 3). Low-elevation aspen stands are also likely to have been affected by 20th century fire exclusion, because fire intervals were historically shorter at lower elevations (Sherriff 2005). Declining stands at low elevations comprise about 20% of the aspen stands and 15% of the aspen forest area on the landscape (Table 4).

*Low-elevation, self-replacing aspen stands* also have 85% aspen by basal area and are found below 2600 m (Table 3). They differ from other low-elevation stands by their uneven age distributions (Figs. 3c, 4b) and higher densities of aspen regeneration, which may be up to five times that of conifer regeneration (Table 3). Self-replacing aspen stands are found on sites similar to other low-elevation stands and may show evidence of severe and chronic ungulate browsing (Table 3), but their extensive regeneration appears to overcome browsing pressure and recruit into the canopy. Self-replacing stands comprise about 24% of the aspen stands and 19% of the aspen forest area on the landscape (Table 4).

*Low-elevation aspen stands mixed with ponderosa pine* are uncommon, but are defined by a significant ponderosa

pine cohort mixed with aspen at elevations <2650 m. The oldest aspen stems typically are up to 50 years younger than ponderosa pine in these stands (Table 3) and represent <60% of stand basal area. The density of conifer seedlings is nearly double that of aspen suckers (Table 3), suggesting a trend toward increasing conifer cover (Fig. 4c). Similar to other stand types at low elevations, both the bark of mature trees (mean = 55%) and aspen suckers (mean = 75%) exhibit significant ungulate browsing (Table 3). Mixed aspen-ponderosa pine stands include only 2% of the stands and 2% of the aspen forest area on the landscape (Table 4).

*Low- to mid-elevation aspen stands seral to mixed conifers* are small stands found between 2350 and 2650 m on the CLD. In contrast to aspen stand mixed with ponderosa pine, they are defined by older aspen components that account for 50% of total basal area and a younger cohort of Douglas-fir with an occasional very old ponderosa pine (Fig. 4d). Browsing damage to the bark of mature trees (mean = 64%) and aspen suckers (mean = 45%) is relatively low (Table 3). Mixed conifer-aspen stands include 4% of the stands and 3% of the aspen forest area on the landscape (Table 4).

*Low- to mid-elevation, self-replacing aspen stands on silty soils* are the largest contiguous aspen stands in the CLD at elevations <2700 m, are nearly pure (90% aspen) and often occur as forested "islands" along moist drainages within the open grasslands in the northwest portion of the CLD. They are found on loamy soils, which characterize less than 20% of the area, but support 27% of the aspen forest area (USDA Soil Conservation Service 1994). Aspen density is very high (>2000 stems/ha) in these stands, which are also self-replacing or even increasing in aspen density (Fig. 4e), and the density of aspen suckers is an order of magnitude higher than that of conifer seedlings (Table 3). Aspen stems (mean = 72%) and regeneration (mean = 58%) experience fairly heavy browsing damage from both domestic grazers and wild ungulates (Dockrill et al. 2004). Self-replacing aspen stands on silty soils include 6% of the stands on the landscape (Table 4).

*High-elevation aspen stands seral to Engelmann spruce and subalpine fir* are rare, typically small in area, and are

TABLE 3. Extended.

Aspen suckers (stems/ha)		Conifer seedlings (stems/ha)	Browse (%)	
<1 m	>1 m		Bark	Regeneration
1425 (989)	267 (325)	1518 (606)	52 (35)	65 (22)
1707 (1506)	786 (674)	171 (208)	13 (11)	12 (7)
1302 (1499)	161 (202)	1884 (1297)	42 (30)	53 (24)
1318 (631)	1581 (432)	118 (193)	72 (15)	58 (32)
1500 (2507)	288 (129)	963 (165)	64 (41)	45 (29)
1275 (1749)	450 (182)	700 (424)	55 (21)	75 (21)
1823 (1748)	747 (1075)	160 (310)	73 (30)	65 (23)
2010 (2480)	225 (387)	213 (427)	80 (21)	62 (28)
0.09	0.03	<0.0001	< 0.0001	0.0002

restricted to cool drainages or wet seeps at elevations >2740 m on the CLD. In these stands, the oldest aspen stems are often older and fewer than the spruce and fir present in the stand (Figs. 3d, 4f), with conifers representing about 60% of stand basal area (Table 3). Conifer regeneration is significant and may be an order of magnitude higher than aspen regeneration (Table 3), suggesting increasing conifer cover with time. Aspen in these stands are some of the oldest in the CLD, including some nearly 200 years old, and they represent 12% of the aspen stands on the landscape and 8% of the aspen forest area.

