

WILLOW RESILIENCE ON YELLOWSTONE'S NORTHERN
ELK WINTER RANGE: A FUNCTION OF
ENVIRONMENTAL GRADIENTS

by

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A thesis submitted in partial fulfillment
of the requirements for the degree

of

Master of Science

in

Land Rehabilitation

MONTANA STATE UNIVERSITY
Bozeman, Montana

April 2005

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ACKNOWLEDGEMENTS

This project was partially supported by NSF Grant # 6113839-0216588, Biocomplexity: Complexity Across Boundaries - Coupled Human and Natural Systems in the Yellowstone Northern Elk Winter Range.

Foremost, I would like to thank my major professor and this Biocomplexity research group for allowing me to be a part of this project, as it was truly an eventful journey and at times a test of endurance. While numerous individuals helped with this research and thesis, there are a few I would like to specifically acknowledge.

- Duncan: For your mentorship, friendship, patience, and encouragement!.. Thank you for the endless hours spent planning, setting up sites, in the field, and offering guidance.
- Brian and Cathy: For your support, advice, and insightful comments.
- Yellowstone National Park, Gallatin National Forest, and Shoshone National Forest
- Jessie, Amanda, and Levia: For your hard work, and friendship.
- My family: For all your encouragement, confidence, and time. Especially helping collect winter measurements and surveying.
- Denine: For your help in the field, advice, friendship, and computer assistance.
- Thank you for auguring soil cores in the rain, making slurry, hauling 50 pound sand bags uphill, taking photos, pounding in well points, for side-stepping bison and wolves to get data, and tagging and retagging plants. I enjoyed working with all of you.

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ABSTRACT

Willow, a deciduous, woody shrub, is a characteristic and often dominant riparian species (Amlin and Rood 2002) that has been unable to successfully regenerate throughout much of its western range, and Yellowstone National Park (YNP) is no exception (Singer et al. 1994, NRC 2002a). The primary objective of this study was to understand growth and maintenance of established willow stands as a community and as individual species following winter browse. These were based on the premises that (1) different levels of herbivory produce varying levels of compensatory growth (Brookshire et al. 2002), (2) different channel types provide diverse hydrologic conditions for vegetation establishment and maintenance (Patten 1998, Castelli et al. 2000), (3) riparian biodiversity is a function of fluvial dynamics and is increased by the degree of hydrologic connectivity of the system (Amoros and Bornette 2002), and (4) the possibility of willow species being either generalist (showing water source shifts) or specialist (availability doesn't influence water source) (Dawson and Ehleringer 1991, Busch et al. 1992, Schwinning and Ehleringer 2001). Site selection and design, and sampling scheme were designed to evaluate biophysical gradients both within and between sites over time. Gradients of biophysical parameters were quantified throughout the growing season. Regressions were used to identify relationships among physical and biological parameters or characteristics. Vegetative communities were compared using Sorenson's similarity index. Ecosystem functions that influence willow presence on the Northern Range include establishment, browse pressure, and maintenance and resilience or their ability to recover. Establishment of willow was a result of availability of their preferred water source while winter decline was a function of location and herbivore preferential selection. Maintenance and resilience were dominated by soil water use in the early season and groundwater use later in the season but with distinct variations between hydrologic systems. Nutrient availability and hyporheic connectivity, essential to dispersing those nutrients among the plant communities, also may influence growth and resilience of willow plants. However, excess or even "acceptable" levels of only one of the physical factors was not enough alone to control dominant plant growth and response to herbivory.

INTRODUCTION

Biocomplexity Background

The Northern Elk Winter Range (NEWR) extends from within the northern portion of Yellowstone National Park (YNP) into Montana Fish Wildlife and Parks land, Forest Service land, and privately owned lands in Paradise Valley (McGinnis and Bennett 2001). Throughout this area, there are increasing human encroachment and land ownership changes. As a consequence, the seasonal migration patterns of and vegetation utilization by resident elk herds are being influenced through diverse personal values and land management decisions (NRC 2002a).

According to scientific literature and local residents, there is evidence of progressive decline in both willow and aspen populations (Singer et al. 1994, NRC 2002a). Causes of the degradation are considered to be a combination of local and regional activities in human and natural systems. Understanding the complexity of this integrated system is the basis for a National Science Foundation biocomplexity project.

The study *Complexity Across Boundaries – Coupled Human and Natural Systems in the Yellowstone Northern Elk Winter Range* (NSF#: 6113839-0216588) is an interdisciplinary research project that integrates the biophysical sciences, social sciences, and information science in an effort to couple the human and natural systems through integrative models (McGinnis and Bennett 2001). A goal of this biocomplexity project is to better understand the relationship between human decision-making and ecosystem dynamics in order to construct a modeling framework that captures the complexity of the

system and aids in the development of future management scenarios (Figure 1) (McGinnis and Bennett 2001).

