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WILLOW THICKETS PROTECT YOUNG ASPEN FROM ELK BROWSING AFTER WOLF REINTRODUCTION

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Aspen (*Populus tremuloides*) is the most widely distributed deciduous tree in North America (Bartos 2001). However, long-term assessments of its status indicate a decline in abundance throughout the western United States during much of the 20th century (Kay 1997, Bartos and Campbell 1998, Bartos 2001). In Yellowstone National Park, aspen decline has been noted on the "northern range," the wintering grounds for the park's largest elk (*Cervus elaphus*) herd. As one of the principal deciduous woody species found in Yellowstone National Park, aspen contributes to ecological diversity by providing habitat for numerous vertebrate and invertebrate species, supports a variety of plant associations, provides browse for ungulates, and has aesthetic appeal for park visitors.

Concern about the loss of aspen on the northern range began in the 1920s and has been the subject of debate and research ever since (Warren 1926, National Research Council 2002). Most research has attributed the park's aspen decline primarily to long-term browsing pressure by elk (see National Research Council 2002 for review). Influences such as fluctuations in climate, altered fire regimes, and conifer invasions have been identified as potentially contributing to aspen decline (Romme et al. 1995, Yellowstone National Park 1997, Meagher and Houston 1998).

Vegetation on the northern range consists of sagebrush (*Artemisia* spp.) steppe, primarily big sagebrush (*A. tridentata*), and grassland interspersed with small stands of trees, primarily Douglas-fir (*Pseudotsuga menziesii*) and aspen (Despain 1990). Aspen covers approximately 1% of the northern range landscape (Ripple et al. 2001). Existing riparian areas are dominated by sedge (*Carex* spp.) and grass-dominated meadows with patches of willow (*Salix* spp.).

Ripple and Larsen (2000) discovered that the decline of aspen began with the extirpation of wolves (*Canis lupus*) from Yellowstone National Park in the 1920s. They hypothesized that the failure of aspen to reach tree height over the last half century may be due to changes in northern range trophic structure involving the gray wolf, elk, and elk herbivory on aspen. Following wolf extirpation from Yellowstone National Park, aspen sprouts and other deciduous woody species were browsed more heavily, changing their growth form dramatically and sometimes increasing mortality (Singer et al. 1998, Barmore 2003). In recent decades neither willow, aspen, nor cottonwood (*Populus* spp.) has been able to grow above the browsing level of elk, resulting in low stature throughout most of the northern range (Barmore 2003, Beschta 2003, Larsen and Ripple 2003).

The elk of Yellowstone National Park lived in an environment free of wolves for approximately 7 decades, from the mid-1920s until 1995, when wolves were reintroduced. By the end of 2001, nearly 80 wolves lived on the northern range of Yellowstone National Park (Smith et al. 2003). In recent years, following wolf reintroduction, elk have altered their movements and foraging patterns to minimize their risk of being preyed upon by wolves (Ripple et al. 2001, Ripple and Beschta 2003). Some young willow and cottonwood have been growing taller along various stream reaches in recent years in northern Yellowstone National

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Park (Ripple and Beschta 2003), though suppressed aspen sprouts generally have not been able to escape browsing (Smith et al. 2003).

Field observations in late summer 2003 indicated that young aspens are growing taller within willow clumps along parts of Crystal Creek near its confluence with the Lamar River. Linked mechanisms for why (1) willow is growing taller and (2) aspen in willow is growing taller include the following:

1. Increased predation risk following the reintroduction of wolves caused less browsing by elk and the growth of taller willow plants (Ripple and Beschta 2003). Taller and denser willow thickets contributed to increased predation risk, thus further reducing browse intensity (Ripple and Larsen 2000, White et al. 2003).
2. Willow provides physical protection from browsing for young aspen stems as well as visual protection, making the stems often indistinguishable from those of willow ("safety in numbers").

Our objective was to test the hypothesis that taller willow represents a mechanism for aiding aspen tree growth in an ungulate winter range by addressing 2 questions: (1) Are aspen within willow clumps growing differently from those growing in adjacent but relatively open areas? (2) Is there a direct positive relationship between heights of aspen sprouts growing in willow and heights of the willow?

In August 2003 we searched for aspen growing in willow clumps along a 500-m reach of Crystal Creek. Whenever we encountered aspen sprouts within willow clumps, we obtained plant height measurements on (1) the aspen plant within the willow clump, (2) the tallest willow leader in the same clump, and (3) the nearest aspen growing outside the willow clump <5 m away (Fig. 1). Plant measurements were used to evaluate the recent history of plant heights and browsing levels (Keigley and Frisina 1998, Keigley et al. 2003). Since browsing usually removes the terminal bud, causing growth to emerge from a lateral bud, the stems grow in a zigzag pattern, leaving behind stubs representing annual segments that can be measured (Keigley et al. 2003). Thus, to assess plant growth history, we measured the height of annual terminal bud scars (or annual segments) for the previous 3 years (2000–2002). For browsing intensity we determined whether each annual leader segment had been browsed for each of the last 3 years.