*High-elevation aspen stands located on steep, rocky slopes* are distinctive as stunted aspen stands often found above 2860 m in the midst of boulder fields or talus slopes. Because their surroundings are natural barriers to elk and other ungulates, and because they are found almost exclusively in the summer elk range, these stands are well protected from browsing, with <15% mature stems or regeneration having browsing damage (Table 3). Aspen represent over 75% of stand basal area, and aspen regeneration is nearly five times that of conifers. They are typically self-replacing and are characterized by very broad age distributions (Figs. 3e, 4g); the low numbers of young trees may indicate that self-replacement is not assured under current conditions. These stands represent 8% of the stands on the landscape and 7% of the aspen forest area (Table 4).

*High-elevation aspen stands seral to lodgepole pine* are the most common aspen stands in the CLD, are small, and are found within a matrix of lodgepole pine forests at <2800 m. They typically occur as small pockets of live aspen surrounded by large areas of dead aspen overtopped by lodgepole pine (Parker and Parker 1983, Mueggler 1989a, Kaye et al. 2003). Lodgepole pine forests with dead aspen beneath may extend for many kilometers, usually spatially connecting the small live pockets of aspen (Fig. 3f). The age distribution of live and dead aspen and lodgepole pine stems suggest that the two species established at the same time following a stand-replacing fire (Fig. 5a). Aspen initially

dominated in terms of density and basal area, but decreased as the stems matured and lodgepole pine increased in density and basal area (Fig. 5b). These stands are found nearly wherever lodgepole pine forests are found and represent 24% of the aspen stands on the landscape and 21% of the aspen forest area (Table 4).

#### *Discrimination of aspen trends*

We used discriminant analysis to further examine the ecological factors underlying the variation represented by the eight dominant aspen trends sampled in the intensive study. Stepwise discriminant analysis selected five variables that were most useful in differentiating among the eight stand types: elevation, conifer regeneration density, density of aspen suckers, percentage of mature trees with bark browse, and percentage of aspen suckers with browse, each of which was highly significantly different among stand types (Table 3). These five variables resulted in excellent separation among the stand types in ordinate space (Fig. 6). The first canonical variate (CV 1) related most strongly with elevation and to a lesser extent to regeneration browse; stands scoring high on the first axis generally included those at high elevation, while those scoring low (negative) included those with high values of regeneration browsing damage. The second canonical variate (CV 2) was dominated by aspen sucker density; stands scoring high on the second axis included those with high densities of aspen suckers, and those scoring low had fewer aspen suckers. Thus aspen stands on rocky sites (R), located at the highest elevations and having high sucker density, are located in the upper right corner of the ordination, but those mixed with spruce and fir (SF) are located in the lower right of the ordination (high elevation but low sucker density; Fig. 6). The first three canonical variates accounted for 63%, 90%, and 96% of the cumulative variance (see Appendix B for full table of discriminant analysis results). The discriminant function had an overall classification accuracy of 86%, and the jackknifed classification rate was 66%, indicating that the *a priori* classification of stands into the eight groups was largely unbiased (Gotelli and Ellison 2004).





FIG. 3. Aspen stand structure for a subset of aspen stands sampled in the Canyon Lakes District of the Arapaho-Roosevelt National Forest in Larimer County, Colorado: (a) and (b) stands at low elevation showing evidence of ungulate herbivory and little regeneration; (c) stand at low elevation with multi-aged structure; (d) stand with spruce/fir understory at high elevation; (e) stand on steep, rocky slope at high elevation; (f) aspen stand within a matrix of lodgepole pine. See *Results: Heterogeneous dynamics in aspen stands* for detailed description of each stand.

