Ecological Applications, 15(4), 2005, pp. 1284–1295
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EFFECTS OF CONIFERS AND ELK BROWSING ON QUAKING ASPEN FORESTS IN THE CENTRAL ROCKY MOUNTAINS, USA

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Abstract. Elk browsing and conifer species mixing with aspen (*Populus tremuloides* Michx.) present current challenges to aspen forest management in the western United States. We evaluated the effects of conifers and elk browsing on quaking aspen stands in and near Rocky Mountain National Park using tree rings to reconstruct patterns of aspen establishment, growth, and mortality over the past 120 years. High conifer encroachment and elk browse were both associated with decreased aspen recruitment, with mean recruitment dropping over 30% from pure aspen to mixed stands and over 50% from low-browse to high-browse stands. Maximum aspen recruitment was lower in mixed stands than in pure stands with the same tree basal area. High levels of elk browsing were also associated with a 30% decrease in stand-level growth of aspen. Neither high conifer abundance nor elk browse affected the growth of individual trees or aspen mortality. Aspen establishment was negatively influenced by conifers and elk browsing; however, aspen growth and mortality appeared to be resilient to these two external influences. Overall, these results suggest that long-term preservation of aspen forests could be achieved by enhancing aspen recruitment.

Key words: *conifers; elk browsing; forest succession; quaking aspen; tree rings.*

INTRODUCTION

Forest management in the intermountain west of the United States balances the complex demands of biological conservation, resource extraction, water yield, recreation, public safety, and other ecosystem services. In the central Rocky Mountains, forest managers are challenged to accommodate two powerful factors: the effects of a century of fire suppression and the recreational demands made by the increasing human population in the region. Management of quaking aspen (*Populus tremuloides* Michx.) forests in Rocky Mountain National Park, Colorado, exemplifies these conflicts because fire suppression, tourism, predator–prey feedbacks, and biodiversity all effect aspen dynamics (Mueggler 1989, Stohlgren et al. 1997, Shepperd et al. 2001*b*, Hessl 2002, White et al. 2003). Quaking aspen is the only widespread deciduous tree species in the intermountain West (Peet 2000), covering <10% of the forested landscape yet providing a disproportionate amount of habitat for a diversity of plant and animal species (DeByle 1985, Turchi et al. 1995, Stohlgren et al. 1997, 1999, Chong et al. 2001). The high-quality habitat ascribed to aspen has generally been associated with pure aspen stands, and managers and ecologist are concerned about the effects that conifers and elk may have on this valued forest type.

Manuscript received 8 December 2003; revised 8 November 2004; accepted 1 December 2004; final version received 6 January 2005. Corresponding Editor: M. G. Turner.

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Previous studies have documented spatial variability in conifers and elk browsing among aspen stands in the Rocky Mountain region. Stands can persist through time as pure aspen (Cryer and Murray 1992, Crawford et al. 1998, Romme et al. 2001), but many stands also include conifer species (Mueggler 1989, Kay 1997, Bartos 2001, Manier and Laven 2001, Rogers 2002, Kaye et al. 2003, Elliott and Baker 2004). Conifers are often described as invading aspen stands, however few studies have differentiated between invasion and co-establishment of aspen and conifers. Elk browsing in the winter range of Rocky Mountain National Park has almost eliminated aspen regeneration (Olmsted 1979, 1997, Baker et al. 1997, Suzuki et al. 1999), whereas surrounding areas within the Park and in the adjacent National Forests show remarkably better aspen regeneration (Suzuki et al. 1999, Kaye et al. 2003). These complex interactions are ideal for an applied historical ecology approach that maximizes the long-term information available to resolve management challenges (Holling and Meffe 1996, Swetnam et al. 1999).

In this study, we used tree rings to reconstruct patterns of forest stand structure and growth over the past 120 years to evaluate the impacts of conifers and elk browsing in aspen stands in and adjacent to Rocky Mountain National Park. Our objectives were to compare aspen establishment, growth, and mortality among stand types to determine how conifers and elk browse effect aspen forest development. We tested the hypothesis that high levels of either browsing or conifer would decrease aspen establishment and growth and increase aspen mortality. Tests of these hypotheses may

TABLE 1. Characteristics of 16 aspen stands sampled in Rocky Mountain National Park and adjacent areas to determine the influences of conifers and elk browsing on aspen stand dynamics.

Stand no.	Browse level	Pure or mixed	Aspect	Slope (degrees)	Elevation (m)	Establishment/ stand age (yr)	Conifer species present†,‡
1	low	pure	S	7	2725	1879/121	
2	low	pure	E	5	2755	1859/140	
3	low	pure	N	3	2685	1890/111	
4	low	pure	NE	10	2713	1880/121	
5	low	mixed	SE	12	2719	1879/121	PICO, PSME, PIFL, ABLA
6	low	mixed	SW	4	2798	1873/126	ABLA, PIEN, PICO, PSME
7	low	mixed	E	3	2576	1893/106	ABLA, PIEN, PICO, PSME
8	low	mixed	N	2	2609	1862/139	PICO, PIEN, ABLA, PSME
9	high	mixed	NE	7	2585	1866/134	PIPO, PIEN, PSME, ABLA
10	high	mixed	E	3	2682	1847/154	PICO
11	high	mixed	NE	6	2633	1860/141	ABLA, PIEN, PICO
12	high	mixed	E	10	2688	1873/128	PSME
13	high	pure	SE	5	2566	1897/103	
14	high	pure	NE	3	2583	1876/124	
15	high	pure	NE	2	2586	1871/129	
16	high	pure	E	5	2560	1862/139	

Notes: Browse refers to whether a stand had evidence of high or low levels of elk browsing. Pure or mixed refers to whether a stand was pure aspen or mixed aspen–conifer. Establishment refers to the year that the oldest aspen in the stand established. Stand ages were calculated by using the establishment year of the oldest aspen in the stand as age 0 and increasing the age by 1 with each subsequent year.

† Conifer species are ordered from highest to lowest basal area at the time of sampling.

‡ Species abbreviations: PICO, *Pinus contorta*; PSME, *Pseudotsuga menzesii*; PIFL, *Pinus flexilis*; ABLA, *Abies lasiocarpa*; PIEN, *Picea engelmanii*; PIPO, *Pinus ponderosa*.

provide a foundation to develop management prescriptions for the conservation of aspen stands in the central Rocky Mountains.