Confidence intervals (±95% CI) were plotted to assess significant differences between height of aspen sprouts in the willow and height of adjacent aspen sprouts in the open. Linear regression was used to test the null hypothesis of no relationship between height of willow and height of aspen sprouts growing in the same willow.

Along the 500-m transect we found 16 young aspen plants growing within clumps of 3 species of tall willow, including Bebb willow (*S. bebbiana*), Booth willow (*S. boothii*), and Geyer willow (*S. geyeriana*). Heights measured during late summer 2003, after the summer growing period and before winter browsing, indicated that aspen growing in willow clumps were significantly taller ($\bar{x}$ = 180 cm, 95% CI ±19.7 cm) than aspen growing in the open ($\bar{x}$ = 104 cm, 95% CI ±13.7 cm), but not significantly different from their protecting willows ($\bar{x}$ = 181 cm, 95% CI ±17.9 cm). We found a strong linear relationship between willow height and height of aspen growing within the same willow clumps ($r^2 = 0.71$, $n = 16$, $P < 0.01$; Fig. 2).

In addition, aspen stems growing inside willow clumps were significantly taller than aspen growing in the open adjacent to willow clumps in 2000, 2001, and 2002 (Fig. 3). We found no significant differences in willow heights and corresponding aspen heights in willow clumps for 2001 and 2002 (Fig. 3). Leaders browsed each year between 2000 and 2002 ranged from 81% to 100% for willow, 73% to 94% for aspen growing in willow, and 93% to 100% for aspen growing in the open.

These results suggest that, on sites suitable for both willow and aspen regeneration, tall willows can play a supportive role in aspen recruitment success by providing protection from ungulate browsing. These findings are similar to those of Ripple and Larsen (2001), who determined that aspen sprouts were escaping severe browsing and growing taller where dead conifer trees had recently fallen and created protective "jackstrawed" barriers to elk movement. The multi-stemmed configuration of willows probably contributes to their effectiveness in protecting aspen sprouts from browsing. It also appears in at least some cases that the annual growth rates of aspen leaders

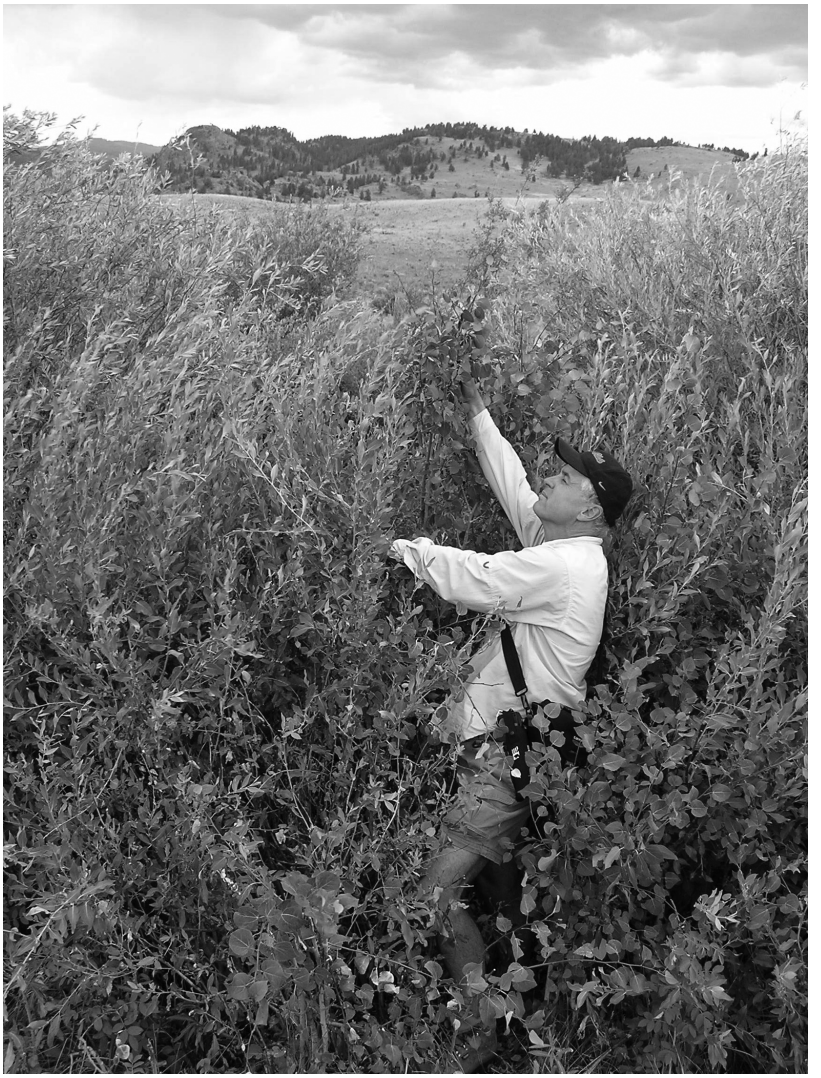

Fig. 1. Photograph showing tall willow and aspen on Crystal Creek in August 2003. The maximum height of young aspen leaders here was 238 cm (above the subject's right hand), the tallest willow stem adjacent to the aspen was 222 cm, and the aspen leader outside the willow clump measured 125 cm (in front and to the right of the subject). These willows and aspen appear to be growing much taller since wolf reintroductions of 1995/1996.

equal or exceed those of willow, increasing the likelihood that these aspen may grow into large-stemmed trees and not be overtopped by willows.

