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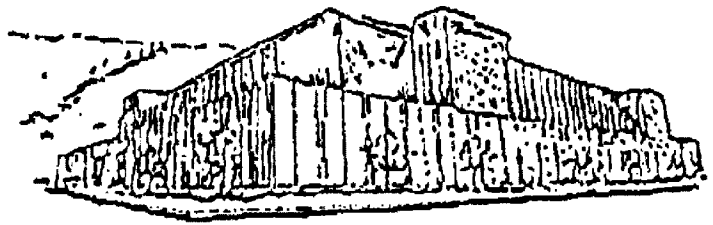
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**REPRODUCTIVE ECOLOGY AND RELATIVE UTILIZATION OF SALIX BEBBIANA
(BEBB WILLOW) IN SOUTHCENTRAL IDAHO AND SOUTHWESTERN MONTANA**

by Todd Hoitsma

B.S. Lewis and Clark College, 1984

presented in partial fulfillment of the requirements


for the degree of

Master of Science

The University of Montana

1997

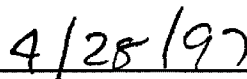
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Reproductive Ecology and Relative Utilization of *Salix bebbiana* (Bebb willow) In Southcentral Idaho and Southwestern Montana (66 pp.)

Director: Paul Hansen *PH*

Despite recent advances in the classification of riparian communities and our understanding of riparian ecology, the autecology and life history of many riparian species is relatively unknown. I collected descriptive data in seventy-four plots across the Intermountain West to describe the reproductive ecology, population structure and relative browse utilization of *Salix bebbiana* (Bebb willow). The most common mode of regeneration was stump-sprouting. Establishment of new individuals from underground suckering, and especially from seed was infrequent. These reproductive patterns are consistent with the clumped spatial distribution and the dominance of mature and decadent plants in nearly all *Salix bebbiana* willow stands. In addition, browse preference for *Salix bebbiana* or any other associated willow species was infrequent. In 60 percent of the plots, browsing by domestic and native ungulates was either too light or heavy on all willow species to observe interspecific discrimination in a single site visit. The few distinct instances of discrimination between willow species suggests that height and accessibility of browse may be some of the most important factors in interspecific willow utilization patterns. The relatively large diameter trunks and long life-span of mature *Salix bebbiana* plants appear to be a major factors in the species' ability to survive longer than most other willow species on sites exposed to long-term grazing and browsing pressure.

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INTRODUCTION

Salix bebbiana (Bebb willow) is a common but variable willow of Alaska, both coasts and the boreal zone of Canada, and the Rocky Mountains (Petrides 1992). In the Rocky Mountains it ranges from low to high elevations (1,000-2700 m; 3,300-9,000 ft) and is best represented in riparian communities of the Douglas-fir zone and mountain big sagebrush habitats (Brunsfield and Johnson 1985). Like other willow species, *Salix bebbiana* exhibits a shift in habitats across different elevations. At lower elevations it is generally restricted to moist riparian sites with heavy soils and at higher elevation sites it tends to occur in drier riparian settings (Brunsfield and Johnson 1985).

In the northern part of its range (Alaska and Canada), *Salix bebbiana* is one of the most common willows, occurring as scattered individuals in most forest and shrubland types (Viereck and Little 1972). It is the most common species in willow stands that follow forest fires in Alaskan "upland" sites, and also occurs in the vicinity of streams, swamps and lakes. In the interior of Alaska, *Salix bebbiana* is an important browse species for moose. During winter, heavy snows may bend branches down so that they are accessible to both moose and snowshoe hares (Viereck and Little 1972).

In the northern Rocky Mountains, *Salix bebbiana* displays several ecological characteristics distinct from adjacent willows. First, it seldom forms dominant, mono-specific stands but appears as scattered individuals even when habitat conditions appear to be ideal. Second, on a continuum of Rocky Mountain willow habitat conditions - from wet, boggy conditions to topographically drier margins of streambanks and riparian meadows - *Salix bebbiana* generally is observed on the drier end of the continuum (Dorn 1969). The third distinct ecological characteristic of *Salix bebbiana* is that unlike many other willow species, it does not regularly occupy early successional, alluvial streamside sites.

Although *Salix bebbiana* is a minor component of riparian areas of the Montana, Idaho and Utah (Hansen and others 1995, Youngblood and others 1985) it is a highly visible willow species. In dense, mixed willow communities it generally stands several feet taller than more common willow associates such as *Salix geyeriana* (Geyer willow), *Salix drummondiana* (Drummond willow) and *Salix boothii*. (Booth willow). In moist valley bottoms where long-term livestock grazing and agriculture activities have reduced willow coverage, the large single trunk, medium height, and

clumped distribution of *Salix bebbiana* makes it easy to recognize, even from a considerable distance.

In fact, the prominent regional riparian vegetation classification systems recognize *Salix bebbiana* vegetation types only in its more visible condition as a resilient component of heavily grazed sites. In Montana (Hansen and others 1995) and Utah (Youngblood and others 1985) describe similar community types for *Salix bebbiana*. Hansen and others (1995) report a *Salix bebbiana* community type. Both of these types are recognized as minor components of the riparian landscape and are often associated with heavy grazing (Hansen and others. 1995, Atchley 1988, Padgett and others 1989, Hansen and others 1988). Individual *Salix bebbiana* plants in these types tend to have a distinct browse line and characteristics of old plants such as a well developed canopy, relatively tall height, and large diameter trunks. Associated shrubs tend to be *Rosa woodsii* (wood's rose) and *Crataegus* spp. (Hawthorne)- those with mechanical protection from browsing. Herbaceous species are often dominated by introduced species such as *Poa pratensis* (Kentucky bluegrass), among others.

This study was in part motivated by an easily observable and repeated pattern related to the distribution and architecture of these *Salix bebbiana* stands on fenced rangelands exposed to long-term cattle grazing (frequently classified as *Salix bebbiana* Community Type). Often, adjacent roads and fence lines provide accidental "controls" to these disturbed sites by apparently excluding domestic livestock and most native ungulates, while having similar soils and moisture conditions. Vegetation in these sites is distinct, and frequently dominated by dense willow thickets comprised of multiple willow species. *Salix bebbiana* generally occupies a small portion of the willow coverage in these areas.

Based on this pattern, Hansen and others (1988) observed that on severely disturbed sites *Salix bebbiana* is often the last willow to leave a site - implying that *Salix bebbiana* is a remnant of the original pre-grazing willow community, and that other willows were eliminated. A potential mechanisms suggested for this pattern is that relative to other willow species, *Salix bebbiana* is more physiologically tolerant to browsing (Hansen and others 1995).

Knowledge of the regenerative strategies and the role of different modes of reproduction for *Salix bebbiana* and other willows is limited. Such information can be directly used in the management of riparian and wetland areas. For example, specifics on the regenerative capacity of *Salix bebbiana* or other willows is needed to help predict the response of the species to altered grazing strategies, complete rest from livestock grazing, or altered stream flows.

Additionally, the literature is limited and contradictory on the subject of relative browse use and palatability of willows in the Intermountain West. If certain willow species are utilized to a greater degree than others, this could, for example, have implications on the selection of species in riparian restoration projects. A better understanding of feeding preferences of dominant ungulates could also further our understanding of riparian successional patterns and how succession may be modified by ungulates.

OBJECTIVES

Twenty years ago only the most dedicated botanists were able to identify common willows down to the species level. Now, due to increased interest in the management, preservation and restoration of riparian zones, and the development of recent riparian publications, public awareness is increasing. Still, the level of understanding of the ecology and function is at a relatively early stage, especially in contrast to the adjacent forested and grassland upland environments. Therefore a basic goal of this study was to help expand the knowledge base of riparian ecology by focusing on the autecology of *Salix bebbiana* and associated willow species across a wide variety of site conditions and geographical areas within the Intermountain West. The specific objectives were as follows:

- 1) Describe the relative contribution of asexual and sexual regeneration in the establishment of *Salix bebbiana*;
- 2) Describe the age-class composition of *Salix bebbiana* stands;
- 3) Assess whether *Salix bebbiana* may be more or less palatable than associated willow species to both wild and domestic ungulates; and
- 4) Qualitatively describe germination and establishment requirements for *Salix bebbiana* seedlings.

STUDY AREA DESCRIPTION

Four general study areas were used in this study. Three of them were located in south-central/southwest Montana and one in southeast Idaho. These areas represent a large cross-section of physiographic and climatic diversity found in the Intermountain West. Riparian ecosystems sampled include dry valley bottoms and mountain canyons of the Idaho desert, low gradient meandering river habitat dominated by cottonwood forests, heavily wooded mountains dominated by small streams, and cool, high elevation basins. Administered by Federal agencies, the most common land use on these study areas is livestock grazing, as well as varying amounts of recreational use, logging, mining and other uses. Although *Salix bebbiana* occurs widely on private lands which often border Federal lands, few of these lands were sampled.

Table 1 provides summaries of mean annual precipitation, mean growing season precipitation, mean annual snowfall, mean quantity of days above 32° C (90° F) elevation of weather station, and mean length of growing season (Caprio and others 1994). Each data set was obtained at the weather station closest to each study area location. Due to the remote location of many of the sampling locations, and varying distance from weather stations, these summaries should be considered generalizations. Figure 1 displays locations of each study region.

Table 1. Climate summaries for each study area

SITE	Mean annual precip. (cm)	Mean precipitation April-July (cm)	Mean annual snowfall (cm)	Mean length growing season (days)	Mean no. July days > 32 ° C	Elevation (m)
Blackfoot R.	30-35	10-12.5	65-125	70-90	6	1,100
Headwaters	25-30	12.5-15	125-250	50-60	2	1,500
Idaho BLM	30-40	12.5-15	100-200	40-50	0	1,200
Red Rocks	50-60	18-20	350-400	30-50	0	2,000

Blackfoot River Study Area

Reaches of the upper Blackfoot River, just east of Ovando, Montana in Powell County were included in this study. This portion of the Blackfoot is a low gradient, meandering river dominated by cottonwood forests, dense willow thickets, and coniferous forests. Riparian zone width is considerable in most reaches and as wide as 400 m (1,300 ft) in places. Parent materials

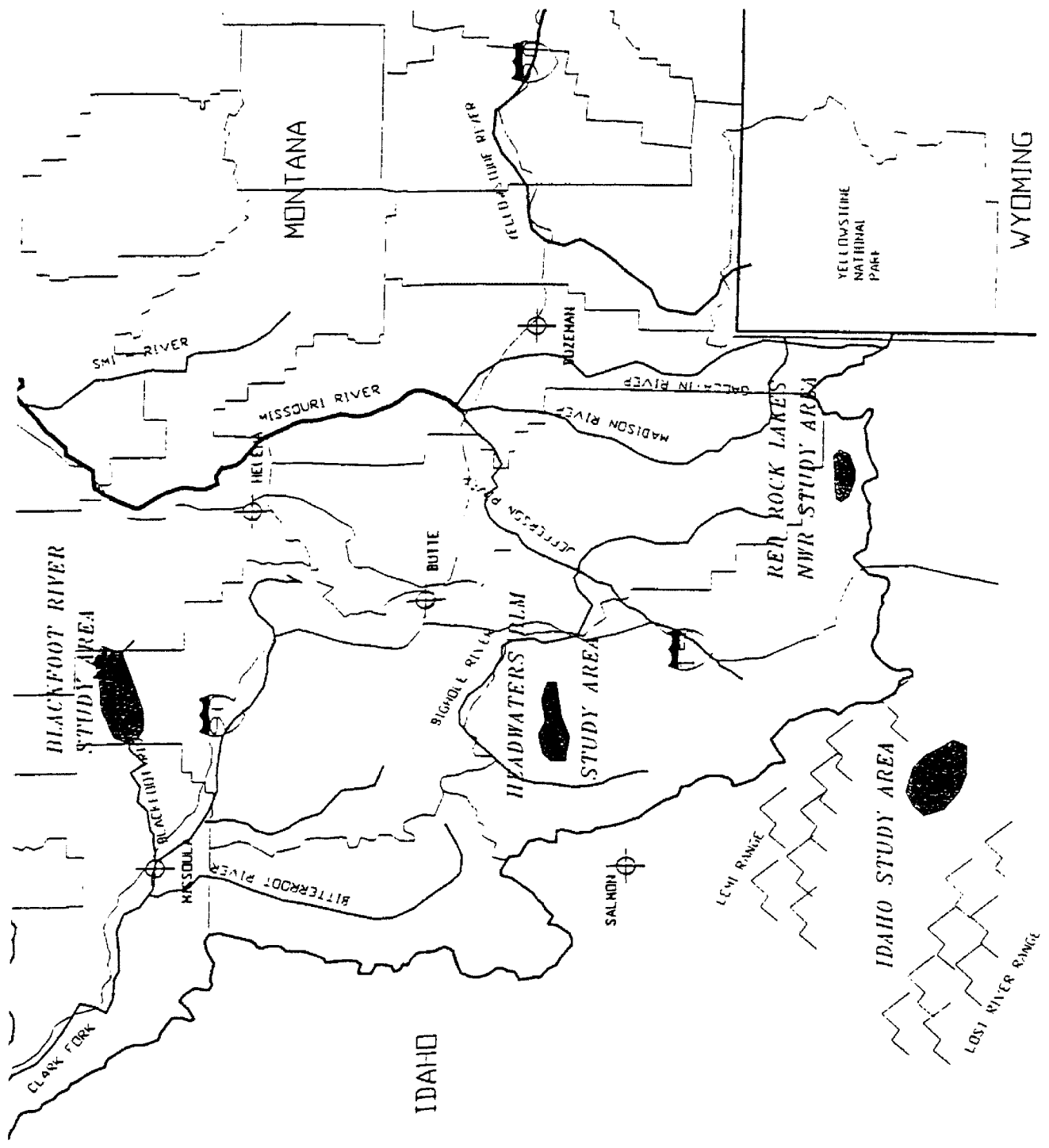


Figure 1. Map of study area

are primarily glacial deposits, and tertiary basin fill (Alt and Hyndman 1986). The climate in the Blackfoot River valley is influenced more by the maritime factors than by any other selected study area. During the winter and early spring, a prevalent westerly and southwesterly flow of maritime air brings frequent precipitation and relatively moderate temps to much of the Pacific Northwest. The western part of study area shows December-January peak precipitation characteristic of this region. The study areas lies in a region of transition between the maritime climate characteristic of northern and western Montana and the continental climate of the east of the Continental Divide.

Land ownership along the Blackfoot River is a mosaic of private, state and federal lands, but most of my sampling was restricted to land administered by the Bureau of Land Management (BLM). In contrast to the other study sites, large portions of BLM land along the Blackfoot River was inaccessible to cattle, so sampling included lands with distinctly different grazing histories. Moose, elk and deer were common along most of the Blackfoot River.

Headwaters Study Area

Located west of Dillon, Montana in the Beaverhead mountains, the Headwaters study site is administered by the Bureau of Land Management. This area is south of the Pioneer mountains and is characterized by sagebrush and grassland dominated valleys bordered by forested mountains. A large portion of the riparian areas are wide, low gradient, willow-dominated types, with narrow higher gradient riparian types common in the mountains. The elevation of this study area ranges from 1,500-2,000 m (5,000 to 7,000 ft). A wide variety of geological parent materials occur in this study area including Paleozoic limestone and sandstone, with inclusions of tertiary granite and granodiorite, and tertiary basin fill in valley bottoms (Alt 1986). Moose, elk, deer and antelope are common in most of this study area.

Southcentral Idaho Study Area

This study area is located in Bureau of Land Management managed lands in valleys and adjacent drainages in Lemhi County, Idaho. The topography of the study area includes sub-parallel faulted mountain ranges separated by broad valleys to the west and the Snake River basaltic plains to the east. The mountains, averaging over 3,200 m (10,500 ft) in elevation are the southern end of the Lost River and Lemhi Ranges. Valley base elevations are about 1,525 m (5,000 ft). Precambrian quartzite and Paleozoic limestone and dolomite are the major types of rock constituting the three ranges (Alt and Hyndman 1989).

The study area lies in a region influenced by the continental climate of the southeast part of the state. Winter high pressure of the Great Basin brings frequent clear skies, extreme temperatures and low precipitation. The dry summers are influenced by high pressure systems with frequent afternoon thunderstorms.

