TROPHIC CASCADES AND HISTORIC ASPEN RECRUITMENT IN THE GALLATIN ELK WINTER RANGE OF SOUTHWEST MONTANA

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✦ ABSTRACT

The extirpation of the gray wolf (*Canis lupus)* by 1930 in Yellowstone National Park (YNP) provided us with an opportunity to study historic aspen (*Populus tremuloides*) recruitment with and without a top carnivore predator present. Herbivory, climate trends, fire records, and current conifer invasion were also examined within the context of aspen recruitment. We obtained tree cores and diameter at breast height measurements to create an aspen age-diameter relationship which we used to approximate aspen origination dates. One elk (*Cervus elaphus*) exclosure, erected in 1945 within the same elk winter range, was compared to the rest of the winter range. Consistent recruitment inside the exclosure began in the 1940s and has continued into the present. Outside of the exclosure, aspen recruitment began decreasing in the 1930s and ceased in the 1950s. Within the scope of the study, we found little correlative evidence between aspen decline and climate trends, conifer invasion, or fire suppression. The results are suggestive of a trophic cascade between aspen recruitment, and historical elk browsing activities as affected by the absence or presence of wolf predation.

✦ INTRODUCTION

The decline of quaking aspen in the Greater Yellowstone Ecosystem (GYE) and YNP has been documented for decades (Warren 1926, Grimm 1939, Barmore 1965, Houston 1982) and continues to be of concern to scientists and natural resource managers (Romme *et al.* 1995, NPS 1997, Meagher and Houston 1998, NRC 2002). Concern over aspen recruitment is due to frequent observations of deteriorating aspen stand structures characterized by mostly mature trees. Due to its widespread decline in YNP, understanding the historical processes that have lead to a decline in aspen is needed to enhance future aspen survival.

Aspen largely reproduce vegetatively (Jones and DeByle 1985), producing genetically identical stems known as ramets. Aspen can also reproduce by seed, but seeding events in the YNP are rare due to the infrequent fire events that promote aspen seed regeneration (Romme *et al.* 1995) and the exacting conditions necessary for successful germination (Jones and DeByle 1985). Thus, because seeding is such a rare event and many aspen have not successfully reproduced vegetatively, the future of aspen persistence in the YNP is unknown.

Aspen decline has been variously attributed to fire suppression, natural stand dynamics, climate trends, and ungulate browsing (Houston 1973, Loope and Gruell 1973, Romme *et al.* 1995, Meagher and Houston 1998, Singer *et al.* 1998). It is also possible that large carnivore presence can influence both ungulate population size and behavior, and in doing so, affect aspen population dynamics (White *et al.* 1998, Ripple and Larsen 2000, Ripple *et al.* 2001, Mao 2003, Hebblewhite *et al.* 2005, Fortin *et al.*

2005, Binkley *et al.* 2006). In YNP, it is therefore possible that the extirpation of the gray wolf in the 1920s lead to changes in both elk browsing behavior and elk density, thus impacting aspen recruitment (Ripple and Larsen 2000). This ability of a carnivore to indirectly impact vegetation is known as a trophic cascade.

Ripple and Larsen (2000) conducted a comprehensive historical aspen study in the park's northern range, the location of the park's largest wintering elk herd. The study concluded that a decline in aspen recruitment inside the park coincided with wolf extirpation. Other studies within the park examining willow and cottonwood have also found associations between low recruitment, wolf extirpation, and elk browsing (Beschta 2003, Ripple and Beschta 2003, Beschta 2005). Though these studies have not found direct evidence that wolves influence elk, other studies have more directly found an association between wolf reintroduction and changes in elk densities and behavior in the park (Childress and Lung 2003, Laundré *et al.* 2001, Mao 2003, White and Garrott 2005).