METHODS

Study area

The study area was between 2400 and 2800 m elevation in the eastern slope of Rocky Mountain National Park and the Arapahoe and Roosevelt National Forests, in the Colorado Front Range of the Rocky Mountains. Average annual minimum and maximum temperatures near Estes Park (105°30′ W, 40°24′ N) at 2400 m elevation are −1.5 and 14.0°C. Growing season (May–October) temperatures average 4.0 to 21.0°C, with an average of 370 mm/yr precipitation (NOAA data, *available online*).[4] Vegetation types include ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.); lodgepole pine (*P. contorta* Dougl. es Loud.); mixed conifer including ponderosa pine, lodgepole pine, Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), subalpine fir (*Abies lasiocarpa* Hook. Nutt.), and Engelmann spruce (*Picea engelmanii* Parry ex Engelm); and spruce–fir forests, as well as wet and dry meadows, riparian corridors, alpine tundra, and quaking aspen forests (Peet 2000).

Field and laboratory methods

We sampled four types of aspen stands in a 2 × 2 factorial design comparing pure aspen and mixed aspen-conifer stands (hereafter called "pure" and "mixed" stands) and stands with high and low levels of elk browse intensity. Thirty-five potential study sites were identified on USGS 1:24 000 topographic maps with current aspen stands mapped from aerial photographs (1:15 800) of the study area. We only considered stands located between 2400 and 2800 m and excluded stands on steep slopes. The 35 stands were visited in random order to determine which stands met the following criteria:

1) Stand radius >20 m;
2) Not within a riparian zone, meadow edge, or ridge top;
3) Slope less than 30 degrees; and
4) Conifers present must not be older than the aspen. This was determined by collecting increment cores from two or three of the oldest looking aspen and conifer trees in the stand during field reconnaissance and in the laboratory dating the timing of establishment of each sampled tree using the tree-ring analysis methods outlined below.

Stands with major influences of processes not included in this study (e.g., hydrology, species range, or extreme microsite conditions) were eliminated. Stands were evaluated until four stands of each type ($n = 16$ total) were selected (Table 1). Aspen stands were classified as pure aspen (if they had no conifers reaching 1.37 m in height) or mixed (if conifer basal area was >5 m²/ha). Aspen stands that had visible signs of elk browsing on aspen sprouts and stems were classified as high browse level and stands that had no visible signs of elk browsing were classified as low browse level.

[4] (http://cdo.ncdc.noaa.gov)

We established a circular 10-m radius plot (314 m^2) in 14 of the 16 stands and adjusted the radius to 8 m and 18 m in the most dense and sparse stands, respectively, to ensure a similar tree sample size. Within each plot, tree-ring samples were taken from all living and dead aspen and conifer stems (>1.5 m tall and >4 cm diameter at core height) at 20–30 cm above the root collar. We collected increment cores or cross-sections cut with a handsaw from all dead aspen and conifer stems with bark or beetle galleries to assure the ability to identify the last year of cambial growth of each dead tree. The presence of beetle galleries on a dead aspen stem indicates that the outermost ring on the tree is preserved because bark beetles build their galleries in the vascular cambium, which is located between the outer-most ring (xylem) and inner bark (phloem). Diameter and core height, bark thickness, and tree species were recorded for each sample.

Core samples were mounted and cores and cross sections were sanded with progressively finer sand paper ranging from 250-mm to 15-μm grit to maximize tracheid and vessel definition and distinguish annual growth rings. All samples were examined under a binocular microscope, skeleton plotted, crossdated, and calendar years were assigned to each ring (Stokes and Smiley 1968). Radial growth rates near the pith were examined to identify any trees that may have persisted for many years as sprouts due to elk browsing before experiencing a growth release to reach tree size. Suppressed growth near the pith would indicate a time lag between sprouting and tree establishment and our goal was to reconstruct the timing of tree establishment. If a radius did not intercept the pith, concentric circles were used to estimate the number of rings between the innermost rings and the pith (Applequist 1958, Biondi 1999). We assigned (estimated) establishment dates to all samples and death year was estimated with the date of the outer-most ring on dead samples. Ring-width series were created for each sample by measuring annual rings with a slide stage micrometer of 0.01-mm accuracy interfaced to a personal computer. A master tree-ring chronology was created from the ring-width series of 54 of the oldest aspen stems with the program COFECHA (Holmes 1986). Dated ring-width series of living and dead aspen were compared with the master chronology to confirm the accuracy of the crossdating and the establishment and death dates.

Data analysis

To assess influences of conifers and elk browsing on aspen establishment and mortality, establishment and mortality dates of aspen and conifers were aggregated into decadal frequencies (due to the resolution of establishment and death dates; Veblen 1992), and decadal frequencies of establishment and mortality within the plot were scaled to a hectare basis (stems·ha^{-1}·$decade^{-1}$).

To evaluate the influence of conifers and elk browsing on aspen growth, tree-ring data were used to reconstruct stand basal area (BA; m^2/ha; see below for derivation of terms), total basal area increment (tBAI; $m^2 \cdot ha^{-1} \cdot yr^{-1}$), average basal area increment per tree (aBAI; cm^2/yr), and tree density (stems/ha) for conifers and aspen for each stand from the time of stand establishment (time zero) to the present. Stand establishment was identified as the pith date of the oldest aspen stem sampled in the plot. To calculate basal area and BAI the radius of each tree for each year was first calculated with the following equation:

$$R_y = (\mathrm{DCH}_y/2) - \mathrm{BT}_y$$

$$R_{(y-t)} = R_{(y-t+1)} - \mathrm{RW}_{(y-t)}$$

where y = the year the stand was sampled (either 1999 or 2000), t = number of years prior to y, ranging from 1 to the age of the oldest aspen stem, R_y = tree radius measured in the field for year y, DCH_y = tree diameter at core height for year y, BT_y = bark thickness measured in the field in year y, $R_{(y-t)}$ = tree radius for t years before y, $\mathrm{RW}_{(y-t)}$ = ring width measurement for year $y-t$. The annual radius of a tree for each year was converted into annual basal area with the following geometric equation:

$$\mathrm{BA}_{(y-t)} = R^2_{(y-t)}\pi$$

where $\mathrm{BA}_{(y-t)}$ is tree basal area for year $y-t$. Annual basal area increment was calculated based on annual basal area:

$$\mathrm{BAI}_{(y-t)} = \mathrm{BA}_{(y-t+1)} - \mathrm{BA}_{(y-t)},$$

where $\mathrm{BAI}_{(y-t)}$ is the tree BAI for year $y - t$.