Vegetation in valley bottoms consists of species found in the arid sagebrush-grassland zone. A significant portion of the valley bottoms have been altered by agricultural development. Xeric tall shrub communities frequently occupy transitions between sagebrush-grass zone and the sparse forested zone, which consists of several conifer species.

Study sites were located in larger valley bottom streams and in the drainages of the adjacent mountains. Valley bottom sites occurred on low gradient cottonwood dominated creeks fed by mountain tributaries, and a unique set of streams recharged by large springs. These spring-fed creeks are hydraulically connected to the groundwater and consequently display relatively constant annual hydrographs (Raleigh 1992). The dynamics between stream flow, channel morphology and riparian vegetation are fundamentally distinct in spring-fed systems (Raleigh 1992). Associated with agricultural land of valley bottoms is extensive development of irrigation systems which include both stream flow diversions and groundwater pumping. Upper reaches of mountain streams are often bounded by steep canyons, but contain a variety of riparian habitat such as wet meadows, mesic streamside communities and willow thickets. Lower reaches extend across wide, flat alluvial deposits and are often ephemeral, with less habitat diversity. Being closer to agricultural land, the lower reaches frequently have been impacted from instream diversions. Additionally, groundwater pumping occurs widely on the valley floor, impacting groundwater levels and associated streamflow recharge.

Throughout the study area, the importance of riparian areas is magnified by the dry climate and associated lack of both large woody cover and water. In the hot summer months riparian corridors provide invaluable forage and habitat for both wild and domestic ungulates, even if surface water is seasonally absent.

Red Rocks National Wildlife Refuge Study Area

This study area is in the Red Rocks National Wildlife Refuge, located in the Centennial Valley, Beaverhead County, Montana. The Red Rock Lakes lie in a fault block basin at 2,100 m (6,600 ft) in elevation. The Centennial Mountains, which lie on the border between Idaho and Montana, rise abruptly to nearly 3,000 m (10,000 ft). Directly to the south and the foothills of the Gravelly Range lie to the north. Summers are short and cool, winters long and cold.

Administered by U.S. Fish and Wildlife Department, the refuge's primary land uses are preservation of trumpeter swan (*Olor buccinator*) habitat, cattle grazing and associated haying. Recreational use is heavy in certain locations. Red Rocks National Wildlife Area provides excellent habitat for moose, elk and mule deer. In the 1950's over-use of browse from an increasing moose population led to the use of hunting for population control, and by 1969 the moose population was reduced by approximately 50 percent (Dorn 1969).

Specific study sites were located on small streams, many of them ephemeral, which flow from the Centennial Mountains, and in large willow-dominated wet meadows adjacent to Red Rocks Lake.

STUDY DESIGN

Data was collected in the summer of 1994 while working for Montana Riparian and Wetland Association (MRWA), who was contracted to inventory Bureau of Land Management (BLM) riparian areas in Montana and Idaho. These riparian inventories estimated numerous attributes related to riparian vegetation and stream morphology using a "single ocular estimate approach", in which stream reaches up to a mile in length were surveyed on foot, and estimates for specific vegetation and stream channel attributes were recorded.

Since the distribution of *Salix bebbiana* is often discontinuous along stream channels, MRWA riparian inventories were a means to locate *Salix bebbiana* stands. Data from other MRWA field crews working in adjacent drainages was also useful in locating *Salix bebbiana* stands and comparing patterns I had observed. In some instances, MRWA field workers actually collected specific data used in my analysis. Data from Red Rocks National Wildlife Refuge was collected independently of MRWA riparian inventories.

In each drainage surveyed, *Salix bebbiana* plots were delineated whenever the species was located. Traditional plots of a fixed area, or transects of fixed length were not used in this study. Reconnaissance prior to data collection revealed that distribution of *Salix bebbiana* was extremely variable - occurring as single isolated individuals on some streams, evenly dispersed along a narrow stream fringe on other streams, or randomly clumped across wide floodplains in other locations. The use of a single, pre-determined plot size was useful in some situations but failed in others. For this reason, a variable-sized plot was used.

A variable-sized *Salix bebbiana* plot was defined in this study as an assemblage of *Salix bebbiana* plants, or clumps, occurring within 15 m (50 ft) of each other. The minimum plot size, in theory, was the area associated with the canopy coverage of a individual *Salix bebbiana* plant or clump. The maximum length and of a plot was 50 lineal meters (165 ft), measured along the length of a stream. The width of the plot was dictated by the width of the riparian zone. The status of *Salix bebbiana* relative to the dominant plant community (e.g. dominant, sub-dominant, minor component) was not a factor in establishing a plot.

This study was organized into separate sections on: 1) regeneration; 2) age/size class distribution; and 3) utilization. Literature reviews, methods, results, and discussions specific to each subject are described in the appropriate chapter, and a final synthesis relates major findings from each chapter.

CHAPTER 1 REGENERATION

Literature Review

Salicaceous species, including *Salix bebbiana*, establish both sexually and asexually. Sexual reproduction is constrained by a very small and short-lived seed that may lose viability 10-90 days after dispersal, except for seeds of several fall dispersing species of northern latitude willows that remain viable until the following spring (Densmore and Zasada 1983). Seed dispersal in willows generally coincides with the deposition of alluvium by peak streamflows (late May to early June in this study area), so successful seed establishment often occurs on "safe-sites" where sufficient soil moisture, light and temperature conditions exist. Additional factors affecting germination of seed include herbivory, fungal infection, snow, flood and wind (Atchley 1988).

Seed production in willows can be high. In Wyoming, Kay and Chadde (1992) found *Salix bebbiana* to produce an average of 350,000 seeds per square meter of canopy coverage. Densmore and Zasada (1983) reported that fettleaf willow (*Salix alexensis*) dispersed 380 viable seed per square meter. Under ideal greenhouse conditions, Atchley (1988) reported that *Salix bebbiana* seed germination was as high as 90-100 percent. However, in the field less than 1 percent of germinated *Salix bebbiana* seed lived to the end of a three-year study (Densmore and Zasada 1983)

Asexual, or vegetative reproduction is an important element of willow reproductive ecology. Willows, adapted to a heavily disturbed environment, maintain a vigorous underground root system which can produce adventitious shoots or suckers. These vegetative stems, initially attached to the parent plants, are known as ramets (from the Latin root meaning a branch, as in ramification) (Barbor and others 1987). Such connections become broken or non-functional as suckers develop their own roots (Burrows 1990, Sheppard 1993). As a result of successive generations of shoots arising from a continually expanding root system, willows, and especially *Populus tremuloides* (aspen) may occur in large clones of genetically identical species (Schier 1974, Sheppard 1993).

Pitkella and Ahumum (1985) observed variation among clonal species to the extent in which root connections remain functional in the movement of resources shared between ramets. It was speculated that connections between ramets should depend upon the strength and distance between the resource source and sink. Suckering, or ramet production may also help clonal species colonize less than ideal abiotic conditions, or enable a genotype to monopolize an occupied area (Sheppard 1993).

Another type of asexual reproduction, and analogous in many ways to ramets or suckers are stump-sprouts (ortets). The literature is extremely scarce on ortets of any Salicaceous species. In *Salix bebbiana*, initial investigations suggested that ramets may occur as far as 5-10 m from a parent plant, whereas ortets sprout from original plant of the clone at the base of the trunk (Kozlowski 1971).

Although little literature exists on sucker or ramet production in willows, Schier (1974, 1985), Kaufmann (1990) and Sheppard (1993) have studied suckering in *Populus tremuloides* (quaking aspen), another highly clonal member of the Salicaceae family. These researchers observed a scarcity of regeneration associated with decadent *Populus tremuloides* stands throughout the Intermountain Region. Since establishment from seed is very uncommon in this species (as with *Salix bebbiana*), it has been hypothesized that suckering is inhibited by auxins from apically dominant meristems. Pyle (1995), in comparing burned to unburned *Populus tremuloides* plots in eastern Oregon, observed stem density of seedlings (less than 50 cm or 1.6 ft tall) increased from 200 to 80,500 per hectare following controlled burns, but only slightly increased (1,300 to 1,400 stems per acre) on six unburned plots. Apparently removal of apical meristems, by disturbance such as fire, decreases inhibitor levels and encourage pre-formed root primordia to develop adventitious roots (Schier 1974).

The same mechanism of apical inhibition may occur with willows, as fire has been observed to promote heavy re-sprouting of stems and suckers. In eastern Oregon, Pyle (1995) observed that 35 of 46 (78 percent) mature willows (comprised of *Salix lemonii*, *S. boothii*, and *S. geyeriana*) resprouted and survived following an experimental control burn. Additionally, I have observed willow clumps in willow-dominated valley bottoms of southwest Montana respond vigorously to natural fires.

Other disturbances which remove apical meristems also trigger rapid re-growth of willows through suckering or simply regrowth of buds. For example, the process of coppicing is a technique widely used in the discipline of biotechnical and soil bioengineered slope stabilization. Coppicing is a method of pruning or timber harvesting that involves the production of new trees and shrubs from old stumps that is sometimes used to provide bioengineered slope stabilization (Gray and Sotir 1996). It is recognized that many tree and shrub species (including willows) have the ability to regenerate from dormant buds along the lowest parts of their trunks.

The greatest success with coppicing has been obtained if the stumps are cut after leaf drop in late fall or winter (Ecabert 1993). Some maple and locust species have reported more than six feet of

growth in the first season (Gray and Sotir 1996). However even summer harvesting can generate tremendous regrowth. Coppicing is practiced to deal with one of the few adverse effects of using woody plants in bioengineered slope stabilization - susceptibility to wind-throw. Pruning or harvesting of large old trunks and branches encourages stump sprouting and reduces the chances of windthrow, but retains the benefits provided by a trees' root system (Gray and Sotir, 1996).

A final type of asexual reproduction is dislodged stems or branches that get buried and then re-sprout. These are established by means similar to stem cuttings, which are currently used in the propagation of willows in riparian revegetation projects. Dormant adventitious root primordia are pre-formed nodes which lie embedded in willow stems of all ages (Carlson 1950). When stems become dislodged and fall in water or moist soil, they enlarge rapidly and differentiate into roots. Although most willow species readily form rooted cuttings, certain species root more easily than others (Burke, personal communication). In two separate studies of *Salix bebbiana*, a 40 percent (Atchley 1988) and 42 percent (Holloway and Zasada 1979) success of producing roots and shoots from stem cuttings was achieved. Unpublished data from Bitterroot Restoration and personal experience however, have achieved approximately 80 percent success in rooting *Salix bebbiana* cuttings.

Studies evaluating the relative contribution of sexual versus asexual reproduction in members of the Salicaceae family are few. In Alaska floodplains, Krasny and others (1988) studied the establishment of four Salicaceous species by propagating seeds in several soil types in both field and greenhouse conditions, and determined the relationship between root suckering and soil type. Sexual reproduction was of secondary importance in establishment of *Populus balsamifera* (balsam poplar), *Salix alexensis* (feltleaf willow), and *S. interior* (interior willow). Expanding root suckers (ramets), stem sprouting (ortets) and lodging of root and shoot fragments were most important in colonization and recolonization of river sites for the species.

In regard to sexual reproduction (genets), Atchley (1988) conducted greenhouse experiments on temperature requirements for seed, seedling response to different light intensities, and the effect of soil type on establishment and biomass production of seed and stem cuttings. Regarding temperature effects, she found that germination is rapid and successful at warm temperatures (15-25 C) and significantly poorer at cooler temperatures (5-10 C). Experiments on seedling response to light were only significant at light intensities representing heavy shade, where seedlings did not survive. At higher light intensities seedling response was significantly variable. Nonetheless, trends indicated that seedling height and weight increased with increasing light intensity. In these studies field soil type affected neither seed nor stem cutting establishment. It appears

however, that potential treatment effects from soil type were obscured by the fact that all soil types were kept saturated. That is, soil types were selected to represent different water holding capacities found in streambanks, but constant watering obscured actual differences in water holding capacity that would have been revealed as soil water was reduced.

In the Intermountain West, a considerable amount of published information on riparian ecology has resulted from the development of classification systems (Youngblood and others 1985, and Hansen and others. 1995) and technical willow guides (Brunsfield and Johnson 1985, Heinz 1994). These sources provide general patterns of species regeneration, but offer little in the way of species specific information on willow regeneration.

Methods

Data Collection

A total of 70 plots were sampled for regeneration data, with over half (38) in Idaho, followed by 14 plots at Red Rocks National Wildlife Refuge, 11 plots at Blackfoot and 7 plots at Headwater. This portion of the study investigated the relative contribution of: 1) asexual and sexual reproduction to *Salix bebbiana* populations; and 2) the occurrence of seedlings (genets or ramets) in specific biotic and abiotic site conditions.

To investigate reproductive ecology, the proportional coverage of all *Salix bebbiana* regeneration within a plot was estimated for each "type" of regeneration (genets, ortets, and ramets). Coverage values were then placed in one of the following 12 cover classes:

Trace (0.5-1.0%)	2 (15.5-25%)	5 (45.5-55%)	8 (75.5-85%)
Present (1.5-5%)	3 (25.5-35%)	6 (55.5-65%)	9 (85.5-95%)
1 (5.5-15%)	4 (35.5-45%)	7 (65.5-75%)	Full (> 95%)

Regeneration was considered any plant with a stem in the seedling or sapling size-class. A seedling is a stem less than 30 cm (11.8 in) tall and less than 1.5 cm (0.6 in) in basal diameter and a sapling is greater than 1 cm (0.4 in) basal diameter and less than 2 m (6.6 ft tall).

Seedling/saplings of sexual origin were called genets, and those established asexually were considered either stump sprouts (ortets) or stump sprouts (ramets).

Distinguishing between genets, ortets, and ramets was rather imprecise in the field, and required certain assumptions, based on initial field reconnaissance, excavations of several ramets, and a review of literature. As such, distance from potential parent plants was a primary break between the three "types" of regeneration. For example, ortets (stump sprouts) were defined as regeneration occurring and within 15 cm (5.9 in) from the main stem (trunk) of a parent plant. Ramets (suckers) occurred a distance of at least 15 cm (5.9 in) from, and within 5 m (16.4 ft) the main stem. Any seedling regeneration found more than 5 m (16.4 ft) from a seed-producing plant and not obviously sprouting from an underground root system, or not re-sprouting from a detached branch or buried log was considered a genet (sexual origin). Because it is possible for genets to occur within 5 m (16.4 ft) of a potential parent plant, these assumptions may underestimate the quantity of genets.

A series of qualitative observations were made in each plot regarding the amount of regeneration occurring under specific biotic and abiotic conditions expected to influence *Salix bebbiana* regeneration. A primary biotic factor affecting successful regeneration of *Salix bebbiana* was considered to be herbivory. Therefore, in each *Salix bebbiana* plot with regeneration, it was assessed whether seedlings were restricted to locations where ungulate access was limited, and if so, the source of the restricted access was identified. Possible sources include roads, fences, and downed logs, deep water, among others.

Two major factor abiotic factors promoting regeneration were presumed to be the existence of suitable seed germination sites and moist sites. Areas of "recently deposited alluvium" are areas of bare soil deposited by peak flows, and were considered "safe sites" for seed reproduction. Indicators of gradients of soil moisture expected to promote *Salix bebbiana* regeneration include the bankfull channel area, floodprone area, and wet meadow/seep areas. Bankfull and floodprone areas are qualitative indicators of relative inundation frequency and floodplain moisture regimes. Bankfull discharge occurs several days in a year and is related to the 2 year recurrence interval discharge (Leopold and others 1993, Rosgen 1993) and is that portion of the channel and streambank surface inundated by bankfull discharge. The floodprone area is the width occurring at an elevation of twice the maximum bankfull depth (Rosgen 1993). Wet meadow/seeps are sites where soil is saturated for at least part of the growing season and obligate or facultative wetland plant species dominate as a result of topographic moisture or minor groundwater outflow. In attempt to positively identify genets, the presence, if any, of regeneration occurring at least 10 m (32.8 ft) from the nearest parent plant was also recorded. Written descriptions of any other notable reproductive microsites were also noted.

