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Response of Aspen Suckers to Simulated Browsing

Dale L. Bartos, Koketso Tshireletso, and John C. Malechek

Heavy and repeated ungulate browsing on reproductive suckers has limited quaking aspen (*Populus tremuloides* Michx.) regeneration on many Western landscapes. However, little is known about the specific effects of season and intensity of browsing. The objectives of this study were to determine the effects of season and intensity of clipping (simulated browsing) on density and growth characteristics of suckers. Three randomly selected stands were clear-felled in mid-July 2005 and fenced. Simulated browsing intensities of 0, 20, 40, and 60% removal of the current year's growth on aspen suckers were randomly applied in early, mid, and late summers of 2006 and 2007 on permanently demarcated quadrats. Sucker density and sucker height were monitored in each quadrat. Changes in annual sucker numbers for the ends of 2006 and 2007 were compared with declines found that reflected both winter and summer (2007 only) mortality. Mortality was not found for suckers clipped in early summer compared with mortalities of 48 and 46% for mid and late summer clipped suckers, respectively. However, even at the highest mortality, there were still ample numbers (~25,000/ha) of suckers for stand regeneration. At the end of the study, sucker height was reduced by all summer treatment intensities. After adjustment for the controls, clipping (of current year's growth) at 20 and 40% in mid and late summer resulted in suckers that were 47 and 41 cm tall, respectively. However, clipping at 60% resulted in suckers that were only 20 cm tall. Application of information found in this study to new areas under similar circumstances suggests that browsing of terminal leaders at intensities $\leq 40\%$ in midsummer for 1 or 2 years would not have a substantial impact on aspen regeneration.

Keywords: quaking aspen, browsing intensity, browsing season, herbivory, *Populus tremuloides*

The decline of aspen (*Populus tremuloides* Michx.) stands on Western landscapes has been widely documented (Campbell and Bartos 2001, Hessel and Graumlich 2002). Although the factors contributing to this decline are varied and difficult to separate, it has been partly attributed to excessive browsing of reproductive suckers by ungulates (Kay 1997, Bartos and Campbell 1998, Kilpatrick and Abendroth 2001, Shepperd et al. 2001). However, beyond that fact, very little is known about the responses of suckers to browsing, especially how it is affected by intensity and season of browsing.

In the West, large numbers of suckers are usually produced the first or second year after a stand is disturbed. In some areas, where alternative forage for ungulates is limited (because of overuse or poor growing conditions), animals will concentrate on browsing aspen suckers where they are available. Even when there is an abundance of usable forage, ungulates (particularly elk) will sometimes seek out and avidly consume aspen suckers (Shepperd et al. 2006). A certain amount of browsing can be tolerated by the regenerating aspen; however, in some instances total use of the suckers occurs. We¹ have observed cases in which stands have been browsed repeatedly (taken

down to ground level), and total elimination of the stand has occurred in as few as 1 or 2 years. When there are no aspen stems growing aboveground, the root system will eventually die due to lack of photosynthesis. In other instances, suckers may only be hedged, but with repeated browsing, usually by deer (*Odocoileus hemionus* Merriam) or elk (*Cervus elaphus* L.), 30- to 40-year-old stems cannot grow above 0.5 m high and are generally hedged back to the snow line during the winter or early spring.

In general, herbivory on most plant species is most detrimental during the early and/or late growing seasons, depending on the amount of plant tissue removed (Garrison 1963, Cook 1971, Bergström and Danell 1987). During the early stages of growth, plants invest much of their root energy stores in physiological processes required by the recently activated plant. At this stage, the plant cannot satisfy all of its metabolic demands through photosynthesis. Although root carbohydrate reserves do not influence aspen sucker initiation, they are important to early sucker growth when the photosystem is not fully functional (Frey et al. 2003). Therefore, herbivory during this early part of the season is thought to constrain the plant because of the depletion of root energy reserves before the

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Affiliations: Dale L. Bartos (dalebartos@fs.fed.us), USDA Forest Service, Forestry Sciences Laboratory, Logan, UT. Koketso Tshireletso (ktshirel@bca.bw), Botswana College of Agriculture. John C. Malechek (john.malechek@aggiemail.usu.edu), Wildland Resources Department, Utah State University, Logan, UT.