Basal area and BAI of each tree in a plot, as well as the number of trees, were summed to create time series of annual aspen and conifer growth and tree density starting from time of stand origin. Annual values of basal area, tBAI and aBAI, and density were averaged by decade to create decadal time series that accentuate lower-frequency (>10 yr) variability in aspen and conifer growth due to stand dynamics rather than high-frequency (<10 yr) variability due to annual climate fluctuations. Time since death of samples from across the study area was evaluated to assess how far back in time aspen establishment, growth, and mortality could be reconstructed reliably (Johnson and Fryer 1989).

Decadal time series of the means of five measurements (establishment, BA, aBAI, tBAI, and mortality) were compared among stand types for periods beginning at the time of stand origin (stand age = 0 yr) and ending with the decade when less than three stands had data. We used repeated measures analysis to compare means of the five measurements reconstructed as time series and determined the significance of time, conifers, browsing, and the interactions between these variables ($\alpha = 0.05$). Based on the time span of reconstructions, repeated measures analysis and comparisons of means

were conducted to compare decadal averages of aspen data for two stand age periods: 0–129 yr (13 decade values) and 70–129 yr (six decade values). The second period of 70–129 yr was chosen for two reasons: 1) to emphasize the dynamics of "mature" stands and 2) to isolate trends in the data for recent periods when limitations of tree-ring reconstruction methods would be less influential.

Stand basal area of pure aspen (m^2/ha of aspen) and of mixed aspen–conifer (m^2/ha of aspen and conifers) was treated as a continuous independent variable for regression analysis to determine whether the presence of conifers in mixed stands had a different effect on aspen stand development than the effects of aspen alone in pure stands. Exponential decay models were fit to the relationship between stand basal area (in pure and mixed stands) and aspen measurements. Stand basal area and aspen measurements were converted to a log scale and slopes of regression lines were compared with ANCOVA analysis to determine if the rate of response (slope) of aspen measurements to stand basal area were different in pure and mixed stands This analysis was only conducted on aspen variables that were not found to have time as a significant effect in the repeated measures analysis because basal area of stands increased (covaried) with time.

To further investigate the effects of increased elk populations following the initiation of the policy of natural regulation in the Park, aspen establishment in stands with high levels of browse was compared with ANOVAs between the three decades before and after 1968. Additionally, aspen establishment in the three decades following 1968 was compared between stands of low and high levels of browse.

Rates of density-dependent aspen mortality were compared among stand types by transforming the data to the format of the −3/2 thinning rule (also known as the self-thinning rule or the 3/2 power law of self thinning: Yoda et al. 1963). Density (stems·ha^{-1}·yr^{-1}) and basal area (m^2/ha) were natural-log transformed from 10 stands that initiated with an even-aged cohort of aspen establishment. Best-fit regression lines were calculated for each stand starting with the year of maximum density and continuing to the year when the stand was sampled. Slopes of lines were compared among stands and to the expected slope of −3/2.

Results

All stands with high levels of browse were located within Rocky Mountain National Park and three of the four stands with low levels of browse were located adjacent to the Park in the Arapahoe and Roosevelt National Forests. In total, tree core samples were collected and analyzed from 643 living aspen, 548 dead aspen, 327 living conifers, and 37 dead conifers. The correlation in patterns of ring widths among trees (the interseries correlation) was $r > 0.6$ for aspen and $r > 0.5$ for conifers. All living and all but nine dead stems were crossdated. For these nine samples, ring-width series of samples with the same diameter and core height and degree of decay were substituted. Pith was present on 46% of the samples and 0–4 yr were estimated between the inner ring on the core and the pith on >92% of the samples. Over 98% of dead stems had visible beetle galleries on the surface of the stems and death dates were assigned to each stem. Dead aspen stems were preserved for up to 92 years within the stands and 7% of dead stems were smaller than 5 cm diameter. The number of dead aspen recorded per decade dropped steadily from 1950 back to 1900. Low levels of conifer mortality were recorded in three of the eight mixed stands and no mortality was found in the remaining five stands.

Patterns of aspen stand development

The majority of aspen establishment in all stands occurred within the first 30 years of stand development, with continued pulses of recruitment (Fig. 1a and b). Aspen basal area increased steadily from the time of stand establishment to the present, with no decline apparent by the time stands reached 120 years of age (Fig. 2a and b). Stand-level basal area increment (tBAI) of aspen reached a plateau between 40 and 90 years (Fig. 3a and b) and average basal area increment per tree (aBAI) either continued to increase, stayed relatively constant, or decreased depending on the type of aspen stand (Fig. 4a and b). Dead aspen stems began to appear in stands after 10 to 50 years of development and increased in numbers up to the present (Fig. 5a and b). No stands experienced pulses of synchronous aspen death (i.e., clusters of death dates within a decade of each other) that would indicate a stand disturbance such as a blow down or a tent caterpillar (*Malacosoma disstria* Hubner) outbreak.

Time was a significant variable for the period 0–129 years in repeated-measures analysis for all factors except aspen establishment (Table 2a). Time was not significant for mature stands (70–129 yr) for tBAI, aBAI, and mortality (Table 2b). Due to significant interactions of time with conifer and aspen basal area, we only regressed aspen establishment data (no significant interaction with time) with stand basal area of pure and mixed stands (see results below; Fig. 6).

Patterns of conifer development

The initiation of conifer establishment in mixed stands ranged from 10 and 80 years after initial aspen establishment. Conifer establishment occurred throughout stand development, with peaks present early in stand development and after 100 years (Fig. 1c). Conifer basal area (Fig. 2c) and basal area increment (data not shown) increased continually with stand age. Average basal area increment per tree remained constant or decreased slightly as stands aged. Conifer mortality was minimal in all stands and in percentage of total stems (0–9%).