Data Analysis

Histograms of the distribution of regeneration type data at each site indicated a non-normal distribution and strongly bi-modal tendency. Attempts to normalize data through transformations were unsuccessful. Therefore the distribution of coverage values for each regeneration type was analyzed with side-by-side boxplots. Boxplots for each regeneration type were then pooled across all study regions. To compare significance of median values, 95 percent confidence intervals were used, and are included in figures with boxplots.

No statistical analysis on the data regarding biotic and abiotic conditions affecting regeneration was conducted because of limitations of the study design. For example, the amount or presence/absence of specific abiotic or biotic conditions, such as recently deposited alluvium, in each plot was not noted. The amount of regeneration related a certain biotic or abiotic condition may correspond to the absence of those sites for regeneration to occur, rather than the ability of the species to utilize such "safe sites".

Results

As shown in the series of boxplots (Figures 2-4), in all study areas ortets (stump sprouts) were substantially more common than either ramets or genets. The median coverage value for ortets was between 80 and 100 percent coverage in all study regions. Since the confidence intervals overlap at each site such differences are of little consequence. The confidence interval at Headwaters is relatively wide indicating that the true population median may fall somewhere between 30 percent and full coverage. In contrast, Idaho and Red Rock sites show a small deviation from full ortet coverage.

Ramet coverage was consistently low across all study regions and substantially lower than ortet coverage (Figure 3). The median coverage at Blackfoot, Headwater and Red Rocks was "absent" (0 percent), and "trace" (approximately 1 percent) in Idaho. The confidence intervals at Idaho, Headwaters and Red Rocks were narrow, but considerably wider at Blackfoot. At Idaho, Headwaters, and Blackfoot sites a few observations of nearly "full" (nearly 100 percent) coverage occurred.

The median genet (seed) coverage in each study region was "0" (absent), and no genets were observed in the Blackfoot and Red Rock plots (Figure 4). In Idaho, small amounts ("trace" or "present") of genets are reflected on the boxplots as outliers. At Headwaters, the upper ends of the boxplots are pulled to 50 percent coverage by a single observation where genets dominated and a second plot where genet coverage was 60 percent. With the exception of the latter two

95% confidence intervals are shaded, open circles represent outliers, and asterisks represent extreme outliers

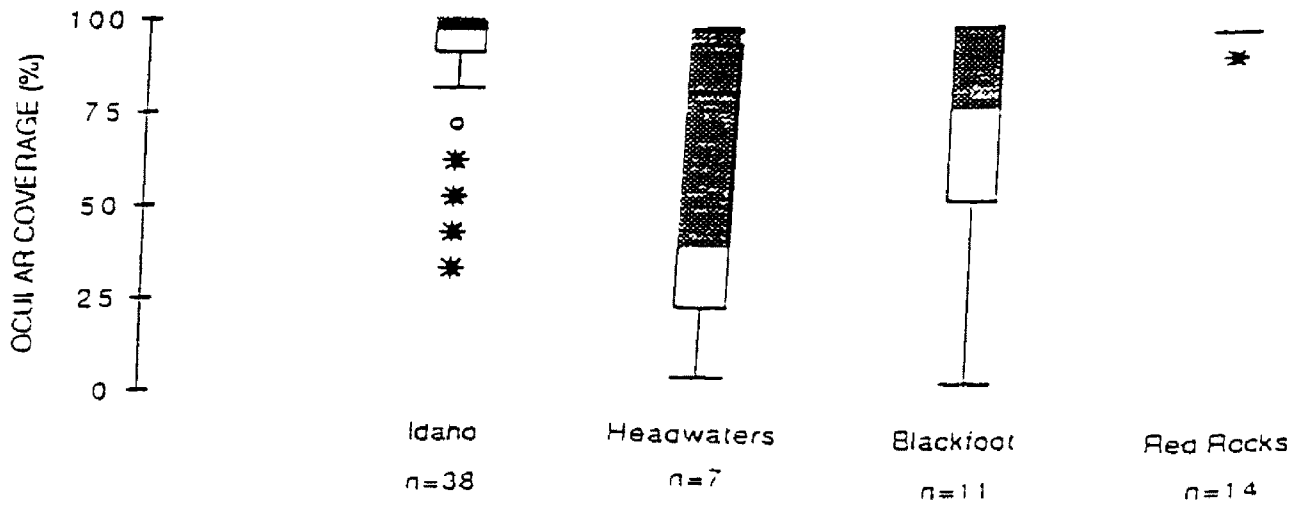


Figure 2. Boxplots of ortets (reproduction stump sprouts) by study region

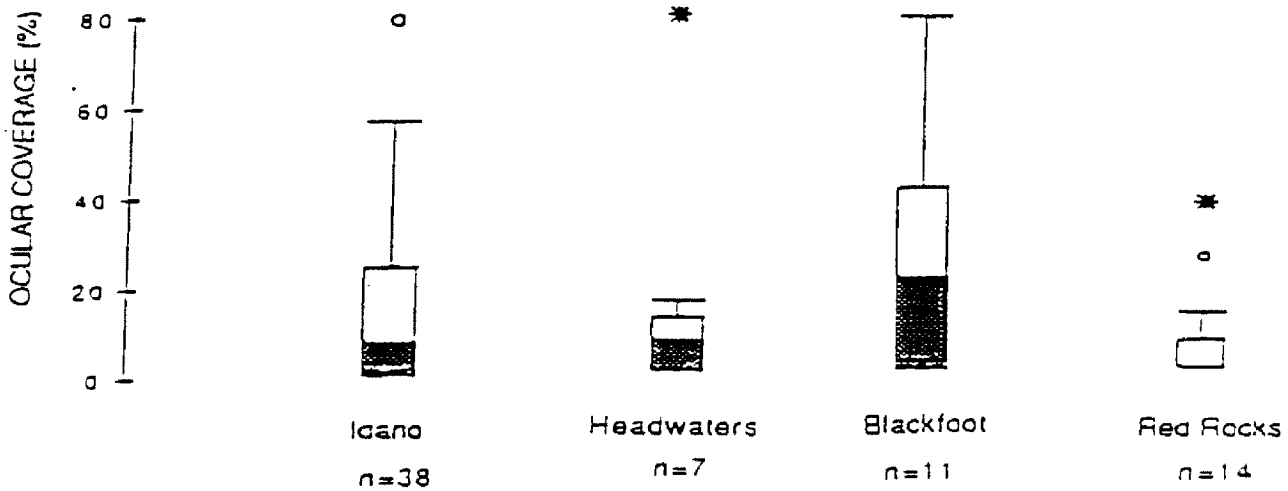


Figure 3. Boxplots of ramets (rhizomonous reproduction) by study region.

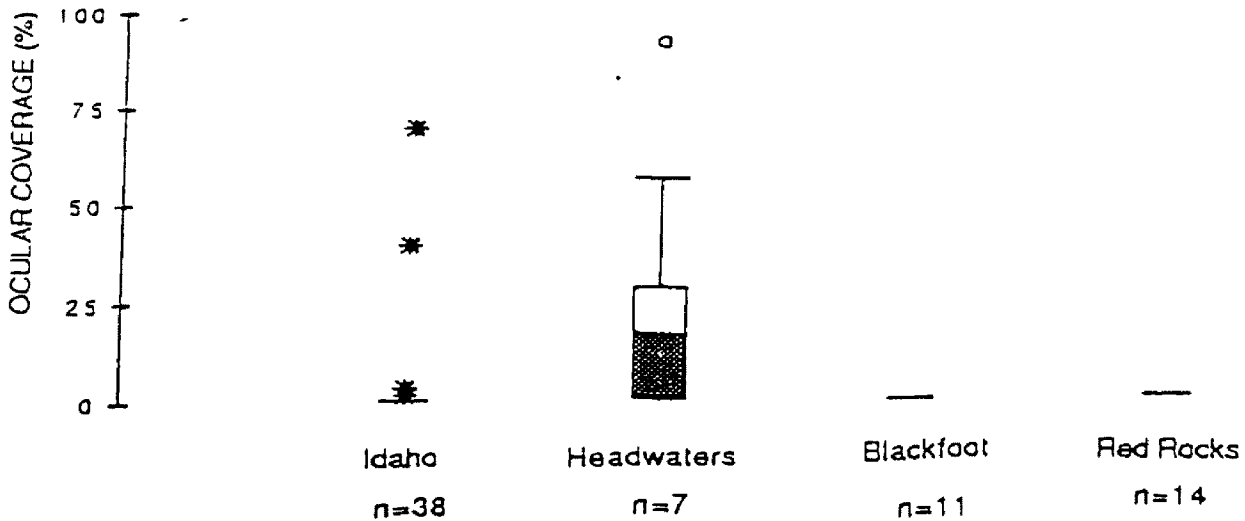


Figure 4. Boxplots of genets (seed-produced reproduction) by study region.

Headwater observations and two Idaho observations, genets were either absent or displayed trace amounts of coverage in all plots.

When data from each region was pooled by regeneration type (Figure 5), the dominance of ortets and the nearly complete absence of sexual reproduction (genets) observed in each region is more profound. The coverage of ortets is statistically greater than both ramets and genets. The median ortet coverage was “full” (nearly 100 percent), compared to “trace” (approximately 1 percent) for ramets, and “absent” (0 percent) for genets. The lack of genets is so extreme that an outlier sits at approximately 1 percent coverage. Both ortets and ramets exhibit outliers, and a range that are in fact, nearly complete opposites. The narrow confidence intervals further suggest the strength of the differences between regeneration types.

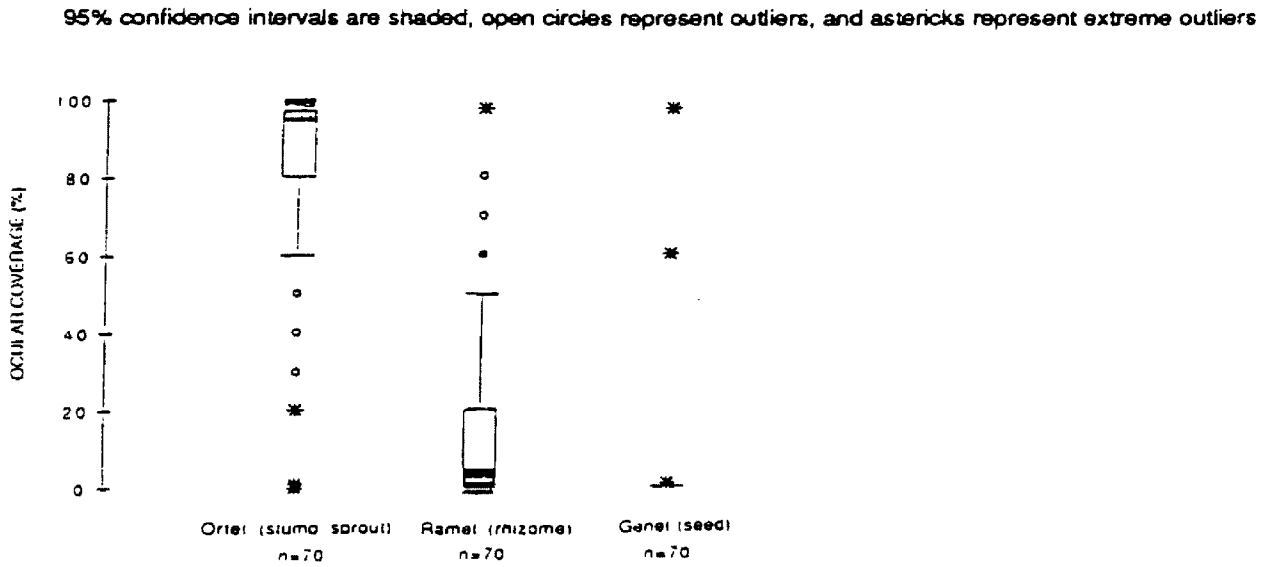


Figure 5. Boxplots of regeneration types for all plots

Conditions associated with regeneration are presented in Table 2. Of the total number of sites where regeneration occurred (n = 63), regeneration most frequently occurred in the floodprone area (present in 67 percent of the plots) followed by bankfull area (46 percent), and seep areas (21 percent). Twenty-four percent occurred greater than 10 m (32.8 ft) from the nearest potential parent plant. At two study sites, all *Salix bebbiana* regeneration was observed on recently deposited alluvium, and these were presumed to be genets because of even-aged nature of the stands. This data needs to be interpreted cautiously since no data was collected on the frequency of plots in which floodprone, bankfull, or seep areas occurred or the areal extent of these types when observed. For example, although regeneration was associated with alluvium in 24 percent

of the plots, no data was collected on the proportion of the plots in which recently deposited alluvium was observed.

Table 2. Abiotic conditions associated with regeneration

Abiotic Condition	Observed Regeneration	
	# plots	% plots
Recently deposited alluvium	2	3
Within 10 m of nearest potential parent plant	13	21
Within bankfull channel width	29	46
Within floodprone channel width	42	67
Within seep area	13	21

Discussion

Knowledge of the reproductive ecology of willow species is essential to expand our understanding of the dynamics of riparian zones and predict the response of these areas to changes in management. Few studies have previously documented the quantities of different types of regeneration for any type of willows, and no such work previously existed on *Salix bebbiana*. These data therefore provide useful information on the reproductive strategies of this species, and helps to explain the distribution of *Salix bebbiana* across the landscape.

The major finding of this portion of my study is that *Salix bebbiana* is a highly clonal species, reproducing through ortets (stump sprouts) significantly more than from either ramets (rhizomes) or genets (seed). Thus asexual reproduction is the primary mode of *Salix bebbiana* regeneration, and sexual reproduction is extremely uncommon. This overall strategy is consistent with the distribution the species over the landscape because *Salix bebbiana* occurs on the landscape in a clumped pattern.

However, ortets, unlike ramets and genets, only extend the longevity of existing *Salix bebbiana* plants and do not add new individuals to a population or allow a species to colonize new locations. Thus from a demographic perspective, ortets may be less important than ramets and genets. With this in mind, the relative importance of each regeneration type may not be consistent with the relative coverage or actual count of number of stems of each type.

Determining whether *Salix bebbiana* juvenile plants originated from seed or suckers can be difficult. In this study, separating ramets from genets was relatively easy in the seedling age class, since seedlings were uncommon. When found, tugging each seedling distinguished between genets (poorly rooted) and ramets (well rooted). In the sapling age class it was impossible in some cases to accurately differentiate ramets from genets because the older plants were more deeply rooted. So, despite some success in distinguishing ramets from genets in the field, conclusions drawn from data regarding the relative contribution of sexual reproduction and asexual production (suckering), especially in the sapling age class, are limited.

However, since ramets and genets were so uncommon in this study it is of little importance whether recruits were established from ramets or from genets. More important is the total amount recruitment of new individuals. Since both ramets and genets are by definition, individual plants spatially separate from parent plants (as opposed to ortets), combining ramet and genet coverage values can measure recruitment of *Salix bebbiana* individuals. Recruitment of new individual plants allows a stand to colonize new areas. Ramets and genets, even if combined, were present in only half the plots where regeneration was observed (although the actual coverage in most of these plots was relatively small).

This study provided one surprise regarding the relationship between regeneration and biotic/abiotic conditions. Only two observations were made of *Salix bebbiana* regenerating on recently deposited alluvium despite an abundance of unvegetated deposits which appeared to be prime sites for genet establishment. Most other associated willow species demonstrated a greater ability to colonize such sites.

As expected, regeneration occurred most commonly along moist sites streambanks and wet meadow/seep areas, but was also found outside the floodprone area and relatively dry riparian sites in a few instances. In addition throughout the three study areas, my results are consistent with Atchley and Marlow (1989) who observed that protection from herbivory does necessarily ensure increased genet or ramet production.

Limited genet production may be attributable to many factors, including light, herbivory, lack of seed, absence of suitable seedbeds. Apparently, the requirements for seed establishment of *Salix bebbiana* are rather strict and establishment of genets may be particularly stochastic.