To understand future aspen dynamics, a first and necessary step is to comprehend historical aspen dynamics. Therefore, the objective of the present study was to examine historical aspen recruitment within the framework of trophic cascades theory in the Gallatin elk winter range, an area to our knowledge where aspen had not previously been studied. The *a priori* hypothesis of this study was that the decline and extirpation of the gray wolf in the 1920s resulted in increased elk herbivory and a subsequent decline in aspen recruitment. Conifer invasion, fire suppression, and climate were also examined as alternative explanations for aspen decline. An elk exclosure, erected in 1945 and located within the same winter range, provided an opportunity to study aspen decline while disentangling the influence of ungulate herbivory and climate. Historical aspen conditions were studied by creating an aspen age-diameter relationship. Long-term climate records, conifer basal area, and historical documents were all examined to study other potential factors that may influence aspen decline.

STUDY AREA

The Gallatin is the main wintering area of the Gallatin elk herd (Lovaas 1970). Elevation ranges between 2400-3000m. Winter precipitation normally occurs as snow and annual precipitation ranges from 50 cm at low elevations, to 150 cm at high elevations (NRCS 1996). Heavy, deep snows in the fall and winter force the elk herd to move to lower elevations that include both the Daly Creek and Black Butte watersheds, a core winter range for the Gallatin elk herd (Lovaas 1970). In the current study, all aspen stands within the Daly Creek and the northern half of the Black Butte watersheds were examined (Figure 1).

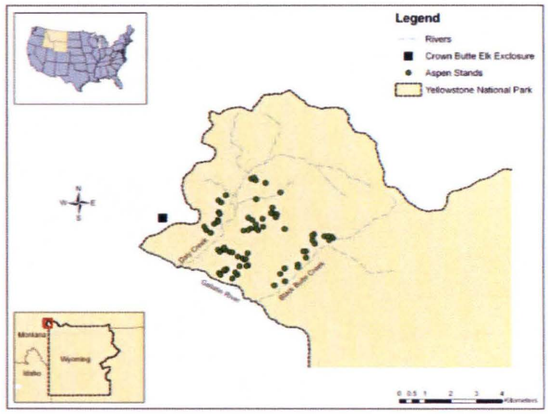

Figure 1. Study location. All data were collected within the Gallatin elk winter range southwestern Montana.

The coniferous vegetation of the Gallatin is comprised of pure stands of lodgepole pine (*Pinus contorta*) or mixed stands of lodgepole pine, Douglas-fir (*Pseudotsuga menziesii*), and Engelmann spruce (*Picea engelmanni*), with willow (*Salix* spp.) the most prevalent hardwood in the Gallatin valley bottom, and aspen the dominant hardwood at higher elevations. Both willow and aspen are minor components in comparison to the conifer species. On open hill slopes, sagebrush (*Artemisia* spp.), rabbitbrushes (*Chrysothamnus* spp.), Idaho fescue grass (*Festuca idahoensis*), wheatgrasses (*Agropyron* spp.), and bluegrasses (*Poa* spp.) are commonly found. Due to their higher nutritional content, preferred elk forage in the winter range include willow and aspen. Elk typically browse coniferous species in the winter range once they have depleted more nutritious forage.

✦ METHODS

During the summer of 2004, we enumerated and visited all aspen stands within the study area with 1:24000 aerial photography and field reconnaissance. We defined a stand as a minimum of three aspen stems with each stem less than 30m away from any other stem. When available, nine diameter at breast height (DBH) measurements representing a range of tree diameters were collected in each stand. Increment cores were similarly taken from the full range of diameters present in the stand.

To examine current aspen reproduction levels, we established a 2x20 m belt transect in every third aspen. Each transect ran from the stand edge toward the stand centroid and the direction of the belt transect was randomly selected with a random number table. Within each transect we collected aspen sprout information, defining aspen sprouts as immature aspen less than 200 cm in height. For all aspen sprouts within each transect, we recorded the total number, height, and previous year browsing (yes/no). We collected conifer basal area data using a basal area gauge (basal area factor = 5) to assess current conifer encroachment. We obtained fire information from historic documents and looked for the presence or absence of fire scars on Douglas-fir while in the field.