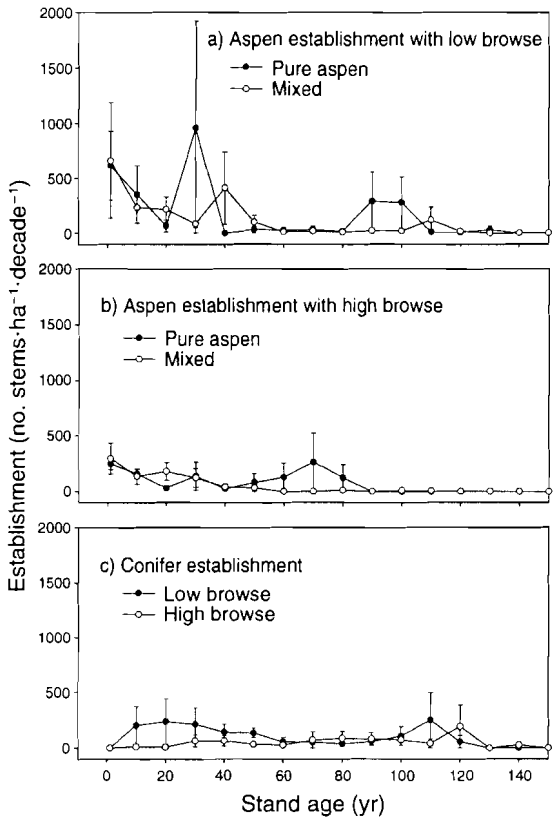

FIG. 1. Establishment of aspen and conifers over 120 years of stand development in 16 aspen stands in the Front Range, Colorado, USA. Each line represents mean values (±SE) of four stands. Four types of stands were sampled: pure aspen stands with low levels of elk browse (panel a, solid circles), mixed aspen–conifer stands with low levels of elk browse (panel a, open circles), pure aspen stands with high levels of elk browse (panel b, solid circles), and mixed aspen–conifer stands with high levels of browse (panel b, open circles). Conifer establishment was sampled in mixed aspen–conifer stands with low levels of browse (panel c, solid circles) and high levels of browse (panel c, open circles).

Influences of conifers on aspen

Due to the large number of decades during which aspen establishment was zero (70% of all potential decades of establishment), we regressed stand basal area in pure and mixed stands with maximum aspen establishment recorded for a given basal area range. For example, a maximum aspen establishment of 477 stems·ha^{-1}·decade^{-1} was recorded in pure aspen stands and 98 stems·ha^{-1}·decade^{-1} in mixed stands for stand basal area values ranging between 10 and <15 m^2/ha (Fig. 6). Maximum aspen establishment decreased exponentially in pure and mixed stands as stand basal area increased (Fig. 6). No pure stand had aspen recruitment when stand basal area was >47 m^2/ha and no mixed stand had aspen recruitment when stand basal area was >38 m^2/ha (Fig. 6). The comparison of slopes of linear regressions of log-transformed stand basal area and maximum aspen establishment values for mixed stands (log[max aspen establishment] = 4.60 − 2.373 × log[stand BA]; $P < 0.001$) and pure stands (log[max aspen establishment] = 4.278 − 1.543 × log[stand BA]; $P = 0.064$) showed the rate of decrease of maximum establishment was higher in mixed stands than in pure stands ($P = 0.026$). Aspen mortality was not significantly different between pure and mixed stands (Table 3).

All measures of aspen growth (BA, tBAI, aBAI) and mortality showed no significant difference between pure and mixed stands for the full period of stand development and in mature stands (Table 3a and b). When plotted, aspen basal area, total aspen basal area increment, and average basal area increment per tree showed

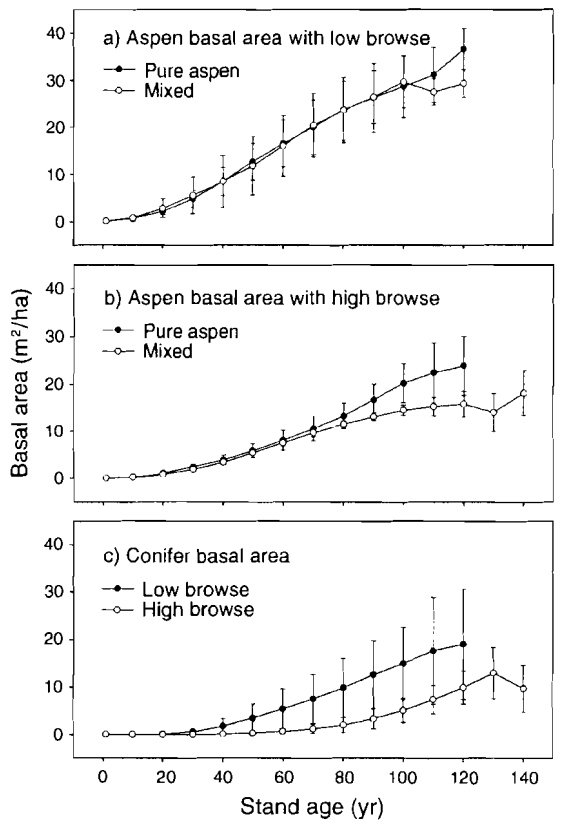

FIG. 2. Basal area of aspen and conifers over 120 years of stand development in 16 aspen stands in the Front Range, Colorado, USA. In each stand, basal area values were averaged by decade. Each line represents mean values (±SE) of four stands. Four types of stands were sampled: pure aspen stands with low levels of elk browse (panel a, solid circles), mixed aspen–conifer stands with low levels of elk browse (panel a, open circles), pure aspen stands with high levels of elk browse (panel b, solid circles), and mixed aspen–conifer stands with high levels of browse (panel b, open circles). Conifer basal area was sampled in mixed aspen–conifer stands with low levels of browse (panel c, solid circles) and high levels of browse (panel c, open circles).