In summary, the proportion of each type of regeneration is consistent with the present distribution and ecological status of *Salix bebbiana*. Ortets play a critical role in the life history of *Salix bebbiana*

by extending the life span of an established plant by many decades. Less frequent are ramets, which appear to be the most regular mode of establishment of new individuals. Their attachment to parent plants allows them to root in sites too dry for genet establishment, and perhaps to be more tolerant of disturbance such as herbivory. Genets, which also establish new recruits, were less common than ramets, and arise infrequently. Although uncommon in the seedling/sapling age class, genets may be important in the distribution of the species over its wide range. The recruitment of new genets and ramets of individual plants is less important on an annual basis for this long-lived species than for most other associated willow species, which are shorter lived.

CHAPTER 2 AGE/SIZE CLASS DETERMINATION

Literature Review

Assessment of the age class structure (or population structure) of plant populations is used as a predictive tool in ecological studies to interpret trends in population replacement with time. It is also used to reconstruct the periodicity of reproductive success of a population, and to reconstruct population response to disturbance such as grazing or fire (Barbor and others 1986). For example, Crisp and Lange (1976) predicted the elimination of an Australian acacia species in much of its current range under continued grazing practices, based in part on a determination of the age class structure of that species. Population structure has also been used in numerous other biomes such as montane forests of California (Runnel 1971), subalpine forests of Appalachians (Oosting and Billings 1953), Canadian boreal forests (Jones 1945) and the Mojave desert (Chew and Chew 1965).

The traditional approach to determining population structure of a community is to quantify the numbers of individuals within a certain age class and then plot the number of individuals per area versus the specific age class breaks (Barbor and others 1987). With some life-forms, such as coniferous trees, age correlates well with diameter, and is readily determined from annual growth rings. In these cases population structure is obtained with relative ease. However, the great morphological complexity and plasticity of other life-forms, such as woody shrubs, make them among the most difficult life-forms on which to conduct population studies (Harper 1977).

Clonal woody shrubs are difficult subjects for study for several reasons. First, clonal species have two quite different age structures - that of above-ground shoots and that of the underground system (Harper 1977). Secondly, the multi-stemmed habit of some species may make it extremely difficult to distinguish between an individual plant and a clump, and separate modes of regeneration into components (Harper 1977). Additionally, tree-like species such as *Salix bebbiana* and *S. lasiandra* (Pacific willow) often develop cambial die-back and may be impossible to successfully age (Kovalchik 1992). Lastly while clonal woody species life-stage may be a better indicator of reproductive status than age because size is not necessarily correlated with age, especially in heavily browsed sites (Barbor and others 1986).

Despite these difficulties, Busse (1989) compared the population structure of several Salicaceous species in grazed and ungrazed sites in Oregon. Willow clumps were aged by measuring the diameter of the largest stem in each clump and placing these into one of three size classes, with the assumption that an increase in diameter reflected an increase in age. Busse concluded that

regeneration was severely inhibited in sites grazed by cattle based on an absence of small and intermediate diameter classes. In protected (ungrazed) sites a healthy presence of smaller diameter willow stems indicated a well balanced population structure.

Numerous other researchers have observed that younger size classes of Salicaceous species are poorly represented under heavy livestock grazing (Youngblood and others 1985, Atchley 1988, Atchley and Marlow 1989, Padgett and others 1989, Kovalchik and Elmore 1992, Hansen and others 1995) or wildlife browsing (Dorn 1970, Kay and Chadde 1992). Other studies have shown a shift toward aging populations of riparian communities resulting from inhibition of seedling establishment where stream diversions have occurred (Johnson and others 1976, Smith and others 1991).

Another approach to determining the age or stage structure of woody plants is to describe various stages of the life history and quantify the numbers present at each stage. Rabotnov (1969) recognized eight important stages in an individual plant or population: (1) viable seed, (2) seedling, (3) juvenile, (4) immature, vegetative (5) mature vegetative, (6) initial reproductive, (7) maximum vigor (reproductive and vegetative) and (8) decadent. A plant population that shows only the first four stages is invading a community and part of a seral community. A stable population, successfully replacing itself, might show all eight stages. The presence of only the last four stages suggests a population in decline. In theory a mature plant need only produce a single surviving seedling in its lifetime to maintain a population (Barbor and others 1986).

Methods

Data Collection

For this portion of the study, a total of 70 plots were sampled, with half (35) in Idaho, followed by 16 at Red Rocks National Wildlife Refuge, 9 at Headwaters and 10 at Blackfoot (note that the distribution of plots between each study site varies slightly from data in Chapter 1 due to some missing data) To examine the population structure the following data was collected in each Bebb willow plot:

- 1) the proportion (percent canopy cover) of three primary life stages of *Salix bebbiana*;
- 2) diameter of largest *Salix bebbiana* in plot;
- 3) percent canopy cover of dead and dying branches with *Salix bebbiana* plants ; and
- 4) presence/absence of individual *Salix bebbiana* plants with no living stems, shoots or branches.

To determine the age class structure of *Salix bebbiana* plots, the total ocular coverage of *Salix bebbiana* in each plot was divided into three classes or life stages: 1) young; 2) mature"; and 3) old. The "young" class includes seedlings and saplings. A seedling was a single stem less than 30 cm (11.8 in) in height and less than 1 cm (0.4 in) in basal diameter. A sapling was less than 2 m (6.6 ft) tall, and greater than 1 cm in basal diameter. A "mature" plant was greater than 2 m tall, but less than 20 cm (7.8 in) in diameter measured 30 cm (11.8 in) from the ground. An "old" plant was greater than 20 cm (7.8 in) in basal diameter and approximately 30 cm (11.8 in) above the ground. No distinction between rhizomes (ramet), stump sprouts (ortets) or seed (genet) was made. Coverage values were then recorded in one of the following 12 categories:

Trace (0.5-1.0%)	2 (15.5-25%)	5 (45.5-55%)	8 (75.5-85%)
Present (1.5-5%)	3 (25.5-35%)	6 (55.5-65%)	9 (85.5-95%)
1 (5.5-15%)	4 (35.5-45%)	7 (65.5-75%)	Full (> 95%)

The presence or absence of *Salix bebbiana* seedling recruitment within the specified plot was noted. As discussed previously, a seedling was considered any individual willow stem less than 30 cm (11.8 in) in height. This excluded any stems sprouting from the within 15 cm (6 in) of a stump or possible parent plant. I did not attempt to differentiate between seedling produced via genets or ramets but did exclude ortets.

The diameter of the largest single stem or trunk of *Salix bebbiana* within a plot was recorded 30 cm (11.8 in) above-ground. During initial reconnaissance the approximate age of a sample of 20, 1 cm (0.4 in) stems ranged between 3-6 years, 2 cm (0.8 in) stems ranged from 4-11 years, and several cores 20 cm (7.8 in) in diameter were between 40 and 55 years old. Data was recorded to the nearest centimeter.

The percent ocular coverage (using the 12 category scale, above) of dead and dying branches intended to determine the proportion of dead and unhealthy foliage relative to the amount living foliage in each plot.

Data Analysis

The distribution at each site was not normally distributed and strongly bi-modal, and attempts to normalize data through transformations were unsuccessful. Therefore the distribution of coverage values for each age class was analyzed with side by side boxplots. Boxplots for each age class were then pooled across all study regions. To compare significance of median values, 95 percent confidence intervals were used, and are included in figures with boxplots. For diameter

data, mean and standard deviation was determined for each study region and pooled for all regions. The distribution of the percent decadence in each region was displayed with side-by-side boxplots, and also pooled for all regions. These boxplots also display 95 percent confidence intervals to help assess statistical significance between median coverage values of different regions.

Results

The general pattern that emerged from my data was very low coverage of the seedling/sapling age classes, a high presence of the mature age class, and moderate coverage of the old age classes (Figures 6-8). With minor exceptions, this trend held across all study regions.

The seedling/sapling age class for all regions had median values less than “trace” amounts (1 percent) (Figure 6). Headwaters and Red Rocks showed exceptionally low coverage values, with only outliers extending beyond 1 percent coverage. The few instances where seedling/saplings were found in greater than 50 percent canopy coverage occurred at Idaho and Blackfoot sites.

The median canopy coverage value for the mature age classes ranged from a low of 45 at Red Rocks to a high of 69 at Headwaters (Figure 7). These differences were not statistically significant as displayed by the overlap of the 95 percent confidence intervals (shaded gray). The distribution of coverage values at each study region was wide, and outliers were absent. Only at Red Rocks was the median canopy coverage of the mature class lower than the old class.

For the old age class (Figure 8), the median coverage value showed greater range than the mature class. This range extended from a low of 1 percent median coverage at the Blackfoot site to a high of 70 percent at Red Rocks. The only statistically significant difference in median coverage was between Blackfoot and Red Rocks.

By site, Idaho and Headwaters were similar in trend. At these two sites seedling/saplings were nearly absent, and the mature class had median values nearly twice as high as the older age class. The only statistically significant difference was between the youngest age class and the two older ones. The Blackfoot site seedlings/saplings were slightly more abundant than other locations, and there is not significant difference between the old age class and seedling/saplings. At Red Rocks, seedling saplings were nearly absent and significantly less than both the moderate coverage values of the mature class and the more common old class.

95% confidence intervals are shaded, open circles represent outliers, and asterisks represent extreme outliers

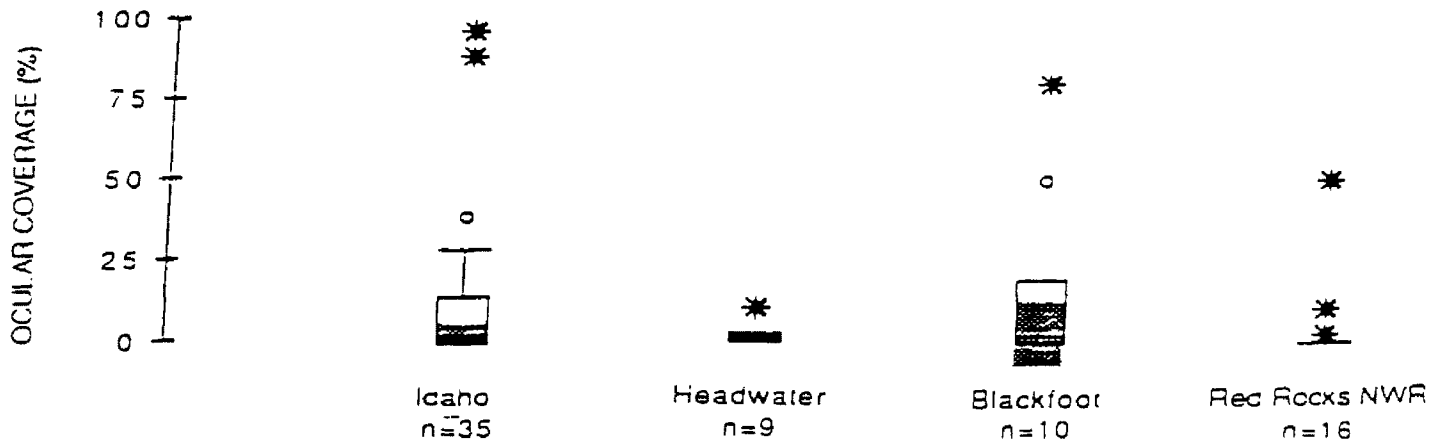


Figure 6. Canopy coverage of seedling/sapling age class by study region

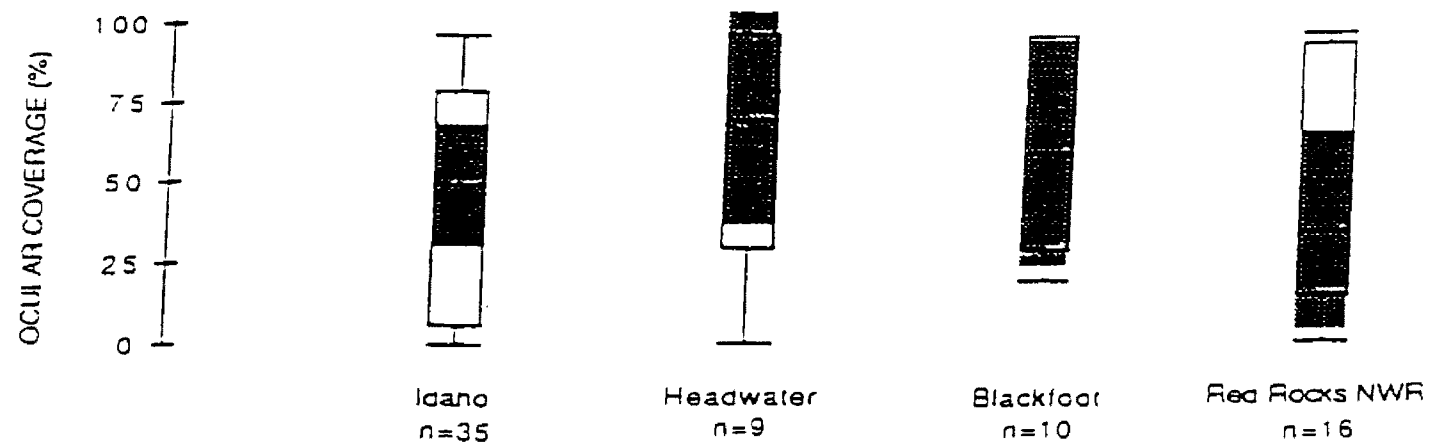


Figure 7. Canopy coverage of mature age class by study region

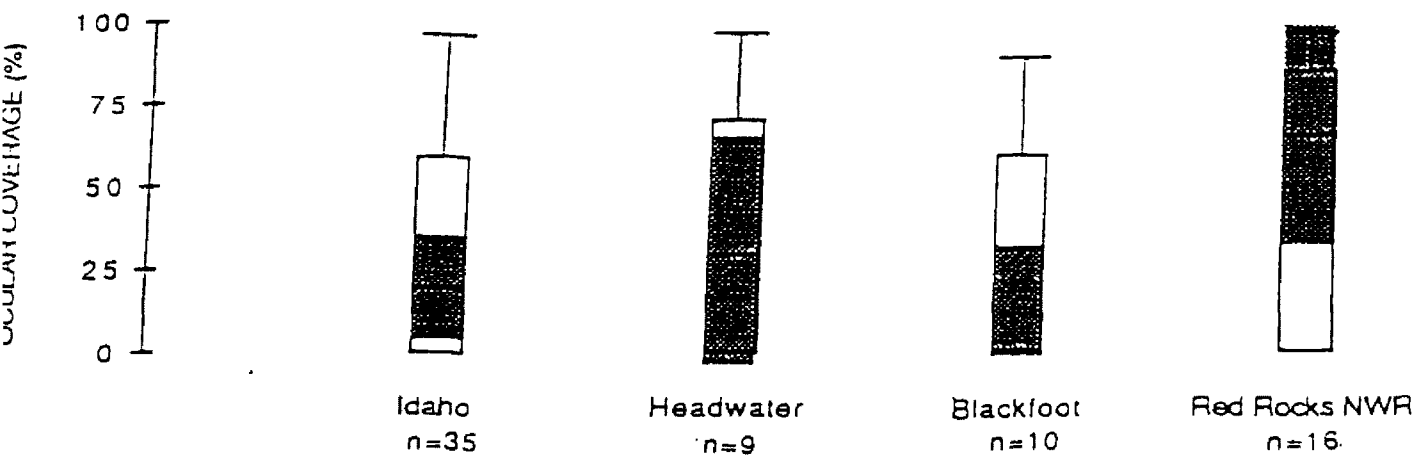


Figure 8. Canopy coverage of old age class by study region

As shown in Figure 9, the median canopy coverage values for seedling/sapling, mature, and old age classes was 1, 50 and 22, respectively. As indicated by the non-overlapping confidence intervals the differences between median coverage for each age class was statistically significant. Each age class had coverage values that covered the range between "0" (absent) and full coverage. However, the seedling/sapling age class values were heavily skewed towards low values, and all observations of coverage greater than 20 percent were outliers. Alternatively, the mature and old age classes were more evenly distributed since no outliers are displayed.