Within the same elk winter range, additional data on aspen was gathered within a 2ha fenced elk exclosure erected in 1945. We collected DBH measurements on all aspen stems greater than 1 cm in DBH and extracted increment cores from stems > 5 cm in DBH.

We used standard dendrochronological procedures (Stokes and Smiley 1968) to dry, mount, and sand each core. Rings on each core were counted with a dissecting microscope. Cross-dating was unsuccessful due to ring complacency. We created an aspen age-diameter relationship from 31 aspen cores and corresponding DBH's. The age-diameter equation was: $Age = 2004 - (2.50*DBH^{1.036} + 5)$. We placed the remaining aspen DBH's into the regression equation to approximate aspen age and year of origination.

We downloaded Palmer Drought Severity indices (PDSI) from the International Tree Ring Databank website to examine climate trends http://www.ncdc.noaa.gov/paleo/treering.html. Created by Cook *et al.* (2004), this long-term climate record is based on climatically sensitive tree-ring chronologies. Average PDSI values have a value of zero. Negative values are indicative of drought conditions (moderate (-2), severe (-3), extreme (-4)), whereas positive values are associated with above average precipitation. We averaged PDSI values from the two nearest records available.

✦ RESULTS

Aspen Stands

From the 71 aspen stands located in the winter range, we collected 462 DBH measurements and an additional 353 DBH measurements within the elk exclosure (Fig. 2). Outside of the exclosure, the decline in aspen began in the late 1930s and completely ceased in the 1950s (Fig. 3), illustrating a large gap in tree recruitment from the 1950s through 1999. In contrast, aspen numbers originating within the exclosure began to increase following fence construction and has continued inside the exclosure through 1999, (Fig. 3).

Figure 2 A.

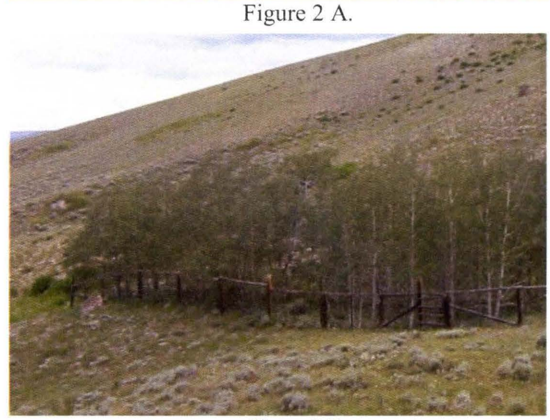

Figure 2 B.

Figure 2. A typical winter range stand (A), and aspen in the Crown Butte Exclosure (B). Note our ability to see through the typical winter range stand and lack of aspen recruitment. Note the lack of recruitment outside of the Crown Butte exclosure and the greater aspen stem density inside the exlcosure.

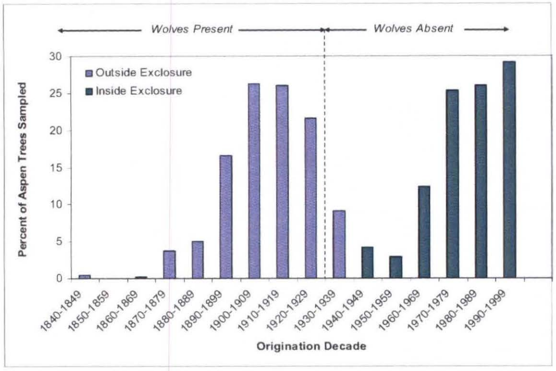

Figure 3. Winter range aspen origination within and ouside the elk exclosure. Outside of the exclosure, no aspen were found originating after the 1950's. Consistent recruitment was found inside the exclosure after its erection.