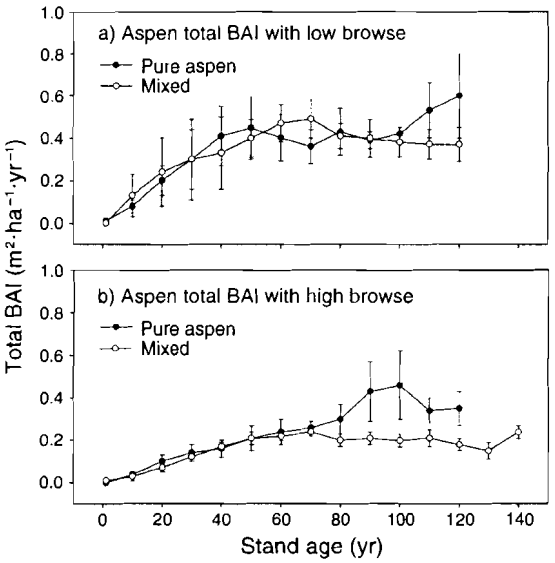

FIG. 3. Total basal area increment (BAI) of aspen over 120 years of stand development in 16 aspen stands in the Front Range, Colorado, USA. In each stand, total BAI values were averaged by decade. Each symbol represents mean values (±SE) of four stands. Four types of stands were sampled: pure aspen stands with low levels of elk browse (panel a, solid circles), mixed aspen–conifer stands with low levels of elk browse (panel a, open circles), pure aspen stands with high levels of elk browse (panel b, solid circles), and mixed aspen–conifer stands with high levels of browse (panel b, open circles).

no evidence of decline in mature mixed stands, and average tree-level BAI appeared to be increasing even when these stands were older than 100 years (Figs. 2a, b, 3a, b, and 4a, b). Aspen mortality was higher in pure stands than in mixed stands, although the difference was not significant (Table 2 and 3).

Influences of elk browsing on aspen

Aspen establishment over the full period of stand development was significantly higher in stands with low levels of browse than stands with high levels (Table 2a and 3a; Fig. 1a and b). Despite overall higher levels of aspen establishment in low-browse stands, at some ages (e.g., 60–80 yr) aspen establishment was higher in stands with high levels of browse (Fig. 1a and b). In stands with high browse levels, aspen establishment was not significantly different ($P = 0.74$) in the three decades before 1968 (41.1 ± 26.2 stems·ha^{-1}·decade^{-1}; mean ± 1 SE) and after (61.0 ± 47.2 stems·ha^{-1}·decade^{-1}). Mean aspen establishment in stands with high levels of browse was not significantly different ($P = 0.56$) for the period following 1968 from establishment values in stands with low browse (128.2 ± 60.9 stems·ha^{-1}·decade^{-1}). Repeated-measures analysis comparing establishment before and after 1968 found time to not be a significant factor ($P = 0.61$).

Measures of stand-level aspen growth (BA, tBAI) were consistently and significantly lower in stands with high levels of elk browse (Table 2 and 3, Fig. 2a and b, 3a and b), while average tree growth (aBAI) was not significantly lower in stands with high browse levels than those with low levels (Table 2 and 3, Fig. 4a and b). Time and browse levels interacted significantly for BA and tBAI for the full period of stand development (Table 3a), the only significant time interaction in the data.

Aspen mortality was higher in stands with low levels of elk browse than stands with high levels (Table 3). Mortality during the past 50 years in stands with low elk browse had nearly 70% variance explained by the maximum aspen density recorded in a stand, however this relationship did not exist in stands with high levels of elk browse (Fig. 7). The slope of the self-thinning line of aspen stands showed no pattern relating conifers and elk browsing with density-dependent mortality (Table 4).

DISCUSSION

Aspen forest development over 120 years included long-term trends related to the exogenous influences of conifers and elk browsing as well as intra-specific dynamics. Despite the capacity of living aspen to develop

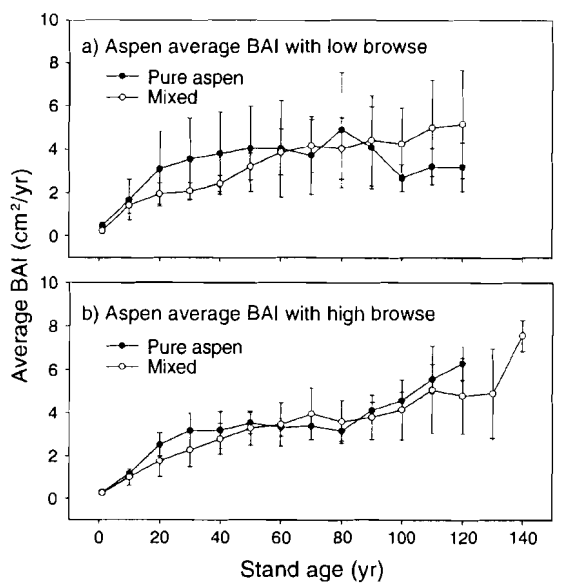

FIG. 4. Average basal area increment per tree (BAI) of aspen over 120 years of stand development in 16 aspen stands in the Front Range, Colorado, USA. In each stand, average BAI values were averaged by decade. Each symbol represents mean values (±SE) of four stands. Four types of stands were sampled: pure aspen stands with low levels of elk browse (panel a, solid circles), mixed aspen–conifer stands with low levels of elk browse (panel a, open circles), pure aspen stands with high levels of elk browse (panel b, solid circles), and mixed aspen–conifer stands with high levels of browse (panel b, open circles).

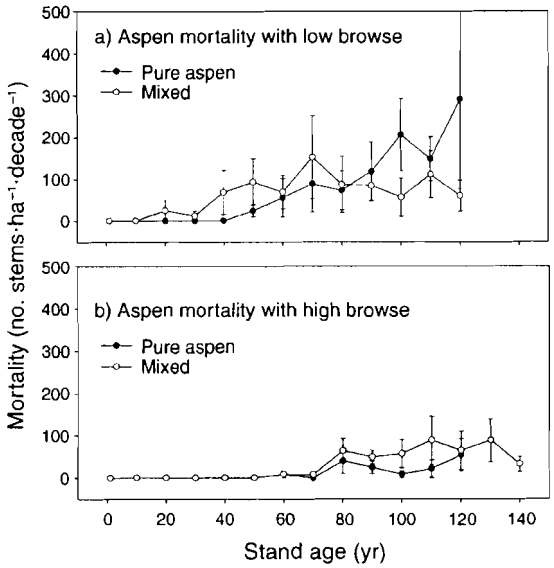

FIG. 5. Mortality of aspen over 120 years of stand development in 16 aspen stands in the Front Range, Colorado, USA. In each stand, mortality values were summed by decade. Each symbol represents mean values (±SE) of four stands. Four types of stands were sampled: pure aspen stands with low levels of elk browse (panel a, solid circles), mixed aspen–conifer stands with low levels of elk browse (panel a, open circles), pure aspen stands with high levels of elk browse (panel b, solid circles), and mixed aspen–conifer stands with high levels of browse (panel b, open circles).