#### DISCUSSION

Our study is consistent with others that have documented highly variable aspen stands in the northern Colorado Front Range (Suzuki et al. 1999, Kaye et al. 2003), and we conclude that “declining” and “persisting” aspen stands are both found on this landscape. Moreover, aspen decline and persistence are affected by multiple factors that occur simultaneously within

specific ecological contexts. We documented aspen stands suffering heavy elk browsing (low-elevation stands), as previously described for this region (e.g., Packard 1942, Olmstead 1979, Baker et al. 1997, Suzuki et al. 1999, Kaye et al. 2005), that may be interpreted as “declining.” However, we also identified stands interpretable as declining (high-elevation spruce–fir and lodgepole pine and low-elevation mixed conifers and

TABLE 4. Coverage and characterization of eight quaking aspen trends in the Canyon Lakes District of the Arapaho-Roosevelt National Forest, Colorado, based on a sample of 91 aspen stands.

Aspen type	Trend	Declining or persistent?	Percentage of stands	Percentage of area
High-elevation aspen/lodgepole pine	seral	declining	24.2	20.9
High-elevation rocky slopes	self-replacing	persistent	7.7	6.6
High-elevation aspen/spruce–fir	seral	persistent	12.1	7.9
Low/mid-elevation aspen on silty soils	self-replacing	persistent	5.5	26.6
Low/mid-elevation aspen/mixed conifer	seral	declining	4.4	2.5
Low-elevation aspen/ponderosa pine	seral	declining	2.2	1.9
Low-elevation self-replacing aspen	self-replacing	persistent	24.2	18.9
Low-elevation aspen	senescing/not self-replacing	declining	19.8	14.7
Total senescing			19.8	14.7
Total low-elevation seral			6.6	4.4
Total declining			26.4	19.1
Total self-replacing			37.3	52.1
Total high-elevation seral			36.3	28.8
Total persistent			73.6	80.9

ponderosa pine) that are experiencing conifer encroachment (Harniss and Harper 1982, Shepperd et al. 2001, Kaye et al. 2005). We also noted the importance of fire exclusion (Romme et al. 1995, Kay 1997b), and fungal infection (Krebill 1972, Patton and Jones 1977, Hart 1987) for aspen stands that may be considered in decline. Likewise, we noted several types of stands that may be considered “persistent,” including those that appear stable even under heavy browsing pressure (low elevation self-replacing stands). Defining the spatial and temporal scales of the range of aspen dynamics, the relative proportion of each type of declining or persistent aspen stand on the landscape, and the factors driving this heterogeneity are therefore critical in creating management prescriptions responsive to the ecological context of each stand.

#### *Spatial heterogeneity of aspen dynamics at low elevations*

Much of the spatial variation in aspen dynamics across the CLD may be explained by differences in natural and human disturbance regimes found between high- and low-elevation landscapes. Forests at low elevations on the northern Colorado Front Range were characterized by historically smaller (<100 ha), more frequent (<35 yr), predominantly low- to moderate-intensity fires that have been effectively excluded for at least 80 years (Veblen 2000, Sherriff 2005). Fires of this type burning through or at the periphery of aspen stands removed small conifers and stimulated aspen suckering (Romme et al. 2001). Thus the current trend toward dominance by conifers in many low-elevation aspen stands (e.g., Fig. 4d) is probably related to fire exclusion in the past century (Loope and Gruell 1973, Houston 1982, Mueggler 1989a, Romme et al 1995, 2001).

Forests at low elevations on the CLD also represent the winter range of ungulates (Baker et al. 1997, Kaye et al. 2005), and severe, chronic ungulate browsing on aspen was highest in stands at low elevations as was the rate of fungal infection, probably as a result of elk browsing on mature stems (Krebill 1972, Hart 1987).