95% confidence intervals are shaded, open circles represent outliers, and asterisks represent extreme outliers

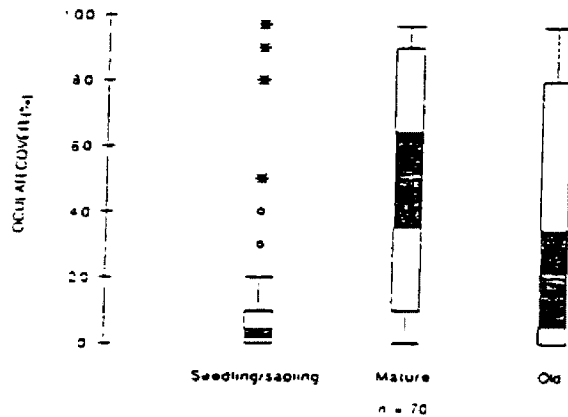


Figure 9. Canopy coverage of three age classes in all plots

The mean diameter of the largest *Salix bebbiana* stem in all plots was 25.7 cm (10.1 in) (Table 3). The Blackfoot River site had the largest willows, with a mean diameter of 34.0 cm (13.4 in) and the two largest multi-stemmed willow trunks, 91 cm and 111 cm (36 and 48 in) respectively. The Red Rock site had the next largest diameters (20.6 cm; 10.5 in), followed by Idaho sites (24.4 cm; 9.6 in), and Headwaters (20.6 cm; 8.1 in). In plots where the largest willows belonged to the mature age class, the mean stem diameter of the largest plants was 9.6 cm (3.8 in). The mean diameter where the old age class occurred was 36 cm (14.4 in).

Table 3. Diameter of largest *Salix bebbiana* in each plot

	Study Region				
	Idaho	Blackfoot	Headwaters	Red Rocks	All Regions
Mean (cm)	24.4	43	20.6	26.7	25.7
St. deviation (cm)	13.2	23.1	10.2	12.4	14.5

The median canopy coverage of dead or dying branches (decadence) between three of the four sites (Idaho, Headwaters and Red Rocks) was not statistically significant and ranged between 30 and 40 percent (Figure 10). The median value at Blackfoot sites was approximately 10 percent, which was significantly lower than Headwaters and Red Rocks. For all plots, the median coverage of dead and dying branches was 30 percent. This value is statistically significant from only Blackfoot River plots.

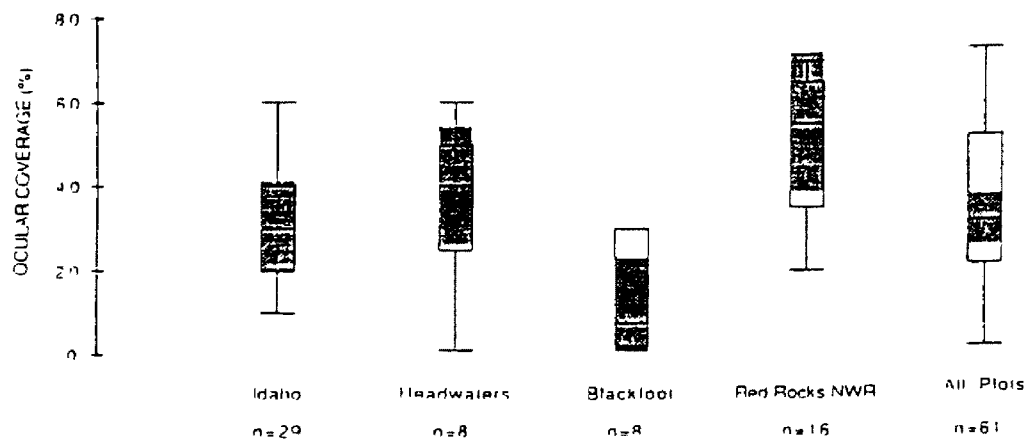


Figure 10. Coverage of decadence by study region

Although efforts were made to core the largest single stem of *Salix bebbiana* in each plot, a large proportion of the cores were of poor quality due to cambial rot. A dozen intact cores of the largest *Salix bebbiana* were obtained. The oldest core was approximately 90 years old, but like most cores, did not reach the pith. Therefore, the real age is probably greater than apparent age measured from cores. Few other native willows of the Intermountain West have stems as large or as old, and when the multi-generational character of *Salix bebbiana* is considered, individual plants may live to be several hundred years old.

Discussion

Determination of the population structure of a species is a method to assess the ecological trend of a species in regard to reproductive success, and response to disturbance such as grazing or fire (Crisp and Lange 1976, Barbor and others 1986). The population structure of *Salix bebbiana* has not been examined prior to this study except for at a single site (Atchley 1988). However, some authors have speculated about the ability of this species to replace itself (Atchley and Marlow 1989) and observed reduced coverage of younger age classes in response to grazing (Hansen and others 1995). This data quantifies the abundance of different age classes, adding

to our understanding of this species, especially when discussed in combination with that learned from regeneration data.

The low coverage of the seedling/sapling age class can be interpreted in at least two ways. First, it can be hypothesized that observed age class distributions of *Salix bebbiana* represent "normal" condition of the species, as slow colonizer, and its mid-seral successional status (relative to other willows). Alternatively, the low proportion of young age classes may be related to certain human-induced factors such as altered streamflows, excessive livestock use, or other factors.

Under the first hypothesis *Salix bebbiana* is not considered a vigorous colonizer, and the age class structure observed in this study is consistent with its present distribution in the Intermountain West as a wide-ranging but sub-dominant species. Several lines of evidence supports this hypothesis. First, in a series of plots with similar physical site conditions along Blackfoot River, my observations suggests that the spatial distribution of *Salix bebbiana* is similar, even as use by domestic and wild ungulates varies substantially. In both grazed (or browsed) and ungrazed areas, *Salix bebbiana* was a subdominant willow, spatially clumped and dominated by old age classes. Second, throughout all study areas, *Salix bebbiana* seedlings were infrequent, even when grazing was absent, seeds present and apparent safe sites for seedling establishment were available. Third, *Salix bebbiana* plants, once established, are long-lived relative to many other willow species (see Chapter 1, Regeneration), and establishment of new individuals can be relatively infrequent compared to willows with smaller diameter stems (and presumably shorter lived) such as *Salix geyeriana* or *S. boothii*. Consequently, the age class composition of *Salix bebbiana* stands, even in the absence of browsing ungulates is considerably skewed in favor of older plants.

According to the alternative hypothesis, *Salix bebbiana* seedling and saplings are poorly represented in this study because of anthropogenic or management related factors. Under this hypothesis, it would be expected that in situations where these conditions are eliminated, the seedling/sapling age class would be better represented. Examples of anthropogenic factors which may impede regeneration success include livestock grazing (as well as trampling and other physical damage), reductions in beaver populations from pre-settlement numbers, streamflow diversions, and reduced fire frequency. Although the objective of my study was not to test or control for these factors, the potential for some of these factors to impede regeneration are worth discussing.

The effects of continuous and long-term livestock grazing (and associated trampling) and ungulate browsing on willow regeneration has been well documented. Although my study was

not designed to test whether regeneration was reduced by grazing, my data showed no observable increase in regeneration in areas where cattle were excluded (due to livestock enclosures or areas where downed logs or other barriers naturally prevented ungulate access). That is, exclusion did not necessarily result in a greater amount of *Salix bebbiana* seedling/saplings, as also observed by Atchley and Marlow (1989).

An abiotic factor that may reduce the sprouting of new willow stems (including ramets and ortets) is the lack of fire. Although the role of fire in arid-region riparian zones is not well documented, some authors report that willows resprout readily after light, quick fires (Viereck and Little 1972, Kovalchik 1985, Pyle 1995). Controlled burns on *Populus tremuloides* (aspen) and mature willow stands promote vigorous post-fire regeneration Pyle (1995). Further studies involving controlled burns or coppicing *Salix bebbiana* clumps could help explain the response of this and other willows to fire and the regenerative patterns following such disturbance.

Reductions in beaver populations from pre-settlement numbers may have reduced safe sites for regeneration. If this were so, areas where beaver populations and associated backwater areas overlap with *Salix bebbiana* populations might show improved coverage of younger age classes. Similarly, sites unaffected by streamflow diversions and associated water table drops during the growing season might also be expected to show better regeneration than hydrologically impacted sites. However, my study did not provide data to adequately address either of these factors.

It is difficult to determine what canopy coverage values of the seedling/sapling age class are a threshold for successful regeneration of this species. On one extreme, the absence of any seedling/saplings is generally indicative that a woody species may not be maintaining itself. Alternatively, an individual *Salix bebbiana* (or any other shrub species) need only to successfully regenerate once during its lifetime to theoretically maintain itself.

This study did demonstrate however, that once established, and especially out the reach of herbivores, *Salix bebbiana* is extremely long-lived for a shrub. Mature *Salix bebbiana* plants tend to be multi-generational, that is, as portions of the upper branches senesce and die, new shoots (stump sprouts) and branches sprout. Often a single plant was, upon closer inspection, a collection of different age stems. It was common to see multiple stems each over 10 cm (3.9 in) in diameter, forming a single trunk nearly a meter in diameter. Although most mature stands showed considerable dead branches and shoots, only several fully dead *Salix bebbiana* were found during the entire study. Even plants with dead canopies had, upon closer inspection, a few healthy stump sprouts.

To summarize, in view of the longevity of a single mature plant, the lack of genets and ramets in ungrazed sites, the clumped spatial pattern, and the sub-dominant character of this species, it is not surprising that the population structure is so dominated by mature and old plants. *Salix bebbiana*, and its limited capacity to colonize sites demonstrates a different reproductive strategy than many adjacent willow species. Due to the relatively large, tree-like trunks and the frequency old-aged individuals, recruitment need only occur very sporadically to maintain existing densities. In short, once a seedling matures, this species has a demonstrated propensity to survive for many years and tolerate a variety of disturbances.

Nonetheless, despite the infrequency of younger age classes, it is very likely that successful establishment of seedlings is further reduced livestock grazing and native ungulates, and other possible anthropogenic factors such as streamflow diversions, beaver control, and perhaps fire suppression in adjacent uplands and grasslands. The degree to which these factors impact *Salix bebbiana* population structure can only be speculated until more extensive studies are undertaken.

CHAPTER 3 UTILIZATION

Literature Review

The literature review in this chapter consists of five sub-sections related to browsing and the grazing of woody shrubs by domestic and wild ungulates, and the responses of shrub species to these activities. The topics include browse studies, chemical defenses of woody plants, ungulate foraging behavior, browse availability, and willow palatability.

Browse studies

Numerous approaches exist to estimate browse utilization by wild and domestic ungulates. These techniques have generally been in response to land manager's demands for managing deer, moose, elk and livestock, and as a result, have been the basis for subsequent management efforts (Lyon 1970). Reliable estimates of browse utilization help in determining the carrying capacity of a specified area or habitat (Heischmidt and Stutz 1991), allocating browse between domestic stock and wild ungulates (Marshall and others 1990), rating the relative importance of woody species as ungulate food sources (Telfer 1969), or interpreting the land use history of a site as related to ungulate or livestock activity (Hansen and others 1995). However, highly variable plant physiognomy, life history, and spatial distribution of browse species pose complex problems in accurately estimating browse use (Pitt and Schwab 1990).

Techniques used to measure forage use of shrubs generally consider some combination of three major requirements: 1) a measure of availability; 2) a measure of loss; and 3) the availability to loss ratio (Thilenius 1988). Aldous (1944) describes one of the simplest approaches to determining browse by visually assessing shrub use in terms of the availability to loss ratio. Although this method is relatively easy, it often fails to provide management agencies with verifiable levels of statistical confidence and precision, and may be subject to observer bias (Pechanac and Pickford 1937). A similar but more statistically valid method of this type was developed by Cole (1963), consisting of a numerical count of browsed and unbrowsed twigs.

Other researchers have attempted to quantify the measure of loss by estimating either the length or weight of the current annual growth (CAG) of twigs removed by browsing. With this information, estimates of the carrying capacity of a given range or habitat can be made. Methods which measure the weight of the forage removed include the weight estimation method (Pechanac and Pickford 1937), the clip and weigh method, and the standing crop remaining in browsed

compared to unbrowsed areas (Rutherford 1979). Clipping, although highly accurate, is also costly, laborious and unavoidably destructive (Pitt and Schwab 1990). The weight-estimation method, is fast and non-destructive, but estimates derived by this method are hard to analyze statistically (Shafer 1963).

More recent developments in ungulate browse inventories rely on correlations between stem or twig measurements and available removed browse. The twig count method (Shafer 1963) converts a count of twigs to weight of browse by using an average weight per twig for individual species. This approach is as accurate as clipping, quick as the weight estimation method and is non-destructive (Shafer 1963). Telfer (1969) refined the Shafer twig-count method by successfully predicting twig weights from diameter measurements for 38 species of northeastern woody species. Thilenius (1988) reports that others (Joyal 1976, Wolff 1976, Parker and Morton 1978) have modified some details of Shafer's method, but the essentials are unaltered.

In a study of an important winter Alaskan moose forage, a regression equation was developed to estimate twig weight of *Salix barclayii*, (Barclay's willow) removed by browsing because longer twigs have proportionally less weight in the distal end than short twigs (Thilenius 1988). The best estimator of twig weight removed by browsing was an independent variable which approximates the volume of the twig attached to the plant. The practical consideration realized for this species is that browsing may be often over-estimated visually because weight is concentrated in the basal end of stems of current annual growth. For example, a 500 mm (19.5 in) twig would have to have between 65 and 70 percent of its length browsed to remove 50 percent of its weight (Thilenius 1988).

Although high correlations among shrub dimensions, browse production and browse use have been successfully used, predictive equations may be highly variable depending on: 1) time year twigs are collected; 2) geographical location; 3) site location; 4) portion of shrub crown from which sample is collected; and 5) age of twig (Pitt and Schwab 1990). Peek and others (1971) found that determining twig diameter to weight relationships using a common regression equation on eight species in seven sites produced significantly different results from site specific equations. Additionally, use of regression equations to predict biomass from shrub dimensions generally requires pre- and post-browsing measurements (Lyon 1970). However, Pitt and Schwab (1990) using the approach of Jensen and Urness (1981), accurately predicted biomass of browse removed from post-browsing measurements during a single site visit on a single willow species and three other associated species in British Columbia.

These techniques all possess inherent strengths and weaknesses depending on specific objectives, the size of the study area, the species of concern, as well as logistical and financial concerns. In situations where the removal of biomass is necessary, a wide range of techniques may be also be used. Many of these methods require use of predictive regression equations, multiple site visits and considerable time and effort.

If determination of the biomass of browse removed is not necessary, relatively simple methods can be employed. In such cases, the presence or absence of browse lines on shrubs, the amount of species specific regeneration, and determination of the population age class distributions are excellent qualitative indicators of browse use. Additionally, large ungulates especially cow, elk, and moose may cause extensive physical or mechanical damage to shrubs (and soils) due to hoof impact, rubbing and trampling - without actually browsing shrubs.

Chemical defenses of woody plants

To successfully exploit woody plants, browsing mammals must overcome variations in plant species, growth stages, nutritional value, and both mechanical and chemical defenses (Bryant and others 1991). Although mammals may select their food according to protein, mineral and energy content (Westoby 1974, Belovsky 1982), numerous studies show that food selection may be influenced by plant secondary chemistry (Bryant and Kuropat 1980, Palo 1984). Chemical defenses are especially important since woody plants produce numerous compounds that provide defense against mammals, and some of these may be in response to evolutionary browsing pressure.

Two broad classes of plant defensive chemicals (so-called secondary metabolites) were described by Feeny (1976). Qualitative compounds are those produced at little physiological cost to a plant, and may increase with browsing pressure. The general classes of qualitative compounds include phenols, and alkaloids, which occur in early successional, fast-growing woody trees and shrubs. Quantitative compounds such as lignins, tannins and resins, have high molecular weights, and are associated with slow growing, late successional evergreen tree and shrub species. They tend to occur in fixed amounts, independent of browsing intensity because they are so metabolically expensive to produce.

Recent studies have identified actual chemical substances that trigger a specific response in mammals. Additionally, avoidance or rejection of a plant species has been directly linked to either a plant nutrient deficiency or the presence of chemicals that are unpalatable and negatively affect a mammal's physiology (Bryant and others 1991). Most of this research has been centered on

small mammals such as snowshoe hares, voles, and woodrats (and very little on wild ungulates). One reason for this may be the relative ease in which "cafeteria type" feeding experiments (in which food choices are observed under controlled conditions) may be carried out with small mammals. Extensive amounts of literature are available on the interaction between domestic ungulates and toxic plants.