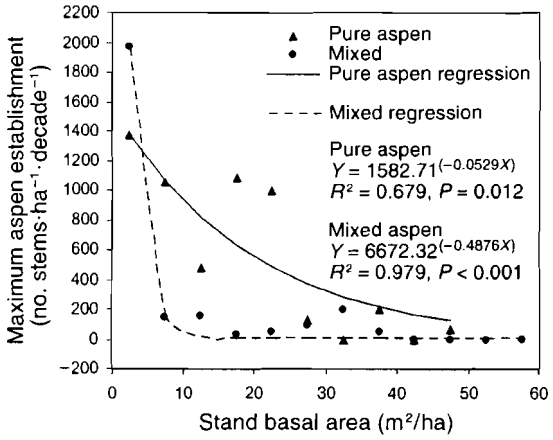

FIG. 6. Maximum values of aspen establishment recorded in eight pure aspen and eight mixed aspen–conifer stands for stand basal areas ranging from 0 to >55 m^2/ha. Each diamond (pure aspen) and circle (mixed stand) represents the maximum establishment recorded for a given 5 m^2/ha increment of stand basal area. Pure stands reached a maximum stand basal area of 50 m^2/ha, and mixed stands reached 60 m^2/ha. Exponential decay regression lines were fit to maximum aspen establishment data from pure stands (solid line) and mixed stands (dashed line). ANCOVA comparison of log-transformed stand basal area and maximum establishment data showed mixed stands to have a more negative slope than pure stands ($P = 0.026$).

heart rot and the species' soft wood, it makes a suitable species for stand reconstructions (e.g., Lieffers et al. 1996, Shepperd et al. 2001*a*, Hessl 2002, Larsen and Ripple 2003, this study). Through reconstructing aspen stand history, we found aspen stands to be highly variable through both space and time in their patterns of establishment, mortality, stem density, basal area, and degree of aspen-conifer mixing within the stands. Despite this variability, clear relationships between aspen forest development, conifers, and elk browsing were evident.

The change in species composition from pure aspen to mixed species is often labeled as conifer invasion. The process begins with aspen stand establishment via

TABLE 2. Aspen establishment, basal area (BA), total basal area increment (tBAI), average basal area increment per tree (aBAI), and mortality for 16 aspen stands in the Front Range of Colorado sampled in a 2 × 2 factorial design; values are means (±SE).

	Establishment (no. stems·ha⁻¹·decade⁻¹)		BA (m^2/ha)		tBAI (m^2·ha⁻¹·yr⁻¹)		aBAI (cm^2/yr)		Mortality (no. stems·ha⁻¹·decade⁻¹)	
	Browse		Browse		Browse		Browse		Browse	
Conifer	Low	High	Low	High	Low	High	Low	High	Low	High
a) Full period (0–129 yr)										
Pure aspen	153.01	100.67	13.06	11.70	0.29	0.24	3.29	3.31	52.12	46.22
	(45.20)	(26.44)	(1.24)	(1.06)	(0.02)	(0.02)	(0.25)	(0.25)	(12.27)	(7.43)
Mixed	181.68	73.85	15.88	9.01	0.34	0.20	3.18	3.41	76.60	23.08
	(50.20)	(15.55)	(1.38)	(0.77)	(0.02)	(0.01)	(0.28)	(0.22)	(13.19)	(4.62)
b) Mature stands (70–129 yr)										
Pure aspen	91.11	16.94	22.73	19.17	0.40	0.30	3.96	4.53	99.19	73.66
	(38.96)	(9.26)	(1.62)	(1.30)	(0.03)	(0.02)	(0.34)	(0.39)	(24.21)	(12.31)
Mixed	75.35	30.62	26.87	15.42	0.43	0.27	3.89	4.59	130.77	45.66
	(32.47)	(21.58)	(1.56)	(0.88)	(0.02)	(0.02)	(0.43)	(0.31)	(24.76)	(8.42)

Notes: The first factor was conifers, and the two levels were pure aspen and mixed aspen–conifer. The second factor was elk browsing, and the two levels were low browse intensity and high browse intensity. BA, tBAI, and aBAI were averaged by decade.

TABLE 3. Results of repeated-measures analysis of time series of aspen establishment, basal area (BA), total basal area increment (tBAI), average basal area increment per tree (aBAI), and mortality for 16 aspen stands in the Front Range of Colorado sampled in a 2 × 2 factorial design.

Factor	Establishment (no. stems·ha^{-1}·decade^{-1})	BA (m^2/ha)	tBAI (m^2·ha^{-1}·yr^{-1})	aBAI (cm^2/yr)	Mortality (no. stems·ha^{-1}·decade^{-1})
a) Full period (0–129 yr)					
Conifer (pure aspen vs. mixed)					
Browse (low vs. high)	**	*	**		
Conifer × browse					
Time		***	***	*	*
Time × conifer					
Time × browse		***	***		
Time × conifer × browse					
b) Mature stands (70–129 yr)					
Conifer (pure aspen vs. mixed)	*				
Browse (low vs. high)		*			
Conifer × browse					
Time		***			
Time × conifer					
Time × browse					
Time × conifer × browse					

Notes: The first factor was conifers, with the two levels being pure aspen and mixed aspen–conifer. The second factor was elk browsing, with the two levels of low browse intensity and high browse intensity. Significant P values ($\alpha = 0.05$) are indicated in three ranges: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. The direction of the effect of conifers and browse for all significant P values was that pure aspen and low-browse sites had higher values than mixed and high-browse sites. Empty cells had no significant effect.