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This article uses metric units; the applicable conversion factors are: centimeters (cm): 1 cm = 0.39 in.; meters (m): 1 m = 3.3 ft; square meters (m²): 1 m² = 10.8 ft²; millimeters (mm): 1 mm = 0.039 in.; kilometers (km): 1 km = 0.6 mi; hectares (ha): 1 ha = 2.47 ac.

photosynthesis rate is high enough to generate full growth. During the late growing season, the plant requires adequate energy before entering dormancy (Cook and Stoddart 1960, Cook 1971, Willard and McKell 1978). This energy is used for over-winter bud maintenance and to support growth when conditions are sufficient in the following spring. Hence, late season use can deplete energy stores that will not be available for growth initiation the following spring. Essentially, for the plants to tolerate herbivory, they must withstand the challenge of annually losing and then replenishing root resources.

Plant developmental stage and timing when herbivory occurs greatly affect the plant's response (Dyer 1975, McNaughton 1983, Keigley and Frisina 1998). Because of their photosynthetic ability, larger plants are able to withstand some level of herbivory, compared with young or small plants. Many woody plants have characteristics that allow them to tolerate some level of browsing (Bilbrough and Richards 1993, Boege and Marquis 2005). Their growth is mediated and controlled by hormonal mechanisms that tend to suppress lateral growing points while maintaining apical dominance (Haukioja and Koricheva 2000). When apical dominance is broken by browsing or other external factors, lower buds are free to open and initiate growth. These mechanisms that regulate plant regrowth are basically the same as those of normal growth (Haukioja and Koricheva 2000). Thus, root reserves can be compensated for. Woody plant canopies expand through regulated growth of individual shoot modules, with those plant parts getting the best access to resources being favored (Haukioja and Koricheva 2000).

The mechanism of increased tissue growth after loss to herbivory has been studied in woody plants and has been described as compensation, undercompensation, or overcompensation (Belsky 1986, McNaughton 1986, Guillet and Bergström 2006). This conceptual framework (herbivore optimization hypothesis) asserts that at low or moderate biomass removal, the plant may be stimulated to produce well above the lost tissue amount. However, beyond a certain critical level of tissue removal, the plant can no longer compensate, leading to undercompensation.

Few studies in the western United States have attempted to document the effects of herbivory impacts on aspen with respect to timing (Carson et al. 2007, Jones et al. 2009) and intensity (Julander 1937, Campa et al. 1992, Osier and Lindroth 2004, Jones et al. 2009) of defoliation. For example, Julander (1937) performed a clipping study over a 4-year period on the Kaibab National Forest in Arizona and found that aspen reproduction deteriorated when 75% or more of the current year's sucker growth material was removed. Clipping aspen at 65–70% removal levels permitted fair growth, but greater growth occurred under lighter clipping levels. Julander did not compare the effects at different seasons.

Tolerance is considered to be an especially viable form of survival in plants with high intrinsic growth rates, large storage capacity, and substantial physiological (e.g., photosynthetic) plasticity, all traits that are characteristic of aspen (Lindroth 2001). However, it remains to be seen how these mechanisms operate in aspen suckers. We initiated this study in 2005 to investigate the response of aspen suckers to simulated browsing under natural environmental conditions at different periods of the growing season. The general area where the study was located is exposed to herbivory by several species of large ungulates (elk, deer, cattle [*Boa taurus* L.], and sheep [*Ovis aries* L.]). Specific objectives of the study were to determine the effects of simulated browsing at four intensities and three seasons on aspen sucker density and sucker growth response (height). We hy-

pothesized that early summer simulated browsing would yield lower aspen density and overall growth than mid and late summer clipping and that both density and growth would decrease as the intensity of clipping increased.