Although fire exclusion may play a role, ungulate browsing at low elevations is probably the most immediate factor causing a paucity of regenerating aspen on the CLD, especially in stands on xeric sites where aspen sucker production is generally lower (Shepperd 1990). Aspen stands that are self-replacing and stable despite heavy browsing on this landscape are often located on mesic sites and thus may be more vigorous (Shepperd 1990). Accurate, spatial ungulate population data do not exist for the CLD, and fully understanding why some heavily browsed stands are still self-replacing is dependent on knowledge of the spatial variability of browsing intensity. Overall, however, >70% of the total aspen area at low elevations on the CLD—most on sites with higher soil moisture—appears stable or self replacing even in the absence of fire and the presence of heavy browsing.

#### *Spatial heterogeneity of aspen dynamics at high elevations*

Forests at elevations higher than about 2700 m are characterized by large (>100 ha), infrequent (>100 yr), stand-replacing fires (Veblen 2000, Bebi et al. 2003, Kulakowski et al. 2003) that are likely the primary mode of aspen forest regeneration on this landscape (Romme et al. 1995, 1997). Naturally long fire intervals at high elevations makes it doubtful that 100 years of fire exclusion in this region has moved patterns of aspen establishment far outside of the historical range of variation (Morgan et al. 1994, Landres et al. 1999, Romme et al. 2001, Kulakowski et al. 2004). Therefore, very long natural fire intervals on this landscape facilitate the persistence of older aspen stands and establishment by conifers (Table 2) independent of fire suppression. More than 81% of the aspen forest at high elevations are mixed with conifers (Table 4); some high-elevation aspen stands in Rocky Mountain National Park have also been shown to have included conifers at the time of establishment (Kaye et al. 2005). Ungulate browsing is a less significant threat at high elevations because this landscape represents the summer ungulate