root sprouting following a stand-replacing forest disturbance, such as fire (Grant and Mitton 1979, Jelinski 1993). In several cases in the West, aspen germination from seed has been witnessed following severe fires (Romme et al. 1997, Quinn and Wu 2001, Turner et al. 2003) however the long-term success of these seedlings has not been determined. Aspen may persist as pure stands (Betters and Woods 1981, DeByle and Winoker 1985, Cryer and Murray 1992, Crawford et al. 1998), but shade-tolerant conifer species often establish in the understory of aspen (DeByle and Winoker 1985, Cryer and Murray 1992). Conifer establishment in our study site began between 10 to 80 years following aspen establishment, similar to the variation reported for aspen in Alberta, Canada (Leiffers et al. 1996). In the traditional succession story, conifers enter what was a pure aspen stand, outcompete aspen, and with time dominate the stand. We found the influences of conifers on aspen forest development to support some aspects

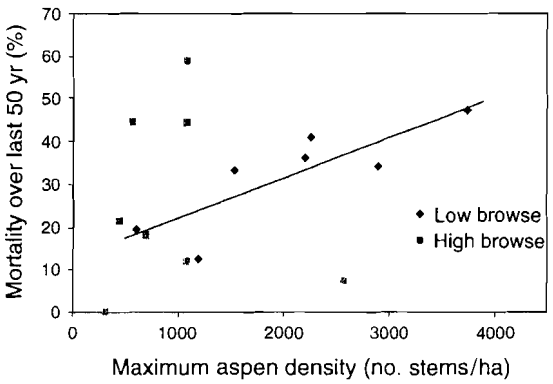

FIG. 7. The relationship between the percentage of aspen mortality recorded during the most recent 50 years and maximum aspen density reached in a stand. Aspen stands with low levels of elk browse (black diamonds) showed a strong relationship between the two, whereas stands with high levels of browse (gray squares) did not.

TABLE 4. Slopes of self-thinning lines of aspen in 10 even-aged aspen stands in the Front Range, Colorado, USA.

Type of stand	Slope of self-thinning line
Mixed, high browse	−0.55
Pure, high browse	−0.72
Pure, low browse	−0.86
Mixed, high browse	−0.93
Pure, low browse	−1.31
Expected	−1.5
Mixed, low browse	−1.67
Mixed, low browse	−2.34
Pure, low browse	−2.6
Pure, high browse	−2.83
Mixed, high browse	−2.99

Notes: The remaining six stands sampled in this study were not even-aged and were not included in this analysis. Slopes were calculated by the regressing of ln(density) against ln(basal area) and were compared to the expected self-thinning rate of −3/2 (Yoda et al. 1963). All regression lines had $R^2 > 0.80$ and $P < 0.001$. Stands are ordered from highest to lowest slope values.

of the traditional idea of invasion, but mostly our findings demonstrate a pattern of a gradual change in species composition driven by species' characteristics such as longevity and level of tolerance to shade.

Our analysis supports the hypothesis that the presence of conifers decreased aspen establishment, but the results fail to support the hypotheses that conifers decreased aspen growth and increased aspen mortality. Aspen establishment was lower in mature mixed stands than in pure stands. Additionally, our data suggest peak aspen establishment would be lower when space in a stand is occupied by conifers rather than aspen. Aspen growth showed no evidence of decline in mature stands, whether they were growing in pure or mixed stands. For example, one aspen stand over 100 years old had conifers exceed a basal area of 40 m^2/ha and still showed increasing aspen basal area and no decrease in average basal area increment per tree. In central Utah, reconstructed stand-level basal area increment was lower in mixed aspen stands than in pure stands, however this conflicting result may be due to two factors in the Utah stands that differ from our sites: aspen and conifers co-established following disturbance and the stands were of low productivity (Shepperd et al. 2001*a*). Aspen mortality was not higher in mixed stands and patterns in aspen mortality did not indicate that past disturbances (e.g., blow down, insect outbreaks) played a role in mortality within our stands. Nearly 70% of the variance of aspen mortality can be explained by the maximum density of aspen measured in each stand with low elk browsing (Fig. 7; see following paragraphs for a detailed discussion of the role of elk browsing).

Our data, combined with previous knowledge of aspen and conifer characteristics, provide the necessary information to update the description of aspen succession to conifers. Previous studies have shown that aspen's ability to sprout from existing roots gave it an advantage over conifers in rapid site recolonization (Peterson and Squiers 1995). Following initial aspen colonization in an area, aspen and conifers infilled aspen stands and as conifer presence increased the potential for aspen establishment decreased. Aspen growth remained resilient to the effects of conifers, possibly due to the ability of individual aspen stems to draw resources from a clonal root system (Jones and DeByle 1985). As time passed, aspen approached its maximum age, which is considered to be approximately <200 years in the Front Range. Concurrently, conifer species that are more shade tolerant and longer-lived than aspen (Aplet et al. 1988, Veblen et al. 1991) established and grew in the aspen stands. With a decrease in aspen establishment, aspen abundance decreased and conifer species began to dominate. Belowground, aspen root systems may remain intact despite a strong presence of conifers aboveground (Shepperd et al. 2001*a*). The succession model presented here would be altered by external and stochastic forces such as insect outbreaks, wildfires, and climate variability (Veblen et al. 1991, Binkley et al. 1997). The results from this study suggest that forest succession from aspen to conifers in our study area can be attributed to the vulnerability of aspen establishment under high levels of conifers rather than the susceptibility of its growth and mortality to the stresses of competition from conifers.

The time course of elk browsing could not be reconstructed in the same manner as the history of conifer arrival and growth in aspen stands, as elk browsing does not leave datable scars on aspen stems. Due to the spatial and temporal limitation of browse information, browsing could only be treated as a binary factor and aspen stands were described as experiencing either high or low levels of browse. In the future, monitoring of both elk activity within a stand and aspen dynamics would yield a more comprehensive understanding of the relationship between the two.

The majority of studies of elk browsing and aspen focus on decreased stem recruitment as the indicating factor of aspen decline. During the winter, elk are restricted to low elevations of the Park, where they browse both aspen stems and sprouts resulting in noticeable scars on mature trees and consumption of aspen recruitment. Ecologists have noted the impacts of elk browsing on aspen stands in the winter range of Rocky Mountain National Park as early as the 1930s (Packard 1942), when the elk population was estimated to be between 300 and 500 head. Recent reports of elk impacts on aspen establishment have coincided with a long-term high of over 1000 elk in the Park following the onset of the policy of natural regulation in 1968 (Olmsted 1979, 1997, Baker et al. 1997, Berry et al. 1997, White et al. 1998, Suzuki et al. 1999, Hessl 2002, Kaye et al. 2003) and spatially expansive studies throughout the West have shown diverse responses of aspen establishment to varying levels of elk browsing (Suzuki et al. 1999, Barnet and Stohlgren 2001, Larsen and Ripple 2003, White et al. 2003). Previous studies have suggested that elk browsing not only decreases aspen recruitment, but decreases the vigor of mature stems and increases their mortality through increased pathogen infection in browsing wounds on the tree stems (White et al. 2003).