Conifer Encroachment

We found a total of 262 aspen sprouts within the 23 transects situated in aspen stands, with a mean sprout density of 2,837 per ha (Lower CL = 1571, Upper CL = 4102). Mean conifer basal area was 14.74 m^2/ha (Lower CL = 10.0, Upper CL = 19.5), and mean live aspen basal area was 21.3 m^2/ha (Lower CL = 14.8, Upper CL = 27.7) in the 23 stands (Fig. 4). We found little association between the proportion of conifer basal area in a stand and current sprout numbers ($F_{1,21}$ = 1.52, p-value = 0.23, R^2 = 0.07).

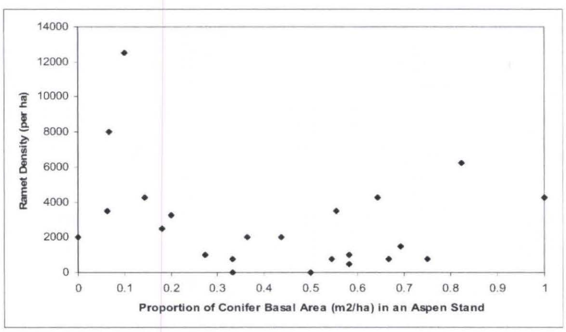

Figure 4. Conifer invasion and aspen recruitment in 23 aspen stands. No relationship was found between current conifer basal area and the density of aspen sprouts ($F_{1,\ 21}$ + 1.52, p-value +0.27, R^2=0.07).

Fire

In his history of the Gallatin elk herd, Lovaas (1970) did not document any fires in the Gallatin elk winter range. We did not observe fire scars on any Douglas-fir trees we opportunistically located in the study area. We therefore concluded there was a low likelihood of high severity fires in the study area since at least the late 1800s.

Climate

A scatter plot of raw annual PDSI values indicated periods of above and below average wetness before and after wolf extirpation (Fig. 5).

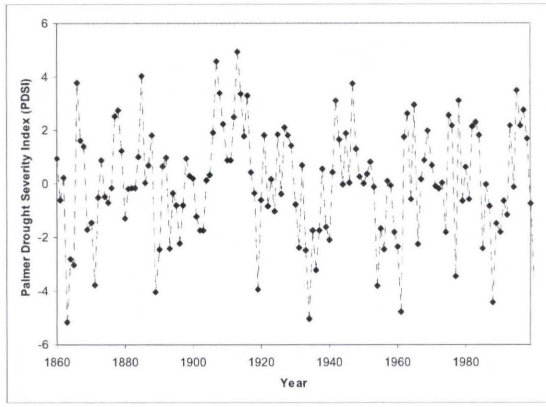

Figure 5. Average Palmer Drought Serveity Index (PDSI).

Herbivory

Of the 262 aspen sprouts measured in the winter range, 94.6% had been browsed within the last year and had a mean height of 26.3 cm (Lower CL = 24.3, Upper CL = 28.4). Within the exclosure, 91.3% of the aspen originated after the exclosure was erected in 1945 (Fig. 2). Outside of the exclosure, we found no aspen trees less than 17 cm in DBH (Fig. 3).

✦ DISCUSSION

Conifer Encroachment

As stands change from aspen to conifer dominated, aspen sprout numbers could decline because conifer trees limit available sunlight to the shade intolerant aspen sprouts (Jones and DeByle, 1985). It would therefore be predicted that aspen stands with greater conifer basal area should have fewer aspen sprouts than those aspen stands with lower conifer basal area. Yet with a mean sprout density of 2837 aspen per ha (Lower CL = 1571, Upper CL = 4102) aspen growth and mortality currently appear to be more problematic than the actual number of aspen sprouts. However, as conifer basal area increases, future aspen sprout numbers could eventually be negatively impact.

Fire Suppression

If fire suppression was the predominant process causing a decline in aspen numbers, few aspen should recruit without fire. However, aspen recruited into the 1950s in the winter range despite no fires reported in historic documents since at least the late 1800s. In addition, the high density of aspen in the elk exclosure illustrates fire is probably not a necessary requirement for aspen to recruit in this area.