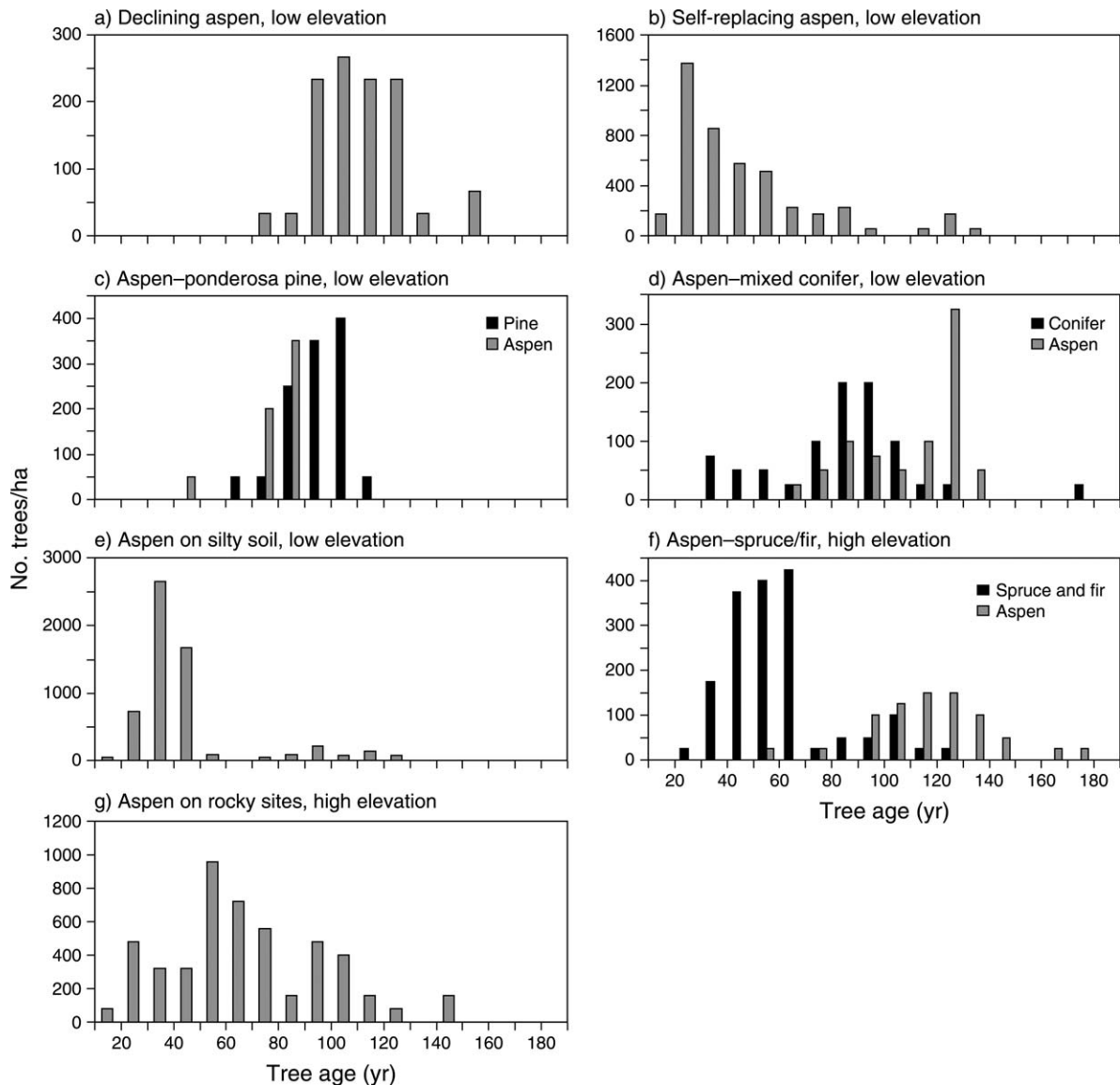


FIG. 4. Age distributions (by density) of aspen and conifer (where applicable) trees in each of eight stands sampled to represent the range of aspen successional trends in the Canyon Lakes District of the Arapaho-Roosevelt National Forest in Larimer County, Colorado, USA. See *Results: Heterogeneous dynamics in aspen stands* for detailed description of each stand.

range where browsing is neither as heavy nor as chronic as on the winter range. Self-replacing stands at high elevations are found mainly on steep, rocky slopes and ridge tops (Table 4) where aspen sucker production is low but ungulate accessibility is limited.

#### *Temporal heterogeneity of aspen dynamics*

Conifer encroachment into aspen stands by lodgepole pine on the CLD highlights the importance of considering temporal scale in assessing the condition of aspen forests and applying appropriate management prescriptions. Replacement of aspen by lodgepole pine is common at high elevations on the CLD and would be defined by previous studies as classically “declining”

aspen (Harniss and Harper 1982, Bartos et al. 1983, Mueggler 1989b, Shepperd et al. 2001). However, this replacement is cyclical when viewed over the entire length of the fire interval, because aspen regenerates prolifically and dominates stands for several decades following severe fires (Fig. 5a, b). Thus “seral” aspen stands at high elevations may appear to be “declining” over the time frame of a human life span (<100 years), but are persistent over longer temporal scales that encompass the entire fire cycle on this landscape (100–300 years).

The cycle of alternating aspen–pine dominance is contingent on the ability of aspen to persevere in a suppressed condition in the understory of lodgepole pine

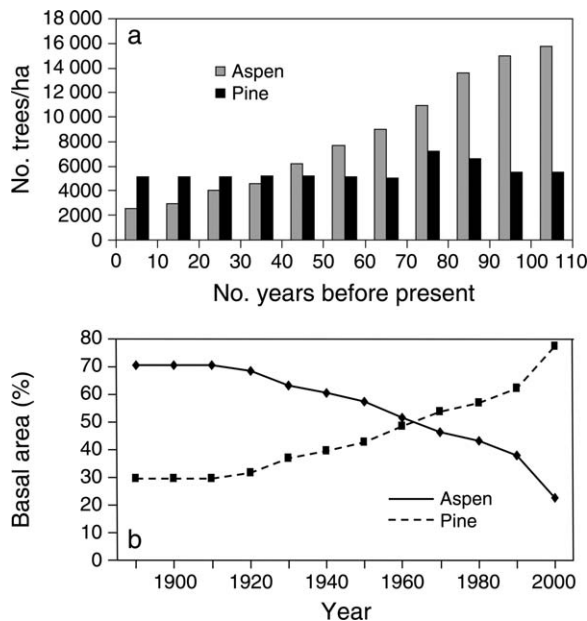


FIG. 5. (a) Reconstructed aspen and pine density and (b) changes in aspen and pine dominance (by basal area) illustrating stand dynamics of aspen stands growing within a matrix of lodgepole pine at high elevations in the Canyon Lakes District of the Arapaho-Roosevelt National Forest in Larimer County, Colorado, USA. Note the differences in x-axis time format between panels (a) and (b).