Methods

The study site was located on the Utah Agriculture Experiment Station Miners Peak, which is privately owned land on Cedar Mountain. This site is approximately 27 km southeast of Cedar City, Utah. The elevation is 2,800 m with a mean annual precipitation of 711 mm from 1970 to 2007. Precipitation is primarily from winter snow and as much as one-third from summer monsoons (Ohms 2003). Annual precipitation during the study was 1,323, 640, and 810 mm for 2005, 2006, and 2007, respectively.

Vegetation of the area consists of interspersed mountain grasslands and woodlands of quaking aspen, with patches of Gambel oak (*Quercus gambelii* Nutt.) (Ohms 2003). Some areas have well-defined shrub fields of mountain snowberry (*Symphoricarpos oreophilus* Gray). The dominant grasses are Letterman needlegrass (*Achnatherum lettermani* [Vasey] Barkworth) and Kentucky bluegrass (*Poa pratensis* L.).

Aspen stands can either consist of numerous aspen genets (from different clones) (Mock et al. 2008) or be a single clone (DeWoody et al. 2008). Individual ramets become less dependent on the parent root system, and within 20–25 years are generally no longer connected and aspen stems function as individuals (Barnes 1966, Sheperd 1993, DeByle 1964, Maini 1968, Tew et al. 1969).

Three aspen stands were randomly selected within a 75-ha pasture on the Miners Peak site (1,310 ha) located at latitude 37°29'652" N and longitude 112°56'247" W. The pasture consisted of a mosaic of quaking aspen and Gambel oak of roughly equal proportions. Independence among stands was established by comparing the tree age of 10 randomly selected aspen trees per stand following the procedures described by Asherin and Mata (2001).

Pretreatment tree density was calculated by counting all aspen trees/suckers within 3 randomly selected belt transects (2 × 30 m). Values are expressed as stems/ha. Most of the mature aspen trees selected for treatment in this study were considered to be independently functioning individuals with their own root systems.

To further characterize the trees, leaf samples were collected from aspen suckers that emerged after treatment and were subjected to DNA extraction. Duplicate leaf samples were taken at five locations on each site for a total of 10 samples per site. Samples were obtained at systematic locations along a line that began at a randomly selected point within each stand. All samples were gathered in July 2006 and were subjected to standard DNA analysis (Mock et al. 2008) at the Genetics Laboratory at Utah State University (Logan, UT).

The stands selected (~0.5 ha each) were clear-felled in mid-July 2005, and logs were immediately hauled off the site using a front loader-equipped farm tractor. This treatment resembled a commercial harvest (clearfell coppice) where big logs are removed, leaving behind the small branches. Aspen removal and soil disturbance by the tractor stimulated sucker emergence by releasing apical dominance.

The cleared stands were immediately fenced with a 3-m high game-proof black plastic mesh fence to protect suckers from ungulate browsing. The fence was laid down in late fall of 2005 just before the snowfall to prevent it from being crushed by the snow. It was replaced in late spring of 2006 as soon as the area was accessible by vehicle. We assumed that suckers would remain covered and

protected by snow through the winter, thus incurring minimal browsing during this period. However, most of the 2005 suckers were browsed in early spring 2006 before the fence could be replaced. This impact was probably caused by deer and elk returning to the area after wintering at lower elevations. For this reason, the fence was left standing at the end of the growing season in 2006 and was not affected by heavy snowfall. Because most suckers that had sprouted in the summer of 2005 were totally consumed by ungulate browsing in early spring of 2006, most suckers that existed in the summer of 2006 began growing in spring or summer of that year.

In June 2006, each stand was divided into three roughly equal portions, and each was randomly assigned to one of the three clipping seasons: early summer (ES), June 15; midsummer (MS), July 30; and late summer (LS), September 15. In each portion, four transects were established, running the entire length of the stand. Transects were placed at a minimum of 2 m of one another. Each transect was randomly assigned a simulated browsing intensity (control and 20, 40, and 60% removal of the current season's growth).

Along each transect, 15 1-m² (square) permanent quadrats were established, using the nearest plant method (US Department of Interior 1996) for monitoring aspen suckers. Quadrats were permanently marked and labeled. The selected sucker served to locate the center of the quadrat.