One of the most intensively studied chemically controlled interactions involves snowshoe hares and winter dormant woody plants (Bryant and others 1980, Bryant and others 1983, Sinclair and others 1989, Bryant and others 1991). In winter, snowshoe hares discriminate between species, growth form, developmental stages and plant parts. Their results suggested that forage nutrient content, tissue energy and digestibility were not correlated to forage preferences. Instead, subarctic browsing vertebrates avoid feeding upon plant tissues that contain high concentrations secondary defense compounds such as terpene and phenolic resins, concentrated in certain age tissues of preferred species of willow, birch, and aspen.

In a study of 44 Scandinavian willow species, two chemical classes, isoprenoids and phenolics, were by weight the main secondary substances (Palo 1984). High concentrations of qualitative defense compounds were concentrated in the current-year shoots and buds. These compounds accumulate during winter dormancy and decline rapidly during periods of growth. Although these compounds may have functions unrelated to plant defense (Jansen and Urness 1981), their high concentrations in the most readily browsed tissues during a season of heavy browsing strongly suggests that phenolic compounds serve as defense compounds to browsing mammals.

Because willows are dioecous (separate male and female plants), plant chemistry is complex. For example, variation in willow defense chemical content is generally greater between sexes than between species (Palo 1984). Possibly in response to these differences, Elmqvist and others (1987), Danelle and others (1985) and Hjalten (1991) reported preferential browsing of male willows by voles. Elmqvist and others (1987) further hypothesized that this might explain female-based sex ratios in boreal willow populations. In Arizona, adult beetles (*Disonchyna* spp.) were very selective and preferred *Salix exigua* (sandbar willow) 93 percent of the time over *Salix bebbiana*, *Salix laevigata* (red willow) and *Salix lasiolepis* (arroyo willow) and they preferred female *S. exigua* over males when offered a choice (Dodge and others 1990).

Clearly, there is evidence suggesting that willow species, sexes of the same willow species and different age shoots may differ in plant chemistry, thus promoting preferential forage selection by small mammals and insects. In contrast, the literature provides few examples of such subtle

discrimination among ungulates. Plant chemistry may play a role in ungulate preference for certain common tree and shrub genera, but factors other than plant chemistry may influence ungulates browse selection at the species level.

Ungulate foraging behavior

Ungulate foraging models predict foraging behavior is based upon body size, metabolic rate, relative rumen and mouth size, and differential nutrient requirements. These theories suggest an animal's foraging effort should relate to nutrient and energetic benefits associated with specific food (Westoby 1974, McCorquodale 1993). The value of a specific food item depends on its nutritional content relative to the cost of acquisition (Westoby 1974). Because quality forage is often patchy, selective use of these forages generally requires high search times with reduced biomass intake. If nutritional quality varies sufficiently among forages, maximum nutrient or energy intake may be obtained by increasing search effort despite reduced intake. Therefore, ungulates should be as selective of high quality forage as they can be, within limits of minimum intake rates (McCorquodale 1993).

Ungulate browsing foraging models have predicted that large ungulates can generally survive on low quality forage associated with relatively non-selective foraging strategy and diets. In contrast, smaller ungulates have lower forage demands and are less limited by minimum intake rates, and thus may be more selective in their food choices (McCorquodale 1993). Field observations are consistent with these predictions. McMillan (1953) observed that deer are relatively selective browsers, pausing very little in one place in contrast to moose, which may remain in one clump of willows for several days.

Dorn (1969) observed that moose browsing consisted of either stripping leaves off stems, or nipping ends of twigs, or a combination of the two. Lacking upper incisors, moose nipped buds by tugging upwards on stems grasped by the lower incisors and upper premaxillaries. The length of twig removed was usually between 5-10 cm (1-2 in). The number of twigs taken in a single mouthful was variable, but was limited to approximately half a dozen. The lack of upper incisors precluded the possibility of browsing large twigs, and the maximum diameter of browsed twig was 0.5 cm (0.2 in). In winter, moose browsed by nipping leaders, often close to the snow level (Dorn 1970). Leaf stripping was observed to remove leaves from 20-60 cm (4-13 in) of the stem, as well as any lateral branches, and often terminal buds (McMillan 1953). Moose efficiently strip leaves from willow twigs at heights over 1 m (3.2 ft) above ground level summer (Dorn 1970).

Moose are able to obtain food from the ground level to as high as 3.5–4 m (10–13 ft) if necessary. In tall willow communities, McMillan (1953) reported that 80 percent of summer browsing heights were less than 1.2 m (3.8 ft), and a maximum of 2 m (6.5 ft) was reported. Winter browsing can be as high as 3.5 m (10.5 ft) above the ground when snow depths are great. Murie (1934) observed summer feeding moose to "ride" down shrubs and break off upper stems. Moose preferentially break stems of moderately large saplings and tall shrubs and often feed upon crown twigs even though younger plants of the same species are available (Dorn 1970). This preference for taller forage may be explained by an evolutionary predisposition of moose.

Elk are more adapted for grazing than moose (McMillan 1953) and apparently better adapted than deer to use a more diverse array of plant species as food. McCorquodale (1993) reported high mobility was associated with low diet diversity and generally reduced forage harvesting rates. Elk were mobile foragers in autumn and spring and relatively sedentary during winter. Mobile foraging occurred during periods of higher quality forage availability. Thus mobile foraging appeared to reflect increased effort when energetic payoffs of selective foraging were enhanced. Further, the degree of dietary specialization was limited by the relative abundance of preferred forages, being greater when grass was more available and less when forb quality was high. This is consistent with Gaffney (1941), who reported that the preference of a species depends largely on the association in which it occurs.

In a Utah summer range, mule deer consumed little or no grass beyond the first two or three weeks of the growing season as compared to the large quantities of grass consumed by elk all summer. Deer diets were generally composed of greater than 50 percent forbs with the remainder being browse (Collins and Urness 1983). Mule deer were significantly more forage selective than elk. Deer were observed to be more discriminating than elk in plant parts, perhaps attributable to reductions in bite size. Conversely, large mouth size relative to size of plants grazed may impede greater selectivity in elk. Contrasts in discrimination may also reflect differences in digestive capacity that dictate the type of forage that can be used efficiently by deer or elk (Van Soest 1980).

Elk were less selective of plant species and they also ingested older and coarser plant parts. The relatively restricted nature of deer diets represented actual physiological limitations since deer could not digest some forages as efficiently as elk. Deer were restricted by interference from unpalatable plant species or plant parts. Thus deer were not capable of using the highly productive meadows to the extent that elk were. This is in agreement with Mackie (1970) who found that elk could more intensively use most plant communities, topographic sites and all forage classes than could mule deer (Collins and Urness 1983).

Hoffman (1989) classifies ungulates into one of three groups of feeding types based on anatomical variations that result from evolutionary trends favoring patterns of food selectivity. Species such as moose and mule/whitetail deer, which evolved before grasses developed, are termed concentrate selectors. These species select plant parts rich in easily digestible and highly nutritious contents, and have limited capacity to digest cellulose due to a primitive rumen. On the other extreme are grass and roughage eaters which include cattle. Their highly evolved digestive system can handle fibrous plant material such as grasses, but can also cope with rapidly fermenting cell contents found in shrubs. Elk are considered intermediate feeders that show adaptations of both extremes and are a highly variable and flexible, seasonally adaptable, and opportunistic feeding type (Hoffman 1989).

Foraging is a dominant activity of ungulates. Wild ungulates typically devote 40–60 percent of each day to finding and consuming food (Wickstrom and others 1984). The selection of forage by ungulates has been described by Heischmidt and Stutz (1991) to operate at several hierarchical scales, from the landscape level down to the plant community level, feeding station level and finally the individual plant level, as described below.

Plant-animal interactions at the landscape level are influenced by proximity to water and cover, accessibility, escape routes and seasonal factors such as snowfall. At the plant community level, selection is dictated by the ability to harvest food material. For example, the greater the quality of forage species, the slower the grazing velocity and the increased residence time. If a community lies between water and thermal cover, site preference may be magnified (Heischmidt and Stutz 1991).

Several interrelated factors are involved at the feeding station level. These include search time, travel time, and biting rates. The interaction between these factors is demonstrated by noting how, for example, biting rates may decrease if traveling time increases. Additionally, patchiness of vegetation at this level has its greatest effects on the distance between feeding stations (Heischmidt and Stutz 1991).

The final level is plant choice, a species by species appraisal of forage (Heischmidt and Stutz 1991). One important consideration at this level is that each ungulate species is, to a certain extent, evolutionarily predisposed to a certain life form. For example, jaw morphology and feeding posture dictate that cattle are predisposed to be grazers and are best adapted to utilize graminoids

and forbs (McMillan 1953). Dorn (1969) further suggests two other factors guiding plant species selection - availability and palatability of plant species.

Browse availability

Availability or accessibility of browse is a rather self-explanatory term (perhaps this very characteristic is the reason it is seldom discussed in scientific literature along with more frequently used terms such as palatability). It refers to how approachable browse is to potential browsing ungulates. Because of the many variables related to browse utilization, such as the growth form of willow species or adjacent plant species present, availability is only used in a relative sense. For example *Salix bebbiana* seedlings may be readily accessible in an open meadow grazed by cattle in the summer, but those same seedlings may be unavailable to moose in the winter, when snow is deep. In this example, the availability of *Salix bebbiana* seedlings may be depend on the season and the species of browsing ungulate.

Willow palatability

Palatability is defined as factors inherent to a plant species that elicits an animal's selective response (Heischmidt and Stutz 1991). Thus a shrub species which is browsed more heavily than others is often said to be more palatable. Palatability is a function of both the chemical constituency of leaves, stems and other plants parts, and factors related to mechanical or physical deterrents. Chemical factors that influence palatability include presence or absence of defense compounds, nutrients, digestibility, fiber content, protein content, and mineral content (Oldmeyer and others 1977). A prime example of physical deterrents are the long thorns of *Crataegus* spp. (Hawthorne spp).

A term closely related to palatability is utilization. Utilization refers to the proportion of available twigs browsed to unbrowsed (Heischmidt and Stutz 1991). A shrub species which is more heavily utilized than adjacent shrubs would be considered more palatable. Another term to describe observed differences in utilization rates is discrimination.

Determining the intraspecific willow palatibility (and shrubs in general) is quite difficult, and consequently the current state of knowledge for willow palatability is considerably less than, for example, that of rangeland grass species. Factors that account for the difficulty in determining willow palatability include:

- 1) the species, size, age and hunger of the browsing animal;

- 2) competition from other animals;
- 3) individual preference of browsing animal;
- 4) growth-form of willow species;
- 5) accessibility of stems, plants or species;
- 6) age of plant, stem, or stand of willows;
- 7) adjacent plant species present;
- 8) snowfall depths;
- 9) number of browsing events;
- 10) separate male and female plants (dioceous) in willows;
- 11) hybridization in willows; and
- 12) the method used to measure utilization, and other factors.

A variety of studies have been designed to control some of these variables. For example, some researchers have conducted controlled food choice studies in which animals select from a palette of potential browse choices. Such "cafeteria" studies control for the herbivore, adjacent plant species, accessibility and other variables. Other researchers have made thousands of observations of ungulate forage choices in the field. Multiple site visits, in which individual stems are tagged, and re-visited, provide seasonal browsing data. Finally, estimations of browse use can also be made from single site visits. Each approach has certain advantages and disadvantages, but no single method can control all variables.

Some of the most intensive research relating to willow palatability has occurred in boreal life zones of Alaska, and Scandinavia. In northern latitudes willows and associated species such as birch, alder and aspen occupy a proportionally greater land area than in the Intermountain West, and their importance to ungulate populations is magnified. As a result, these areas have been relatively well studied, and interactions between woody deciduous species and dominant herbivores animals such as snowshoe hares and moose have been especially well researched.

Many authors in northern latitudes have observed that willow is the preferred forage of most moose populations. The remainder of their diet (in order of preference) in Alaska is comprised of aspen, birch, pine, fir and alder (equal to spruce) (Bryant and Kuropat 1980). Cafeteria type feeding experiments with snowshoe hares (*Lepus americanus*) and mountain hare (*L. timidus*) have validated preference similar to moose. Willows are the preferred boreal woody browse species followed (in order of preference) by aspen, larch, birch, pine, fir, spruce and alder (Bryant and Kuropat 1980). In addition, the juvenile growth-form of *Salix alexensis* (feltleaf willow) are extremely unpalatable to snowshoe hares compared to twigs collected from mature growth-form

trees and shrubs (Bryant and others 1985). Finally, numerous authors have reported that Ptarmigan (*Lagolopus* sp.) preferentially feed upon willows in Alaska, Colorado (May and Braun 1972), Finland (Bryant and Kuropat 1980), and Iceland (Weeden 1967).

In western rangelands, the palatability and physiological tolerances of common grass and forb species to livestock grazing is relatively well understood. The ease in which these herbaceous species can be studied and experimentally manipulated has contributed to the general advanced state of knowledge. In recent years, rangeland managers and researchers have studied cattle use of riparian areas, and especially their effect on riparian shrubs, including willows. But in contrast to herbaceous species, there is little well substantiated information available on the relative utilization of riparian shrub species.

In one of the few studies on shrub utilization, Dorn (1969) documented differential browsing between willow species by livestock. *Salix wolfii* (wolf willow) a dwarf species, was preferentially selected over adjacent (and taller) willow species by cattle in the summer. Dorn hypothesized that the low growth-form of *Salix wolfii* was more suitable to the feeding posture of cattle than were adjacent taller willows. In another study, McMillan (1953) hypothesized that moose avoided *Salix wolfii* because stands comprised of this species lacked the hiding cover provided by taller species and moose had difficulty in accessing this low growing species.

Patterns of cattle use of shrub species has been described by Boggs and Weaver (1992) and Hansen and others (1995). In cottonwood forests of Montana, Boggs and Weaver (1992) observed that cattle grazing has a strong effect on the species composition of the shrub sub-canopy. Ungrazed understories contained a diverse dense mix of shrub species such *Cornus stolonifera* (red-osier dogwood), *Salix* species (willows), *Amelanchier alnifolia* (Saskatoon serviceberry) and *Prunus virginiana* (chokecherry). Moderate grazing reduced the abundance and canopy cover of these species, and increased the coverage of *Symphoricarpos albus* (common snowberry) and *Rosa woodsii* (Wood's rose). Continued grazing, if severe enough, was observed to eliminate shrubs, and replace them with disturbance tolerant herbaceous species. These observations attribute patterns of shrub retrogression to differences in palatability, but the role of differential physiological tolerance to browsing between plant species should be considered as well.

Kovalchik and Elmore (1992) report that willows become a main source of cattle browse after more desirable forage such as grasses and forbs become depleted and their palatability and nutrient content decreases. For these reasons most browsing occurs in late summer. Willow use may occur earlier in the summer if a range allotment is overstocked too long (Kovalchik and

Elmore 1992), but as long as palatable herbaceous forage is available in the riparian zone willow use remains minor (Kaufmann and others 1983).

Many studies investigating the food habits and habitat use patterns of specific ungulates often indirectly provide information on willow palatability. Although such information is not a primary goal of these studies, literature is so sparse on relative palatability of riparian shrubs that these ungulate food habitat studies provide valuable information. These studies often consider a plant important browse species when it is a large component of an ungulate's diet, which relates more to a browse species' relative abundance than to its palatability. Consequently, studies framed in the context of the browsing ungulate may fail to provide information needed to determine the palatability of one browse species from another unless the relative abundance of shrub species is included.

Gaffney (1941), in an observational study, evaluated the use of all elk forage species in two winter range areas of Bob Marshall Wilderness. One winter range was dominated by grasses and forbs but shrubs, although abundant, was used lightly. The second range had fewer graminoids, and as a result, woody species comprised a greater part of the forage. Willows were one of the most consistently browsed shrubs in both areas, with utilization between *Salix bebbiana*, *S. drummondiana* (Drummond willow) *S. exigua* (sandbar willow), *S. geeyeriana* (Geyer willow), *S. lutea* (yellow willow), *S. scouleriana* (Scouler willow) nearly equal with respect to site (5). The abundance of particular willow species had little effect on the degree of utilization, as both scarce and commonly occurring species were browsed similarly. At the winter range dominated by graminoids, all willow species were utilized less than half as much as at the other site. Gaffney (1941) also observed that stems of Salicaceous plants were generally browsed to a greater diameter than *Acer glabrum* (Rocky Mountain maple), *Prunus virginiana* (common chokecherry), and *Amelanchier alnifolia* (Saskatoon serviceberry).