forests over the course of the fire-free interval. We tested the ability of aspen to persist in the understory of lodgepole pine forests and its ability to regenerate following long-interval disturbance events in three 1-ha clearcuts established in the early 1980s by the U.S. Forest Service (D. Virgovic, *personal communication*). Current densities of aspen suckers within these clearcuts suggest that aspen regenerated as vigorously after ~220 years of suppression as they did after ~80 years of suppression (Appendix C). Because typical fire intervals for lodgepole pine forests in this region are in the range of 100–300 years (Veblen 2000), aspen should persist through the fire free interval, and vigorous suckering is likely after each stand-replacing fire (Kaye et al. 2005). Thus aspen may readily persist over long temporal scales in this landscape provided that the natural fire regime remains intact and ungulate browsing does not overwhelm early post-fire aspen regeneration (Bartos et al. 1994, Romme et al. 1995, Baker et al. 1997, Hessl and Graumlich 2002, Turner et al. 2003). This long-term persistence may be important in defining management objectives for preserving aspen forests on this and other Rocky Mountain landscapes (see *Management Implications*).

*Are aspen forests declining on the northern Colorado Front Range?*

We identified a wide diversity of clearly discernable aspen dynamics in the CLD (Appendix B, Fig. 6), such

that a single trend is not adequate to describe the current condition of aspen forests across the northern Colorado Front Range. Ecological studies examining the conditions of a forest type across a broad area are often difficult to translate into specific management prescriptions, in part because ecologists strive for trends or principles that may be generalized across landscapes, while managers struggle to apply these general principles to individual stands on the ground (Shepperd 1990). The issue is not only that aspen decline is ambiguously defined in previous studies, but that multiple, interacting ecological factors leading to many types of aspen decline and persistence are simultaneously present on heterogeneous landscapes (e.g., Hessl and Graumlich 2002, Kaye et al. 2005). Divergent interpretations of aspen decline for a given landscape are therefore reconciled and made useful to managers when the relative importance of the various ecological factors underlying aspen decline and persistence are identified for a particular ecological setting, rather than a general trend for a landscape or region. This spatially and temporally comprehensive framework allows for adaptive management of aspen that is more likely to succeed (Holling and Meffe 1996, Hessl 2002).

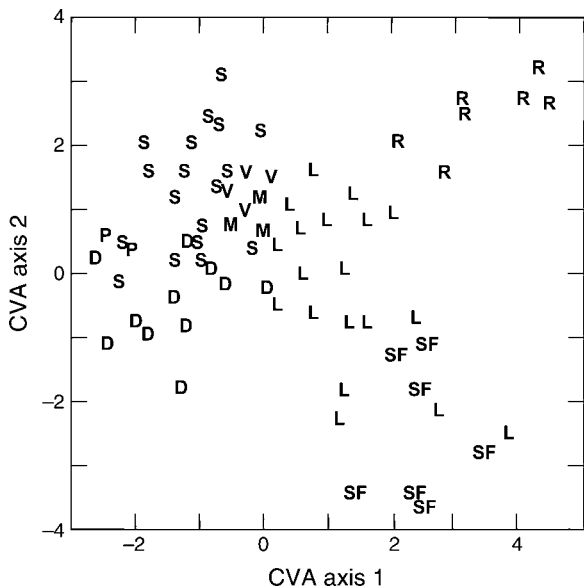


FIG. 6. Ordination of 91 aspen stands sampled across the landscape in the Canyon Lakes District of the Arapaho-Roosevelt National Forest in Larimer County, Colorado, USA, along the first two canonical variates of an analysis of eight aspen stand types. Letters represent stand type: D, low-elevation aspen stands; P, aspen-ponderosa pine stands at low elevations; S, self-replacing stands at low elevations; M, aspen-mixed conifer stands at low elevations; V, aspen on silty soils at low elevations; L, aspen within a matrix of lodgepole pine at high elevations; SF, aspen mixed with spruce and fir at high elevations; R, aspen found on rocky sites at high elevations. See *Results: Discrimination of aspen trends* for interpretation of the ordination.