The same clipping intensities (control and 20, 40, and 60%) were applied to all suckers within each quadrat in 2006 and 2007 for three seasons (ES, MS, and LS). All clipping was completed within 1 week in each case.

Height was measured for the sucker permanently marked in each quadrat to the nearest 0.5 cm. The simulated browsing on sucker heights was limited to measurement of leader growth, which reflects the ability of the suckers to grow out of the reach of ungulates. Density was measured by counting all suckers in each quadrat. Density and height measurements were taken before each treatment for each time and again at the end of the growing year in October 2006 and 2007.

Clipping intensities were achieved using the ocular estimation method (Bonham 1989). This involved clipping and weighing variable percentage amounts of sucker foliage on off-site plants until a satisfactory level of consistency was achieved between estimates and weighed amounts. After clipping and weighing an estimated amount, the remaining portion of the sucker was clipped at ground level and also weighed. The initially clipped material was then expressed as a percentage of the total plant weight to see how close it came to the estimated removal intended. Then, at each treatment quadrat, a specified clipping intensity was imposed on the current year's growth of every branch (including the terminal leader) of each sucker, based on the ocular estimates.

To minimize the chance occurrence of spreading pathogens between suckers, the hand clippers were dipped into 70% alcohol before a new sucker was clipped. Young aspen suckers are known to be very susceptible to pathogens, especially when they are injured (Hinds and Shepperd 1987). However, we observed no incidence of disease on the treated suckers.

All data for sucker density and sucker height were analyzed as a three-way factorial in a split-split plot design with whole plots in blocks by analysis of covariance (ANCOVA) using the PROC GLIMMIX (SAS Institute, Inc. 2010) procedure. The main factors analyzed included three seasons, four clipping intensities, four sampling times (referred to as "time" in the figures), and all possible interactions. Sampling times were before clipping (B06 and B07

during 2006 and 2007, respectively) and at the end of the growing season after clipping (A06 and A07). These data were analyzed using B06 as a covariate, which was used to adjust posttreatment means to common pretreatment heights and densities. Interactions included season, intensity, and sampling time.

Whole plots were seasonally designated portions of the stand nested within sites (blocks), and season was the whole plot factor (ES, MS, and LS). Subplots were transects within the designated portions of the stand, and the subplot factor was intensity (control and 20, 40, and 60%). Transects were measured using subsubplots for time (B06, B07, A06, and A07). Sites were considered random effects. For sucker density, zero values were included in all analyses because they were real data values. However, for sucker height, zero values were treated as missing data in the analyses.

The ANCOVA model described above was used to compare sucker density and height for two different time frames: at the end of the season in 2006 (A06), before clipping in 2007 (B07), and the end of the growing season in 2007 (A07) to before any treatment (B06); and at the end of the growing seasons in 2006 (A06) and 2007 (A07) to evaluate the effects of two consecutive seasons of clipping including winter mortality. A third analysis dealt exclusively with sucker density and their response at the end of the growing season in 2006 (A06) to before clipping in 2007 (B07) to evaluate winter effects on suckers. It should be noted that wildlife migrate out of this area during the winter months because of the deep snowpack; therefore, where they have access to regeneration, they should have minimal impact on aspen suckers during this time.

Multiple comparisons of the least squares means for the fixed effects were made using the Tukey-Kramer significant difference procedure (Dowdy and Wearden 1991). Differences were considered significant at $P < 0.05$. Sucker density data were square root transformed, and sucker height data were log transformed to better meet the assumptions of homoscedasticity and normality for ANCOVA. All means reported herein are descriptive statistics computed using the untransformed raw data.

Results

Stand Descriptions

Pretreatment aspen densities were not statistically different among the three stands ($P \leq 0.05$) with $1,555 \pm 468$ stems/ha. This number is in excess of the 1,250 suckers/ha that Bartos and Campbell (1998) suggested as a lower limit at which a stand would regenerate successfully. Age and genetics demonstrated that the three stands were independent (estimated stand age [\pm SE] was 104 ± 5 , 63 ± 14 , and 27 ± 3 years for the three respective stands; site 1 was genetically uniform, whereas sites 2 and 3 had two different genotypes in each).