Table 4. Utilization and abundance of willow species on elk winter range

Species	Forb-dominated site		Shrub dominated site	
	Utilization (%)	Abundance	Utilization (%)	Abundance
<i>Salix bebbiana</i>	20	S	60	S
<i>Salix drummondiana</i> *	20	A	60	A
<i>Salix exigua</i> **	20	P	40	P
<i>Salix geyeriana</i>	20	A	50	A
<i>Salix lutea</i>	20	A	60	A
<i>Salix scouleriana</i>	30	A	60	A

Abundance: A, abundant; P, plentiful; C, common; M, moderate; S, scarce; R, rare.

* Originally described as *S. subcoerulea*, prior to nomenclature revisions.

** The original work reported data for what now are recognized as two sub-species of *S. exigua*, so the data was pooled.

Dorn (1969, 1970), in an observational study of moose and cattle food habits in southwest Montana, reported that willows were a critical component of cattle and especially moose forage. Dorn determined which willows comprised the bulk of moose and cattle diet, on a seasonal basis, and then evaluated the potential conflict for food sources at a specific study site. Evaluation of the absolute importance of individual plant species to moose and cattle was difficult, but all 15 species of willow were at some time of the year important as forage. For example, *Salix bebbiana* was uncommon, and therefore comprised a small portion of the total moose and cattle diet. However, it was utilized about five times as heavily in the summer by cattle as by moose, and became a very important to moose in late winter because its tall height made it accessible. *Salix geyeriana* (Geyer willow) was used at relatively constant rates both by moose and cattle in the summer and by moose in the winter. Due to its short stature, *Salix wolfii* (wolf willow) was unavailable in the winter to moose (under snow cover), but was used very heavily by cattle in the summer. The most abundant willow, *Salix boothii* (Booth willow) comprised nearly 60 percent of the total summer moose forage, 15 percent of summer cattle forage and 25 percent of moose winter forage and was therefore the most important species overall. A species nearly as common, *Salix planifolia* (planeleaf willow) was utilized significantly less in the summer, but equal to *S. boothii* in the winter.

On the Gallatin River, northwest of Yellowstone National Park, Patten (1968) observed heavy utilization of a willow dominated shrub community comprised of *Salix drummondiana* (Drummond willow), *S. exigua* (sandbar willow), *S. farrae* (Farr's willow), *S. lutea* (yellow willow)

by elk. *Salix exigua* and *S. lutea* were browsed especially hard (40–60 percent utilization, respectively) compared to *S. drummondiana* and *S. farrae* (20–40 percent utilization). Where elk access was limited, reduced browsing pressure and a significant reduction in willow mortality was observed.

In another Yellowstone study, *Salix wolfii* and *S. geyeriana* constituted 75 percent of the moose summer diet (McMillan 1953). Although generally of equal occurrence, significant summer browse preference was demonstrated for *S. geyeriana* over *S. wolfii* by moose, which is consistent with Dorn's observations. Grasses constituted only a small part of the moose's diet (McMillan 1953). Owing to greater species diversity, Murie (1933) found a large percentage of tree and shrub species browsed by moose on Isle Royal, Michigan. In Oregon, Shaw (1992) observed that *Salix lemmonii* (Pacific willow) was heavily used by mule deer, elk and beaver in summer but received little use in winter. In Newfoundland, Parker and Morton (1978) reported that among shrubs, willow had the highest percentage of use by deer, but its lack of abundance reduced its overall importance as browse. While developing foraging models in eastern Washington, McCorquodale (1993) observed that shrubs, primarily willows, were browsed heavily by elk during winter months when snow covered the ground.

Methods

Data collection

A total of 74 *Salix bebbiana* plots in the four study areas were sampled. The seedling/sapling age class was represented in 72 plots and the mature age class occurred in 70 plots. Fifty-five of the seedling/sapling age class plots and 53 of the mature class plots had willow species in addition to *Salix bebbiana*. Therefore, the effective sample size for this portion of the study was 55 for seedling/sapling plots and 53 for plots with the mature age class (Table 5).

Table 5. Distribution of willow species in study plots

Willow Species in Plot	Age Class			
	Seedling/sapling		Mature	
	# plots	% plots	# plots	% plots
<i>S. bebbiana</i> only	17	23	17	24
<i>S. bebbiana</i> and other willows	55	77	53	76
Total	72	100	70	100

To determine if there were differences in utilization (discrimination) between *Salix bebbiana* and adjacent willows, utilization levels of all willow species in each plot was estimated. Within a *Salix bebbiana* plot, utilization of *Salix bebbiana* and other willow species were placed into one of five utilization classes (A = 0-5%, B = 6-25%, C = 26-50%, D = >51%, E = unavailable and F = Full >95%) by species and age/size class (seedling/sapling and mature).

Utilization considered the proportion of available browsed to unbrowsed twigs of the current or previous year. Ocular utilization estimates were supplemented as much as possible by actual counts of browsed to unbrowsed stems on individual plants. These counts were also used to "calibrate the eye", which increased accuracy and precision of ocular estimates within plots, between plots and between observers. The distinction between the age/size categories of seedling/sapling and mature was subjective, but based on diameter and height, relative to the peculiarities of each species, with the basic assumption that generally increased basal diameters and/or increased height represent older plants.

Efforts were also made to determine the ungulate species that commonly used each plot based on knowledge of the study area, browsing patterns, adjacent habitat, condition of browsed twig ends,

or visible tracks, scat, and physical damage to woody plants. This promoted an understanding of certain browsing patterns, that was useful in data interpretation.

Results

The term discrimination describes the differences of at least one utilization class ("A" to "B", "B" to "C", etc.) between one or more willow species. A total of 55 seedling/sapling and 53 mature plots were observed to have more than one willow species. By study region, discrimination was observed at 0 Blackfoot sites, at 1 seedling/sapling Headwater site, at 5 Red Rock sites, and approximately 8 seedling/sapling and 5 mature Idaho sites, as shown in Figures 11 and 12.

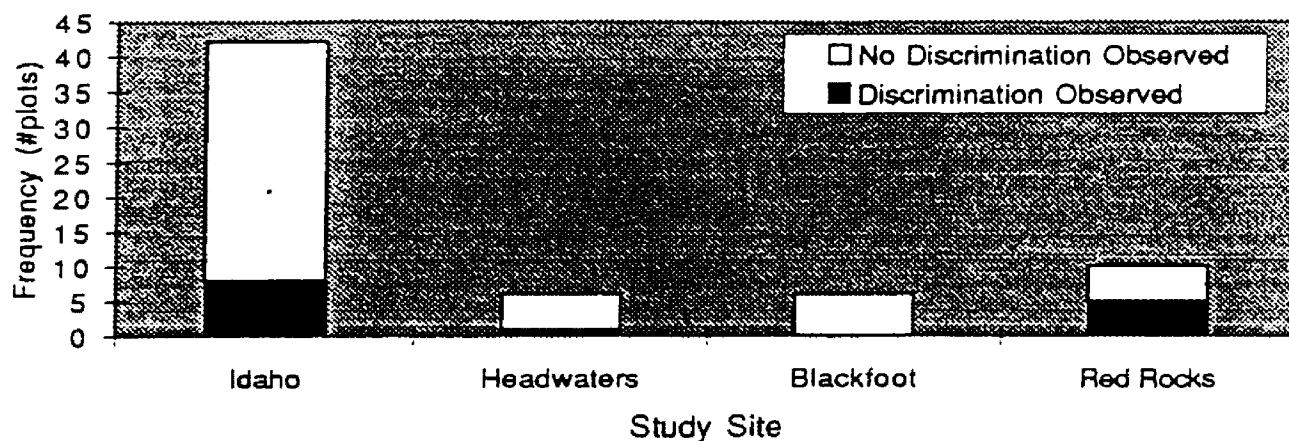


Figure 11. Frequency of observed discrimination in seedling/sapling age class plots by study region

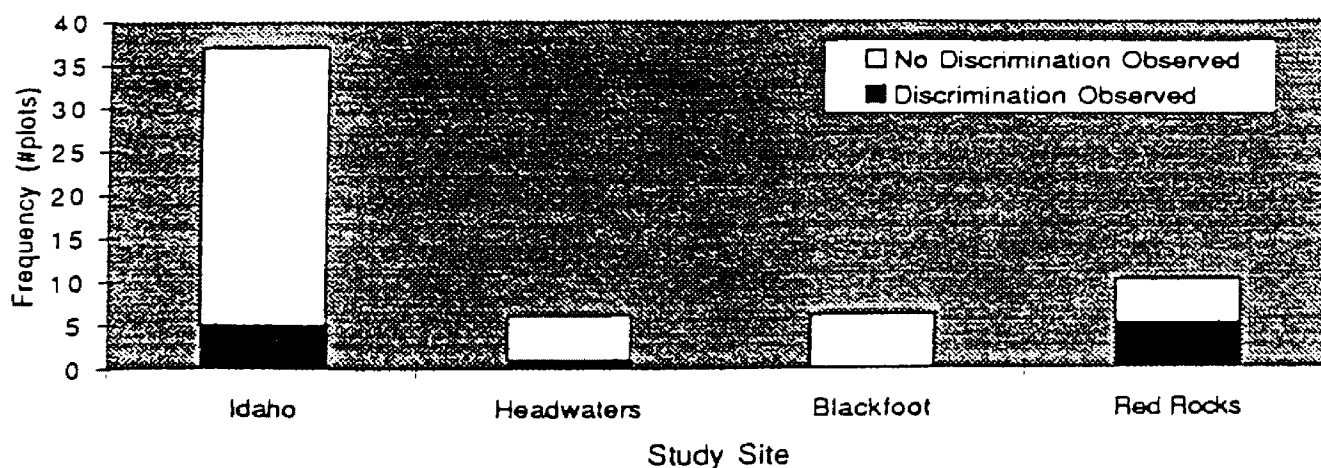


Figure 12. Frequency of observed discrimination in mature age class plots by study region

Discrimination was observed in 15 and 9, respectively, of seedling/sapling plots and mature plots (Figure 13). But where discrimination was observed, *Salix bebbiana* was either the single willow species, or among those willows species preferentially browsed most (93 percent) of the time.

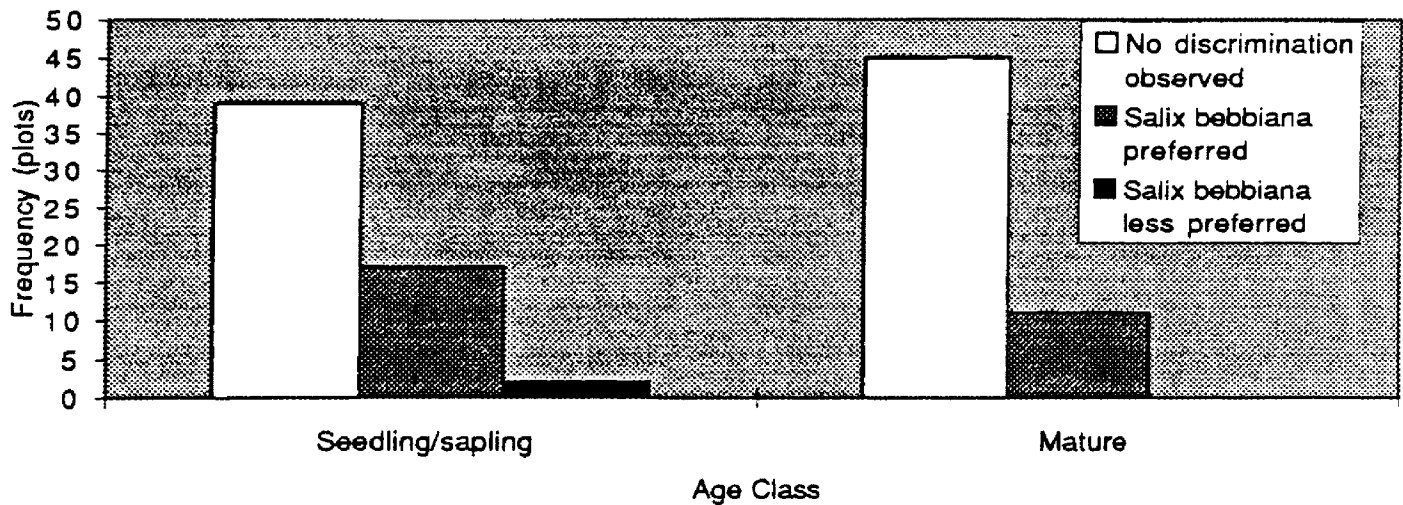


Figure 13. Incidence of discrimination between *Salix bebbiana* and other willow species in all plots with multiple willow species

In approximately one half of the plots where differential utilization (e.g. discrimination) occurred, a single utilization class ("A" to "B", "B" to "C" etc.) separated the less browsed willow species from the more browsed willows (Table 6). In the other half of the plots, two and three utilization classes ("A" to "C", "A" to "D" etc.) separated the less-browsed from the more-browsed willow species. Most (85 percent) of these larger differences in willow utilization within a plot involved *Salix wolfii* and *Salix planifolia*, *Salix boothii*, and *Salix geyeriana* generally were in the same utilization class as *Salix bebbiana* or differed from by a single class.

A large proportion (42 percent) of the plots of the plots reported "full" utilization of available willow browse (Figure 14). About 20 percent of the plots were browsed at heavy levels, and 20 percent showed light or no browsing. The three intermediate utilization classes, when combined, occurred in less than half (40 percent) of all *Salix bebbiana* plots.