Aspen stands are declining at certain fine spatial and temporal scales on the CLD, and individual declining stands within the landscape are certainly important targets for active management (Packard 1942, Krebill 1972, Olmstead 1979, Mueggler 1989b, Baker et al. 1997, Kay 1997a, Shepperd et al. 2001). Long-term persistence of aspen forests is probably most threatened on landscapes like the lower elevations of the CLD, where site conditions are unfavorable or marginal for aspen, stands are small and patchy (95% of stands <2 ha), and ungulate browsing pressure is heavy and chronic (Romme et al. 2001). At least 15% of the total aspen area on the CLD is declining in the sense of a lack of regeneration (Table 4), mostly at low elevations due to ungulate browsing, low sucker production in the absence of fire, or a combination of these factors (Hessl and Graumlich 2002).

Over one-third of the total aspen forest area on the CLD includes seral stands with increasing conifer densities, but we emphasize caution in interpreting all of these stands as “declining.” In low-elevation aspen stands with a significant conifer component (4% of the total aspen area), assuming continued fire exclusion and heavy elk browsing over the next century, we predict increasing conifer dominance and a genuine decline in aspen. In contrast, aspen stands seral to lodgepole pine or spruce and fir at high elevations (29% of the total aspen area) are probably persistent rather than declining at temporal scales appropriate to the long fire intervals on this landscape.

We acknowledge individual declining stands on the CLD, but our study is also consistent with those finding little evidence for extensive aspen decline over broad spatial scales (Suzuki et al. 1999, Kaye et al. 2003, 2005). Across the entire CLD, we estimate that 52% of the total aspen area is stable or persistent over the short term, and 81% is persistent over the long term when long fire intervals at high elevations are considered. Individual aspen stands do not represent the condition of aspen forests across the landscape, and the long-term persistence of aspen forests is favored by the wide range of ecological contexts in which aspen stands are found. We conclude that aspen forests are in no danger of disappearing from the landscape in the northern Colorado Front Range, and recommend that management target aspen decline on an individual stand basis where appropriate.

#### *Management implications*

Because an available range of ecological contexts may drive multiple types of aspen decline or persistence on a landscape, management prescriptions for the CLD should be responsive to the specific drivers of individual aspen stand conditions and developed with clear long- and short-term goals for aspen persistence. The most significant threat to the persistence of aspen stands on the CLD in the short term is a lack of regenerating suckers in existing low-elevation aspen stands, caused by

the lack of periodic fires and ungulate browsing. The absence of new stand establishment over the past 50 years on the CLD (Fig. 3) probably reflects this lack of recent fires at both low and high elevations. Prescribed fires in aspen stands may promote sucker production, but are unlikely to be successful over the long term because regenerating stands may be subject to chronic, intensive browsing following fires under the current browsing regime (Packard 1942, Kay 1997a). Mechanical treatments may be useful in removing conifers from aspen stands, but such prescriptions are often too costly to be successful over large areas. Thus we suggest that the most urgent management priority for aspen in the CLD is controlling excessive elk browsing at fine scales, particularly at low elevations, either by reducing ungulate populations or by protecting currently regenerating aspen stands from browsing using physical barriers (W. D. Shepperd, *personal communication*). Such a strategy should be achievable when targeting individual declining stands.

Landscapes in the western United States are historically fire prone, and managers should consider the likely long-term impacts of future fires for aspen persistence regardless of short-term management prescriptions. The last large fires in the CLD occurred between approximately 1860 and 1890 (L. Huckaby, *personal communication*), which corresponds well to the major period of stand establishment found in this study (Fig. 2). Thus we can expect ample regeneration in aspen stands when future large fires occur, especially in lodgepole pine forests and other areas where ungulate browsing is not excessive. In high-elevation forests with long fire intervals, succession of aspen stands to conifers is a natural dynamic process that will likely be reversed by future stand-replacing fires, especially if the area burned by such fires increases due to climate change (Dale et al. 2001). Thus, active management to preserve these stands in their current form may be unnecessary or even misguided when viewed in the context of this long-term ecological process.