Effects of Intensity and Season of Clipping on Sucker Density Responses

There was a reduction in sucker numbers over the course of the study with sucker density (mean \pm SE) for A06, B07, and A07 declining from $39,900 \pm 3,695$, $29,000 \pm 4,945$, and $25,600 \pm 4,435$ suckers/ha, respectively. There was a 27% reduction in sucker numbers during winter (A06–B07) and a further 12% reduction in the summer of 2007 (B07–A07). Typically, aspen suckers decline within the first or second year after treatment (Shepperd 1993) due to natural causes, self-thinning, browsing by ungulates, or a combination of the three.

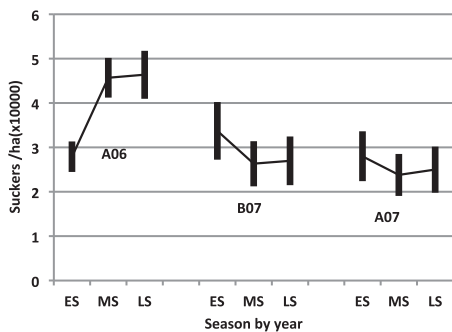


Figure 1. Effect of season of clipping on density of suckers clipped once during the growing season. The sucker numbers for the three seasons were averaged for four clipping intensities. B06 and B07 (A06 and A07) represent before (after) suckers that were clipped at the beginning of seasons in 2006 and 2007, respectively. B06 was used as a covariate in the analysis of these data.

Interactions on density between the season when clipping occurred and the time periods (A06, B07, and A07) are presented in Figure 1. There was a significant difference in density among the three seasons for the first time (A06) clipping occurred ($P \leq 0.0041$). This difference is attributed to fewer suckers that resulted from the ES clipping compared with the MS and LS clippings. ES clipping showed no difference across the three time periods. Differences were found for MS-clipped ($P \leq 0.0006$) and LS-clipped ($P \leq 0.0010$) plots. These differences resulted in fewer suckers for both clipping times in B07 and A07 compared with those for A06.

Sucker density decreased between the end of 2006 and the end of 2007 (A06 and A07) for MS- and LS-clipped plants (Figure 1). This change reflects death over winter (A06 versus B07) as well as summer mortality (B07 versus A07). Clipping in MS and LS caused 48 and 46% reductions in sucker numbers, respectively. However, it is interesting to note that ES-clipped plots endured the same conditions as those for the other two time periods, but sucker numbers remained relatively constant for that season of clipping. This number reflects an increase of new suckers in the ES-clipped plots at the beginning of 2007. Intensity of clipping did not affect the dynamics of suckers differently among the ES ($P \leq 0.0615$), MS ($P \leq 0.6781$), and LS ($P \leq 0.6575$) times.

Effects of Intensity and Season of Clipping on Sucker Height Responses

Sucker height growth for the three sampling times was adjusted using B06 to account for initial heights. The three-way interaction (season \times intensity \times time) for sucker height differences had a value of $P \leq 0.0562$. Decreases as a result of clipping for the three seasons are shown for the three time periods (Figure 2). At the end of the first year (A06), all controls are higher than all the clipped plots; however, this is not the case for either B07 or A07. The difference in the season \times intensity interaction ($P \leq 0.0036$) was a result of the different clipping patterns across the three seasons.

For A06, clipping at 20 and 40% intensities produced similar responses; however, both of these responses were different from the control as well as when 60% was removed in MS and LS. At the end of 2006, in comparison with the control, there was an average reduction in sucker height of 49 cm for the 20 and 40% levels and a 68-cm reduction for the 60% level of removal.