Climate

Climate can influence forage production and the ability of plants to successfully regenerate. Researchers have therefore suggested the decline in aspen is attributable to a changing climate (Houston 1982, Singer *et al.* 1994, Romme *et al.* 1995, NPS 1997, Singer *et al.* 1998). Thus, the lack of aspen since the 1950s in the winter range would be consistent with a drying climate. However, with aspen continuously recruiting into mature stems inside the exclosure since its construction during periods of above and below average wetness (Fig. 5), the climate hypothesis becomes more inconsistent. Specifically, since the exclosure is in the same winter range as the other measured aspen stands, we would expect climate, and therefore its impact on aspen recruitment, to be similar within and outside of the exclosure. Other researchers have similarly found weak associations between climate and aspen, willow, and cottonwood growth in other parts of the Rocky Mountains (Wagner *et al.* 1995, Baker *et al.* 1997, White *et al.* 1998, Hessl and Graumlich 2002, Barmore 2003, Beschta 2003, 2005, Ripple and Larsen 2000, Ripple and Beschta 2004).

Herbivory

For herbivory to impact aspen numbers, recruitment should be minimal within the elk winter range and extensive within the elk exclosure. This assertion is supported by the data (Fig. 3). The only multi-aged aspen stands currently recruiting in the entire winter range study area lie inside the elk exclosure. Aspen have only successfully recruited in large numbers within the exclosure since the 1940s, corresponding to the installation of the exclosure fence in 1945 (Fig. 3). It is only inside the exclosure the distribution of aspen origination ages follows the expected J-shaped distribution of a healthy reproducing plant population. The unimodal distribution of aspen origination outside the exclosure is more indicative of a declining aspen population.

Trophic Cascades

In the current study, no aspen <17 cm in DBH were found outside of the elk exclosure. On Isle Royale, Michigan, McLaren and Peterson (1994) observed that as wolf numbers declined, moose numbers increased causing a suppression of balsam fir. Within the northern range of YNP, a decline in aspen recruitment since the 1930s was reported in the park's northern range (Ripple and Larsen 2000). As with aspen, Beschta (2003, 2005) documented a decline in cottonwood (*Populus* spp.) beginning in the 1920s within YNP and did not find a correlation between cottonwood decline and climate. Thus two browse species growing under different conditions (riparian cottonwood versus upland aspen) concurrently declined during the time of wolf extirpation.

According to general top-down theory, in a two-level trophic system, herbivores directly impact vegetation by reducing plant biomass. Therefore, as herbivore numbers increase, plant biomass should decrease, indicating an inverse relationship between trophic levels. In a three-level trophic system of carnivores, herbivores, and plants, trophic theory predicts predators will lower herbivore numbers and/or alter herbivore behavior, which in turn increases plant biomass. Examination of aspen within the Gallatin elk winter range of YNP yielded little evidence of successful aspen recruitment outside of the elk exclosure following wolf extirpation. Thus, we observed a negative plant response to predator removal outside the exclosure, and a positive plant response under limited herbivory (inside the exclosure), consistent with top-down theory. At this time, uncertainty remains as to whether elk densities and/or behavior will change enough to enable aspen in the Gallatin winter range to persist outside of the exclosure. If elk herbivory patterns do not change, the loss of aspen will change the availability of resources on the landscape potentially resulting in an alternative stable state.

✦ CONCLUSIONS

Due to the loss of many top terrestrial carnivores, terrestrial trophic cascades studies involving large vertebrate mammals are rare. Because most terrestrial vertebrate systems are therefore not fully intact, the information gleaned from a time when the system was more complete becomes valuable. The correlative evidence presented in this study are consistent with a positive top-down influence of wolf presence on aspen via additive predation pressure and a negative top-down influence on aspen when wolves are absent. Therefore, the presence of wolves may be integral to the long-term recruitment of woody browse species in YNP.

✦ ACKNOWLEDGEMENTS

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