We hypothesize that willows along Crystal Creek are growing taller because the proportion of the current year's growth being consumed by elk is less than it was before wolf reintroduction, due to increases in predation risk and associated changes in elk foraging behavior in the presence of wolves (Laundré et al. 2001). With wolves in the system, elk may be spending less time browsing on individual plants and removing a smaller proportion of the current year's growth in areas with high levels of predation risk (Ripple and Beschta 2003). This would account for the taller plant growth even though browsing levels are relatively high as shown by the percentage of leaders browsed annually.

At the landscape scale, willow growing in valley bottoms may be browsed less since elk

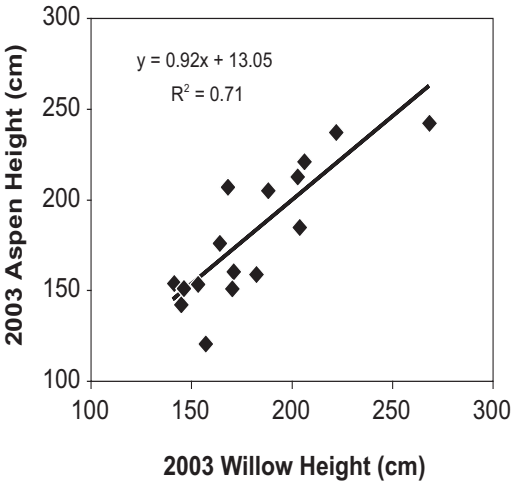

Fig. 2. Relationship between late summer 2003 heights of willow and aspen growing within the same willow clumps in Yellowstone National Park. This regression suggests that willows on these sites are providing protection to aspen from browsing by elk.

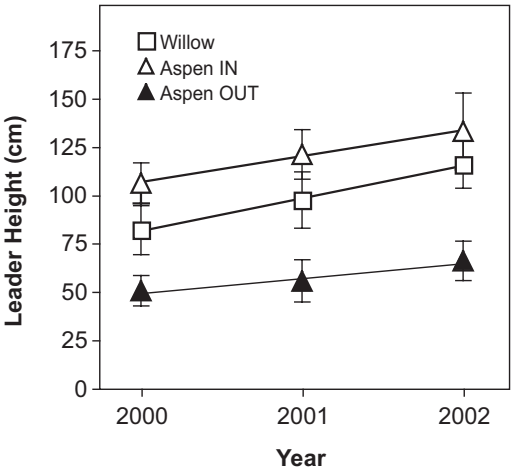

Fig. 3. Heights (means ±95% confidence intervals) of willow and aspen leaders after winter browsing in 2000, 2001, and 2002 based on plant measurements along Crystal Creek. Data include leader height of aspen in willow clumps, height of the tallest adjacent willow leaders, and height of the aspen outside the willow clumps.

may be avoiding certain riparian areas and selecting for higher ground to lower their risk of predation by wolves (Ripple and Beschta 2003). In contrast to many riparian areas, uplands may provide elk with a lower risk of predation, better escape terrain, and fewer escape impediments (Bibikov 1982, Kunkel and Pletscher 2000, 2001). For example, Bergman (2003) found an inverse correlation between distance from streams and successful wolf kills in central Yellowstone National Park. Likewise, Gula (2004), while studying wolves and ungulates in Poland, found that riparian terrain features appeared to be important for hunting strategies used by wolves. He discovered that wolves made most kills (74%) in ravines and creeks where ungulates (mostly elk) may be easier to intercept as they slow down and change their gait. Conversely, this same process of elk avoiding riparian areas could be causing high browsing pressure on upland aspen stands. We know of no current aspen recruitment in the uplands on the northern range within Yellowstone National Park.

Willow typically grows as a shrub with many leaders, while aspen tends to have a single terminal leader that is more susceptible to herbivory by ungulates. This difference in growth form could account for the greater growth of willow than aspen in recent years following the wolf reintroductions of 1995 and 1996. Our paired willow/aspen height measurements indicate that willow is able to withstand more browsing than aspen. The spatial extent of this process whereby tall willows provide browsing protection for aspen is unknown at this time, but we do not expect large stands of mature aspen developing from this process since the occurrence of aspen in willow is not common in the study area. Furthermore, while the increased height growth of young aspen may indicate that some recovery of aspen is underway in the northern range, it is still too early to know if these aspen sprouts, averaging 180 cm tall in the late summer 2003, will be able to overcome browsing by elk, will grow fast enough to not be overtopped by willows, and will eventually grow to tree height.

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