At the beginning of the second year (B07), all the clipped plots

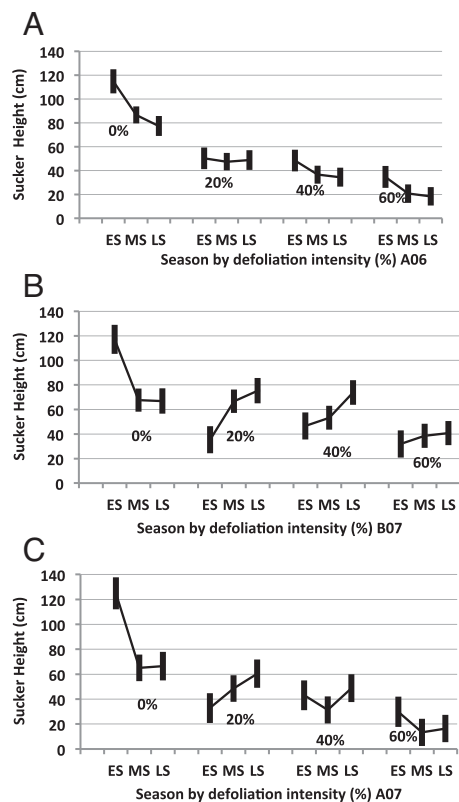


Figure 2. Effect of season (ES, MS, and LS) and intensity of clipping on sucker height at three times: at the end of the growing season in 2006 (A06); at the beginning of the growing season in 2007 (B07); and at the end of the growing season in 2007 (A07).

increased over the season (Figure 2). As we saw above, 20 and 40% treatments were similar but were different from the 60% treatment, and all of the treatments were different from the control during the ES.

At the end of the study (A07), there was no consistent pattern across seasons (Figure 2) for all the clipped plots; i.e., 20% increases, 40% goes down and then up; and 60% goes down and then levels out. Patterns for the control and 60% treatment are similar; however, there is a bigger drop in the control between ES and MS. For this time, clipped plots show differences from the control but are relatively stable overall. Many of the controls are significantly higher than the clipped plots. Seasons are not different within clipping rates and just a few differences exist among the nine intensity \times season means for A07.

Effects of the intensity \times time interaction showed that for the clipped plots B07 was different from the other two times, which were similar. For the control, A06 is higher than A07 but is not significant ($P \leq 0.825$). Therefore, at the end of the growing year, we found that sucker heights were similar across the three seasons. This difference between B07 and the other two time periods can be attributed, in part, to early growth of the suckers before clipping treatments were imposed in 2007. The control for all three times indicates a decrease in sucker heights for the three seasons, which may reflect the slowing of growth as the summer progresses or allocation to root development (Jones and Schier 1985).

Comparison between A06 and A07 (Figure 2) times indicate that, in general, sucker height decreased as the intensity of clipping increased. Averaged for the three seasons, clipping at 20, 40, and

60% intensities caused a 41-, 49-, and 67-cm reduction in height, respectively, compared with the control of 89 cm.

Discussion

Bailey et al. (1990) observed that when aspen suckers were defoliated late in the growing season, the subsequent regrowth did not have adequate time to harden, leaving shoot primordia susceptible to winter kill. Although our design did not allow us to assess exactly when the rather extensive mortality of suckers occurred, it is apparent that many suckers died sometime between late autumn (Oct. 30, 2006) and the following early summer (June 15, 2007), and it is reasonable to assume that the winter conditions exacerbated the negative effects of clipping. Other aspects of our results also appeared consistent with studies done in western Canada on timing of browsing on aspen. For example, Fitzgerald and Bailey (1984) observed that after 1 year of grazing, aspen suckers comprised 29% of the biomass of ES (June) grazed plots, compared with only 2.5% for LS (August) grazed plots. More recent work by Dockrill et al. (2004) showed no difference in stem density of aspen between plots grazed in ES (June) and the control (no grazing) after 2 years.

Bartos and Campbell (1998) documented that an aspen stand will probably fail to regenerate successfully and sustain itself if the density falls below 1,250 suckers/ha. In our study, even though considerable numbers of suckers were lost to MS and LS clipping treatments, sucker numbers were still high (>25,600 sucker/ha) for all seasons of clipping by the end of the second growing season. Whereas these numbers suggest that the stands would successfully regenerate, even at the most severe treatment level, the longer term impact of additional years of clipping remains unknown.