In addition to natural ecological processes, aspen stands on the CLD and elsewhere may respond favorably (though indirectly) to large-scale forest and fuels management occurring in the Rocky Mountains, particularly near exurban areas such as those in the northern Colorado Front Range. Federal legislation such as the Healthy Forest Restoration Act of 2003 (Public Law H.R. 1904) and other state and local legislation have recently mandated fuel treatments including forest thinning over large forested areas each year. Such treatments, if they occur in areas with established aspen stands, may inadvertently favor aspen regeneration in these stands and may therefore increase aspen forest cover over large spatial scales, similar to coniferous forests of the Great Lakes that were logged in the late 1800s (Whitney 1987).

Heterogeneous landscapes in the Rocky Mountains include a wide range of ecological contexts that support

many types of declining and persistent aspen stands. Aspen stands in the CLD and the northern Colorado Front Range have a much larger area of aspen forests that appear to be persistent rather than declining, and management should reflect this diversity of trends in its efforts to preserve this important forest type. If the goal of management is to maintain those individual declining aspen stands, then active management at fine scales is an appropriate action. If, however, management is to maintain aspen forest coverage only within its historical range of variation over broad spatial and temporal scales, then the current diversity of aspen dynamics is likely sufficient to maintain aspen forests within this range even without active management, even if aspen coverage is significantly reduced over short time scales.

#### *Applicability to broader regions*

The wide variability of aspen stand conditions within the CLD cannot necessarily be extrapolated across the entire western United States. For example at regional scales, many studies conducted west of the Continental Divide in Colorado document large, persistent, or even expanding aspen stands (e.g., Crawford et al. 1998, Manier and Laven 2002, Elliot and Baker 2004, Kulakowski et al. 2004) that contrast sharply with the smaller, patchier stands on the CLD. This dissimilarity in aspen stands between regions is driven mainly by differences in soils and climate. In contrast to the drier, coarser-textured soils that dominate the CLD, soils west of the Continental Divide are silty (USDA Soil Conservation Service 1994) and are clearly favorable for aspen persistence based on their limited coverage within the CLD (Table 4). In addition, the climate in this region (based on weather data collected at Steamboat Springs, Colorado, 106°48' W, 30°30' N, at 2050 m elevation) features higher total precipitation and a higher proportion of precipitation occurring as snow than on the CLD, where precipitation occurs mainly during the summer months and is more prone to losses via evaporation or runoff. These broad-scale ecological differences suggest that aspen stand dynamics are not readily comparable across large regions. Our specific results from the CLD and the types of aspen conditions and drivers we describe are probably far more representative of the ARNF and the Colorado Front Range, with similar climate, soils, and land-use patterns, and at most the eastern slope of Rocky Mountains, than of western North America in general. Moreover, spatial variability in ungulate herbivory at low elevations is likely to be a major driver of aspen stand dynamics within the Front Range and in the region. Nevertheless, our data reiterate that no single trend describes the general condition of aspen forests in appropriate detail for managers at spatial scales ranging from western North America to the CLD. Clearly, understanding and characterizing the diversity of ecological contexts that creates a variety of aspen dynamics are key for management in response to aspen decline or persistence.

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#### APPENDIX A

Selected structural characteristics of 91 aspen stands across the landscape in the Canyon Lakes District of the Arapaho-Roosevelt National Forest in Larimer County, Colorado (*Ecological Archives* A017-049-A1).

#### APPENDIX B

Standardized canonical coefficients of the first three canonical variates using five independent variables of quaking aspen stand structure (*Ecological Archives* A017-049-A2).

#### APPENDIX C

Regeneration response of quaking aspen ramets approximately 20 years following clearcutting in lodgepole pine forests of different ages in the Canyon Lakes District of the Arapaho-Roosevelt National Forest, Colorado (*Ecological Archives* A017-049-A3).