Elk browsing negatively affected aspen establishment and stand-level growth in our study, but did not affect the average rate of aspen stem growth and mortality. In recent decades, aspen establishment was neither lower in browsed stands following the onset of natural regulation nor lower than establishment in unbrowsed stands. Interestingly, lower levels of aspen establishment were recorded during the entire period of aspen stand development, but not when exclusively considering the most recent 50 years when the elk population in the Park was largest. Despite the lower elk populations earlier in the century, ecologists noticed elk impacts on aspen in the winter range (Packard 1942). Elk browsing may have been impacting aspen

establishment throughout the Park's history and the recent boom in the elk population has not accelerated a decline in aspen recruitment, although browsing history of the sites cannot be confirmed. Lower rates of stand-level aspen growth in browsed stands also predate the boom in the elk population witnessed in the past few decades. The positive correlation between aspen density and mortality apparent in stands with low browse levels was not present in high browsed stands (Fig. 7), suggesting that elk browsing has the potential to effect the relationship between aspen density and mortality.

Observed differences in aspen dynamics between stands with low and high levels of browse could be the result of methodological shortcomings rather than ecological impacts of browsing. Aspen stands in the elk winter range have supported variable levels of elk browsing since 1915, and differences in aspen establishment, growth, and mortality may reflect many decades of elk impacts. However, lower levels of aspen establishment and growth in browsed stands begin over 100 years ago following stand establishment, a period when elk were absent from the Park. Lower levels of these measurements in the first decades of stand development may occur because the reconstruction does not include some stems that were present during that period and have since decomposed. Two possible mechanisms for accelerated wood decomposition in browsed stands are (1) physical breakdown of dead and downed trees by elk trampling and (2) accelerated wood decomposition due to the introduction of pathogens into aspen wood through browsing wounds. In order to avoid making conclusions concerning the impact of elk browsing on aspen based on a potentially incomplete reconstruction, results from recent decades should be emphasized because reconstruction limitations from loss of wood to decomposition would be less influential. The most recent decades of aspen forest development indicate that elk browsing did not decrease the average rate of tree growth; however, aspen establishment and the total amount of wood in browsed stands was lower.

The combined effects of conifers and elk browsing resulted in aspen forests with the lowest amount of aspen present in the stands and the slowest rate of aspen stand growth. Lower amounts of aspen in stands with conifers and elk browsing were the cumulative result of decreased aspen recruitment into the stands over the full period of stand development. Mortality was lowest in stands with conifers and browsing, which does not support our hypothesis that both factors would accelerate aspen mortality. High levels of mortality in pure stands with low browse may be the result of self thinning, as supported by the positive relationship between the percent aspen mortality and the peak aspen density reached in a stand (Fig. 7).

The comparison of self thinning rates among aspen stands provided further evidence that conifers and elk browsing did not accelerate the rate of aspen mortality. We used the framework of the $-3/2$ thinning law (Yoda et al. 1963) to analyze whether conifers and elk browsing accelerated aspen self thinning, despite the controversy surrounding the method (see Weller 1987, Lonsdale 1990). The slope of the self-thinning line would be steeper if either factor was systematically augmenting the amount of aspen mortality, a pattern that was not evident in our analysis (Table 4). A previous study of the impacts of elk browsing on aspen mortality in the winter range of Rocky Mountain National Park suggested that the amount of aspen mortality was higher in browsed stands and that the size distribution of dead aspen in unbrowsed stands was more skewed to small-diameter trees, however these findings were not statistically tested (Baker et al. 1997). This study did not address the distribution of sizes for dead aspen stems but it found that the lack of difference in thinning rates indicated that increased aspen mortality was not a mechanism contributing to the species transition from aspen to conifers or the possible aspen decline brought about by elk browsing in our study sites.

Management Implications

Adaptive management plans for aspen forests should be based on detailed understandings of the major factors that influence these forests, including conifers and elk browsing (National Research Council 2002). Adaptive management prescriptions can only be made with spatially and temporally comprehensive data documenting the impacts of conifers and browsing (Holling and Meffe 1996).

Our data support the hypothesis that conifers and elk browsing decreased aspen establishment and that browsing decreased stand-level aspen growth. However the results did not support the hypotheses that either factor impacted the growth rate of individual trees or aspen mortality. Aspen's response to conifers and elk browsing can be explained by the species' clonal growth and low tolerance of shade, however further research should test these mechanisms experimentally.

The results of this study suggest that aspen abundance in the Central Rockies can be improved with enhanced aspen recruitment. Once established, its growth and mortality were resilient to both conifers and browsing over the past century. Successful aspen regeneration at small scales (<10 ha) may by achieved with human manipulations such as the physical protection of aspen recruitment from browsing and conifers. Over decadal to centennial time periods and large spatial scales managers may have to rely on disturbance regimes and climate variability. Past pulses of aspen recruitment have occurred following widespread stand-replacing fires (Kulakowski et al. 2004) and during wet periods (Romme et al. 1995), but the recruitment–climate relationship was not detected in one study in the elk winter range of Rocky Mountain National Park (Baker et al. 1997). The 1988 fires in Yellowstone have

demonstrated that aspen colonization will not be successful in the presence of intense elk browsing. Stand-replacing fire regimes combined with suitable climate and/or decades of controlled elk browsing may be a source for the initiation of new aspen stands, and could reduce the concern of forest managers over the loss of older aspen stands to the long-term impacts of 20th-century increases in conifers or elk browsing.

ACKNOWLEDGMENTS

Thanks to Monica Turner, Bill Baker, and an anonymous reviewer for comments on the manuscript. Thanks to Holly Barnard, Suzie Bird, Benjamin Fancher, Jason Kaye, James Riser, and Jessica Worden for assistance in the field and laboratory. This research was funded by the Global Change Research Program of the Biological Resources Division of the U.S. Geological Survey.

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