Previous studies, mainly on herbaceous species, have demonstrated that plants can compensate for and replace tissue lost to herbivores, depending on the timing and intensity of defoliation (e.g., Cook 1971, Gdara et al. 1991). In addition, research has also shown that aspen can similarly compensate for tissue removal below some critical level of natural (Julander 1937) or simulated (Campa et al. 1992) browsing. In our study, 1 year after clipping, ES-clipped sucker heights for all treatment intensities were affected by clipping compared with the control (Figure 2). In contrast, clipping in MS or LS at 40% intensities had no effect on sucker height compared with that for the 20% treatment. Although both Julander (1937) and Campa et al. (1992) reported compensation for aspen clipped at <75% compared with that for the controls, our most severe level restricted height growth for MS or LS treatments, indicating that compensation was incomplete for all clipped treatments. Clipping in the study of Campa et al. occurred in February, a period when nutrients are presumed to be minimal in twigs (Alban 1985). In contrast, summer clipping is associated with high nutrient loss (Bryant et al. 1983), suggesting a major constraint on tissue replacement for the suckers in our study.

Zahner and DeByle (1965) noted that continued rapid growth of suckers indicated that the large, well-developed parent roots serve significantly in water and nutrient absorption for some time. The year 2007 was fairly wet, and soil conditions for plant growth were probably not limiting. Perhaps the marked decrease in sucker growth for the controls in 2007 indicated allocation patterns to belowground root development (Jones and Schier 1985). It was reasonable to assume that the clipped suckers in our study would behave likewise, but rather they demonstrated somewhat more rapid growth in the second year. Other researchers have asserted that

browsed trees grow in such a way as to reestablish their former root/shoot ratio (e.g., Bergström and Danell 1987).

On average, by the end of our study in 2007, sucker heights for all clipping intensities were shorter (47 cm for 20% removal; 41 cm for 40% removal; and 20 cm for 60% removal) than the control (85 cm), a response consistent with the work of Bergström and Danell (1987) on birch plants. Moreover, by the end of the study, neither our control nor clipped suckers had attained the postulated 1.5-m height thought necessary for reducing sucker mortality due to ungulate browsing (Smith et al. 1972, Shepperd et al. 2006). Projecting from the growth responses we observed, by the end of the third to fifth growing season, suckers will have grown and passed this 1.5 m safe height (Shepperd et al. 2006). Thus, from an aspen management standpoint, this calls for several years of regulated browsing in pastures that have been treated to restore aspen. In some instances, it might require 8 to 10 years of normal growth before aspen suckers are no longer impacted by ungulates (Shepperd 2004).

Implications

Our findings suggest that browsing of suckers at intensities $\leq 40\%$ in early to midsummer for 1 or 2 years would not substantially affect aspen regeneration. This is supported by Jones et al. (2009) who studied livestock grazing (area had minimal to no wildlife use) and aspen regeneration in northern California. They recommended that a key management goal should be to minimize use of the terminal leader on an aspen sucker. However, managing aspen on landscapes is greatly hampered by a lack of effective control on browsing by both native and domestic animals. The 40% tolerable level in early to midsummer should be the total maximum browsing of suckers allowable by both native and domestic animals. Current USDA Forest Service guidelines in Region 5, which includes northern California (discussed above), calls for removal of livestock from treated pastures when use on suckers reaches 20% (Shepperd et al. 2006). This guideline is used so that by the time the request for removal of animals is accomplished, ideally the 40% tolerable level is not exceeded. Where cattle are the primary users, grazing should be delayed until midsummer after the treatments to allow sufficient time for preferred forage to grow. This will minimize impacts on the aspen regeneration. However, because of the unpredictable nature of weather conditions, it is critical that strict adherence to the grazing capacity of the pastures is observed closely for at least five growing seasons before the normal grazing schedule is resumed. Presumably, by the end of the fifth growing season suckers will have grown sufficiently to no longer be threatened by overbrowsing by ungulates. Finally, monitoring is critically important to document the progress of the management program. If browsing by livestock and/or wildlife is identified as a problem then managers need to reevaluate their approach and take measures needed to assure successful regeneration.

Endnote

1. Comments based on extensive field observations by the senior author.

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