A total of nine willow species were encountered in *Salix bebbiana* plots, but a strong association was observed between and *Salix boothii* (Booth willow) and *Salix geyeriana* (Geyer willow) (Table 7). In 90 percent of the plots where *S. bebbiana* occurred with other willows, either *S. boothii* and *S. geyeriana*, or both, were present. Individually, these two species were the associated willows approximately 60 percent of the time. The remaining seven other willow species were associated

with *Salix bebbiana* in 22 percent of the plots. The response of both *Salix boothii* and *Salix geyeriana* relative to *Salix bebbiana* was similar. *Salix bebbiana* was preferred over *S. boothii* and *S. geyeriana* in approximately 20 percent of seedling sapling age class plots and a small proportion (10 percent) of the mature class

Table 6. Observed cases of differential utilization by age class and species

Number	Age class ¹	More-browsed species ² / utilization class ³	Less-browsed species ² / utilization class ³
1	S/S	SALBEB/d, SALBOO/d	SALGEY/c
2	S/S	SALBEB/f, SALGEY/f	SALBOO/d
3	S/S	SALBEB/d, SALBOO/d, SALGEY/d	SALWOL/a
4	S/S	SALBEB/f, SALBOO/f, SALGEY/f	SALWOL/b
5	S/S	SALPLA/f	SALBEB/d, SALSCO/b
6	S/S	SALBEB/d	SALGEY/c
7	S/S	SALBEB/c	SALGEY/a
8	S/S	SALBEB/f	SALGEY/d, SALBOO/b
9	S/S	SALBEB/f	SALBOO/d
10	S/S	SALBEB/f	SALBOO/d
11	S/S	SALBEB/b	SALGEY/a, SALBOO/a, SALEXI/a
12	S/S	SALBEB/f	SALBOO/d
13	S/S	SALBEB/c	SALBOO/a
14	S/S	SALBEB/d, SALBOO/d	SALGEY/a
1	Mature	SALBEB/d	SALGEY/c
2	Mature	SALBEB/d	SALBOO/c, SALGEY/c
3	Mature	SALBEB/f, SALGEY/f	SALBOO/d
4	Mature	SALBEB/d, SALBOO/d, SALGEY/d	SALWOL/a
5	Mature	SALBEB/f, SALBOO/f, SALGEY/f	SALWOL/b
6	Mature	SALBEB/f, SALBAR/f	SALPLA/b
7	Mature	SALBEB/b, SALBAR/b, SAL:LUT/b	SALDRU/a
8	Mature	SALBEB/d	SALGEY/c
9	Mature	SALBEB/d, SALGEY/d	SALBOO/b

1 Age classes: S/S = Seedling/sapling

2 Willow species: SALBAR = *Salix barratiana*; SALBEB = *S. bebbiana*; SALBOO = *S. boothii*; SALEXI = *S. exigua*; SALGEY = *S. geyeriana*; SALLUT = *S. lutea*; SALPLA = *S. planifolia*; SALSCO = *S. scouleriana*; SALWOL = *S. wolfii*

3 Utilization classes: a = (0-5%); b = (6-25%); c = (26-50%); d = (51-90%); e = (unavailable) f = (>95%)

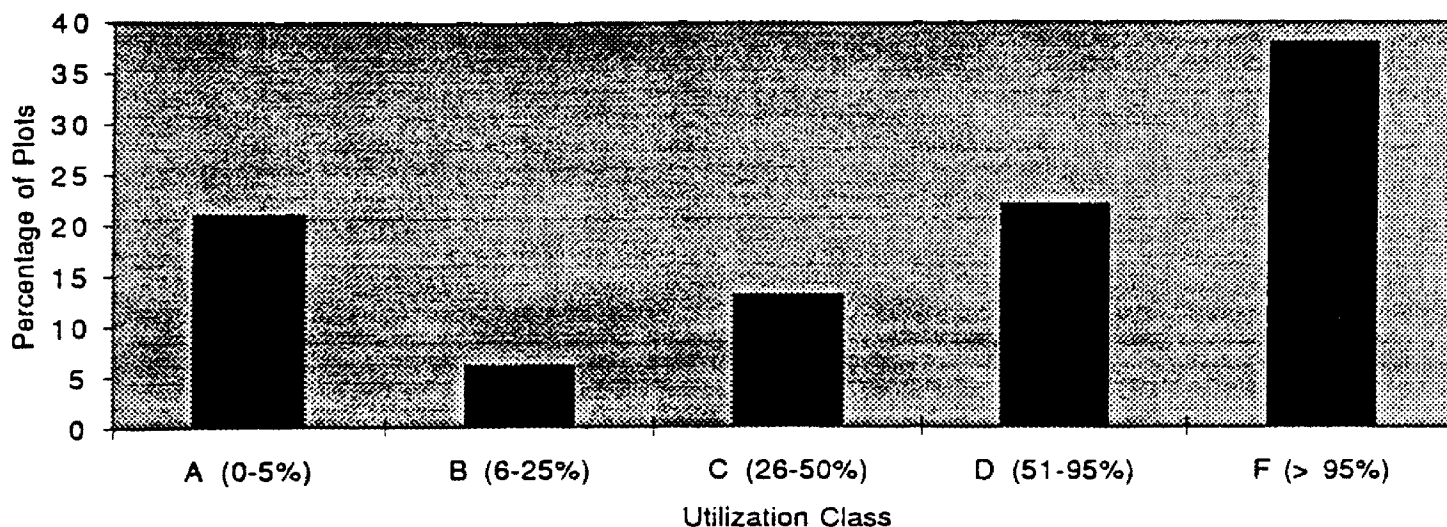


Figure 14. Frequency of utilization levels in plots with more than one willow species

Table 7. Incidence of willow species associated with *Salix bebbiana*

Associated Willow Species	Age Class			
	Seedling/Sapling		Mature	
	# plots	%	# plots	%
<i>Salix boothii</i>	34	61	36	68
<i>Salix geyeriana</i>	35	63	33	62
<i>Salix geyeriana</i> or <i>S. boothii</i>	51	91	47	89
<i>Salix lutea</i>	5	9	5	9
<i>Salix exigua</i>	2	4	3	6
<i>Salix wolfii</i>	2	4	2	4
<i>Salix planifolia</i>	2	4	0	0
<i>Salix drummondii</i>	2	2	0	0
<i>Salix barratiana</i>	1	2	0	0

Discussion

Two somewhat opposing findings resulted from this study. First, in most plots (73 percent) utilization rates between adjacent willow species were approximately equal, suggesting that differential utilization or discrimination between *Salix bebbiana* and associated willow species is not a widespread phenomena. Alternatively, in those few plots where discrimination was observed, *Salix bebbiana* was among those species, or the single species browsed more heavily 91 percent of the time, indicating that at least some differential utilization was occurring, and that *Salix bebbiana* may be a preferred browse species. Each of these results are worth exploring.

Observed discrimination

The greatest and most obvious differences in willow utilization patterns in this study occurred between three medium sized willows (*S. bebbiana*, *S. geyeriana*, and *S. boothii*) and two short willows species (*S. wolfii*, *S. planifolia* variety *monica*). Utilization differed by several classes ("A" to "D", etc.), as the tall willows (mature and seedling age classes) were severely browsed and the short species were relatively untouched. For comparison, nearly all other incidences of discrimination (80 percent) differed by a single class (for example "C" to "D"). Thus the greatest differences in utilization rates in my study occurred in the few plots where willows with distinctly different sizes were adjacent to each other.

The plots where I observed the most significant discrimination (Red Rocks National Wildlife Refuge) were not part of cattle grazing allotments, and were excellent winter moose habitat. Apparently *S. bebbiana*, *S. boothii* and *S. geyeriana* willows were above the snow line and *S. wolfii* and *S. planifolia* were regularly buried by snow and thus inaccessible to browsing moose. A more thorough survey of browsing patterns in Red Rocks area could determine this trend with more certainty, but my findings suggest that accessibility/availability may be more important than palatability in determining browse use by ungulates.

In the remaining plots where discrimination occurred *Salix bebbiana* was consistently preferred more than other willows. However, the differences in utilization classes were usually one utilization class (for example, "B" to "C"). Such a small difference, in view of the variables surrounding browse estimations and potential sampling error is not strong enough to make any conclusive statements regarding interspecific browsing patterns. The large proportion of plots where no discrimination was observed further supports this view

Absence of discrimination

A large proportion of *Salix bebbiana* plots (61 percent) which had at least two willow species provided no data on utilization rates because browsing was either absent (A = 0-5 % utilization), unavailable (E) or full (F = >95% utilization) on all willow species. At such browsing intensities there is little evidence of plant choice (Table 8). Full (F) utilization provides little to no information about the order in which plant species and life forms may have been consumed - in most cases when browsing is full, all available forage was consumed. Similarly, when browsing is light or absent (A), insufficient browsing occurs to note choice between species. But at intermediate (B = 6-25%, and C = 25-50%), and heavy levels (D = 51-95%) browse is available, and the possibility of detecting preference for a certain individual, life form, age class or species of willow is more likely.

Table 8. Frequency of pooled utilization classes with multiple willow species

Utilization Class	Age Class					
	Seedling/Sapling		Mature		All Age Classes	
	# plots	% plots	# plots	% plots	# plots	% plots
Choice (classes B, C, D)	22	40	22	42	44	41
No choice (classes A, E, F)	33	60	31	58	64	59

Another explanation for the lack of observed discrimination is that ungulates, as a group, may not detect any differences in palatability between willow species. The secondary compounds of plant tissue explain insect preference for certain willow species (Boecklen and others 1994, Dodge and others 1990), vole sex-based willow preference (Danelle and others 1985, Hjalten 1992) and hare discrimination between species and age of willows (Bryant and others 1985). However, the scientific literature provided no documentation of ungulate discrimination among willows attributable to palatability. Moose, cattle, elk, and even deer are large generalist herbivores which may not have the capacity to distinguish between species of the genus *Salix*, especially considering the dioecous habit of the genus.

However, ungulates apparently can distinguish between genera of common shrubs. My observations are consistent with those of Bryant and Kuropat (1980), Hansen and others (1995), and others suggesting that alder, birch and spruce are frequently untouched by browsing ungulates, when nearby willows may be noticeably browsed. Thus, ungulates tend to discriminate between genera, but may fail to consistently distinguish between species of willows.

In summary, differential utilization or discrimination was observed in a small proportion (22 percent) study plots, suggesting that discrimination between *Salix bebbiana* and adjacent willow species is infrequent. However, most willow plots sampled in this study (61 percent) were browsed too lightly or heavily to reveal any willow browse preferences that could be observed in a single site visit.

In view of dioecous status of willows, evolutionary predisposition of ungulates for certain life forms, and ungulate foraging energetics, it seems unlikely that moose, elk, cows or even deer regularly distinguish between adjacent willows of similar size. My study suggests that the greatest differences in intraspecific willow browse use may be best observed in willow species of different size. However under most field conditions any actual browse preferences of ungulates may not be detected in a single site visit. Even if preferences for certain willow species exist, they

may be obscured by long-term heavy browsing and associated trampling, erratic annual snowfall amounts, the impossibility of accurately determining the quantity and frequency of ungulate species at a given site, and other factors.

It is well documented, and easily observed in the field that wild and domestic ungulates prefer certain shrub genera, such as *Cornus stolonifera* (red-osier dogwood) over others such as alder, rose, or spruce trees. Although ungulate preference for specific willows species may occur in specific locations due to interactions between species composition, season of use, and other factors, I contend that predictable and consistent ungulate preference for specific willows species (including *Salix bebbiana*) does not occur across a wide geographic area.

CHAPTER 4 SYNTHESIS

This study contributes to our understanding of riparian systems. Specifically, studying the reproductive ecology and relative utilization of *Salix bebbiana* across a wide geographic area provided new insights into management and rehabilitation of this species and willow-dominated riparian areas. It also provides a mechanism explaining why *Salix bebbiana* may survive longer than most other regional willow species under long-term grazing.

I discovered that the reproductive capacity of *Salix bebbiana* is consistent with the spotty distribution and age class structure of this species across the Intermountain West. The predominant mode of regeneration for *Salix bebbiana* is ortets (stump-sprouting), and ramets (suckering) with genets (seed-produced regeneration) being uncommon. It follows that in all study areas *Salix bebbiana* stands were dominated by stump-sprouted clumps of old plants. Young plants, and recently established stands of *Salix bebbiana* were extremely infrequent.

Under existing land use practices it is difficult to say whether *Salix bebbiana* is maintaining itself across the landscape. In comparison to other willows *Salix bebbiana* is a poor colonizing species, but once established, ortets allow it to survive multiple generations. There is no doubt that poor livestock grazing practices, or heavy ungulate browsing can eventually eliminate stands of this resilient species. However, I found no evidence that the absence of livestock grazing necessarily resulted in a noticeable increase in ramet and genet production.

Additionally, I failed to find evidence that domestic and wild ungulates consistently prefer *Salix bebbiana* over adjacent willow species. Although some discrimination between willows was observed, in most study plots willow species were browsed at fairly even levels. My data does not support the assertion that any single willow species will be consistently preferred over other willow species from site to site across the landscape.

This study demonstrated that browsing is a relative event. Among other factors, utilization depends on plant composition, distribution of plant species, time of year and snow levels. The species, age and condition of the herbivore also affects browsing. Based on my literature review, and the willow species I studied (Table 7), I hypothesize that both wild and domestic ungulates base any preference for individual willow species on availability and accessibility of individual plants rather than the chemical or physical characteristics (palatability) of a species.

Finally, this study suggests a mechanism for the apparent ability of *Salix bebbiana* to be one of the last willow species to be eliminated by long-term heavy grazing or browsing. Rather than a high physiological tolerance to browsing, or low palatability relative to other willows, the habit of mature *Salix bebbiana* to form a tree-like trunk allows this species to be relatively tolerant of long-term grazing. The large trunk of mature plants is a relatively resistant to the physical impact (rubbing) of cattle and protects foliage above the browsing line. In contrast, willows such as *Salix geyeriana*, *S. boothii*, *S. drummondiana* which characteristically have clumps of many small diameter stems to support the plant's canopy are more easily bent and broken by the gradual effect of livestock rubbing and trampling woody vegetation. Mature *Populus* spp. (aspen and cottonwood) also share the same physical protection from physical trampling/rubbing and browsing.

Based on its relatively poor colonizing ability, *Salix bebbiana* is a poor choice as the main shrub component in stream restoration projects if rapid colonization and stabilization of streambanks is required. Other willow species such as *Salix boothii*, *Salix exigua*, *Salix geyeriana*, *Salix drummondiana*, and *Salix lutea* might be better choices since these species seem to produce more ramets and genets. Nonetheless *Salix bebbiana* is potentially valuable in restoration projects, in moderate quantities, because of its long-term resiliency and vigorous capacity to stump sprout once tall tree-like plants are established.

Future studies could attempt to quantify many of my observations, or apply similar approaches to other willow species. For example little is known about the actual distances rhizomes can extend from a parent willow. More thorough excavations of rhizomes systems could be valuable in determining distances from parent plants, and establishing whether the parental connection helps willows establish in more difficult conditions. Schier's (1974) hypothesis on apical inhibition of suckering in *Populus tremuloides* might be tested on *Salix bebbiana*, or other species. I suggest one of the following experimental approaches: controlled burns of decadent stands; clipping terminal buds; or sawing older main trunks of individual plants - followed by monitoring of re-sprouting ability.

Regarding discrimination, controlled "cafeteria type" studies could test hypotheses relating to intraspecific willow browse use by ungulates. Such studies could measure cattle utilization of nursery-grown shrub species placed systematically in fenced cattle paddocks. Preferentially browsed species such as dogwood, or species avoided, such as spruce and alder could be used as controls and their utilization could be compared to several willow species. Additionally, a palette of field-planted shrub species could be monitored in locations to observe patterns of native ungulate willow utilization.

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APPENDIX I GLOSSARY

Bankfull Area - That area of a stream channel inundated by a flow that fills the channel to the top of its banks and where water begins to overflow into a floodplain (Rosgen 1983).

Browsing - The process of wildlife consuming shrubby and woody forage.

Community Type - An aggregation of all plant communities distinguished by floristic and structural similarities in both understory and overgrowth layers. A unit of vegetation within a classification (Youngblood and others 1985).

Coppicing - A method of pruning or timber harvesting that involves the production of new trees and shrubs from old stumps that is sometimes used to provide bioengineered slope stabilization (Gray and Sotir 1996).

Discrimination - Differential utilization of one or more shrub species over another shrub species.

Floodprone Area - That area of a stream channel inundated by the two-year recurrence interval flood flow (Rosgen 1983).

Genet - A type of regeneration occurring from seed. Genets are considered sexual reproduction.

Ortet - A type of regeneration occurring from sprouts at the base of a mature stem or "stump". Ortets are considered asexual reproduction.

Palatability - Factors inherent to a plant species that elicit an animal's selective response (Heischmidt and Stutz 1991).

Ramet - A type of regeneration occurring from underground rhizomes that are connected and genetically similar to a parent plant. A form of asexual reproduction.

Utilization - The proportion of available browsed to unbrowsed twigs on a shrub browsed by domestic or native ungulates.

APPENDIX II STUDY SITE LOCATIONS

Blackfoot River; Bureau of Land Management, west of Lincoln, Montana
All sites located along Blackfoot River

Idaho; Bureau of Land Management

Big Butte Resource Area near Howe, Idaho

Big Creek

Breck Creek

Deer Creek

East Fork Bear Creek

Fallert Creek

Horse Creek

Newman Creek

Pass Creek

Sands Creek

Squaw Creek

Williams Creek

Trail Creek

Wet Creek - 2 plots with livestock enclosures

Medicine Lodge Resource Area, near Dubois, Idaho

Cabin Creek

East Indian Creek

Pocatello Resource Area, near Pocatello, Idaho

Moonlight Creek

Red Rocks National Wildlife, Montana

Bear Creek

Un-named creek, one drainage east of Curry Creek

Curry Creek

Red Rock Creek

Meadow, 1 mile east of Red Rock Lake campground; north side of road
Meadows near east end Upper Red Rock Lake

Headwaters: Bureau of Land Management, near Dillon, Montana

Bigfoot Creek

Hay Canyon

High Acre Creek

Tributary to Kilborn Canyon

Tributary to Noble Creek

Tributary to Rocky Canyon

State Creek

Timber Gulch

Whitetail Creek