The model explained below can be separated into four submodel components.

(1) Elk-Wolf Model: model conditions that affect winter feeding habits, (2) Climate & Snow Model: map and model snow depth and conditions based on a set of climatic parameters, (3) Vegetation Model: models the resiliency of willow and aspen to temporal and spatial gradients of browse and water availability, and (4) Human Model: interview stakeholders in the area in order to develop models relevant to the study in a socio-political context.

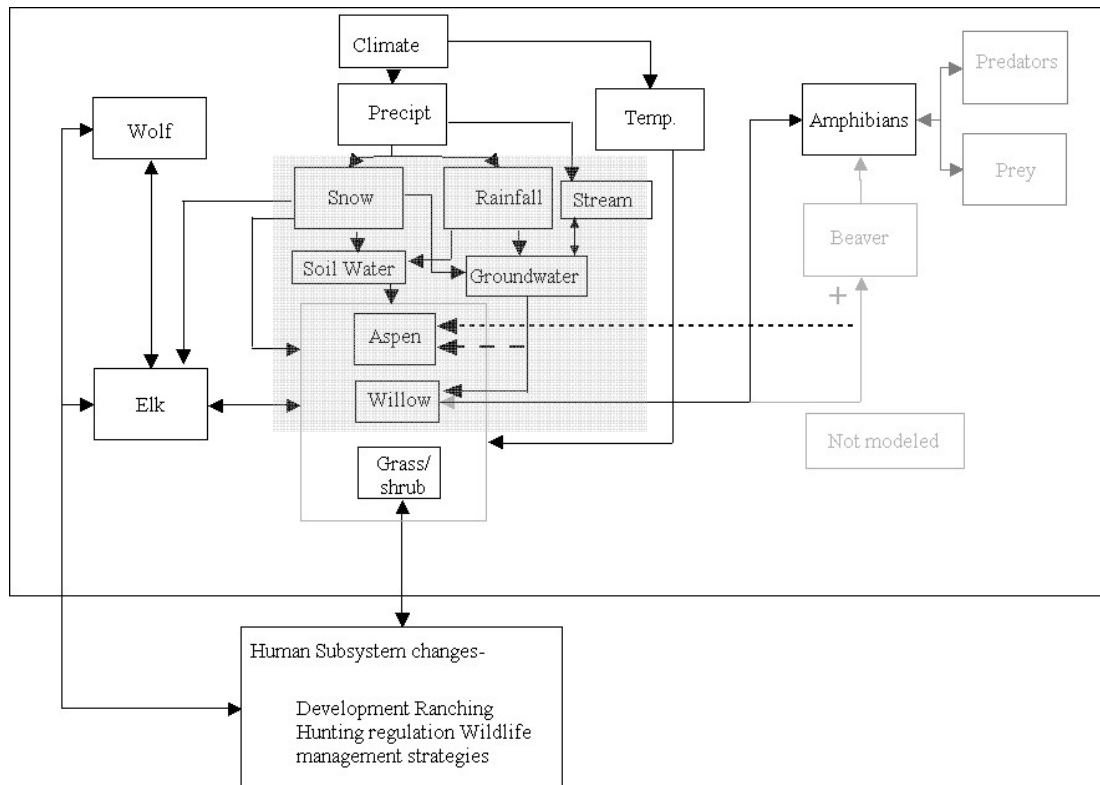


Figure 1: Biocomplexity model being used to integrate the human and natural systems in the NSF Biocomplexity project (McGinnis and Bennett 2001). The vegetation model is highlighted in gray.

The overlap between models is captured in the vegetation model which not only is the main integrator of the biocomplexity study but the primary focus of this research project. For this thesis only the willow (*Salix spp.*) component of the vegetation model will be discussed in relationship to the other system components.

Willow Introduction

Riparian communities provide fundamental ecological functions and values (Johnson et al. 1985, Koehler and Thomas 2000, Beschta 2003) with woody vegetation being key to these processes (Brookshire et al. 2002). These systems provide streambank stability, hydraulic resistance during overbank flows, and enhance organic matter deposition. They buffer water temperatures from extremes, influence nutrient transformation, storage, and cycling (Beschta et al. 1987, Rutherford 1999, Beschta 2003), water quality, and provide wildlife habitat (Castelli et al. 2000).

Willow, a deciduous, woody shrub, is a characteristic and often dominant riparian species in western North America (Amlin and Rood 2002). However, through most of the West, for much of the past century, not only has it been unable to regenerate successfully, but existing stands have been declining (Romme et al. 1995, Kay 1997, Brookshire et al. 2002, Zeigenfuss et al. 2002, Larsen and Ripple 2003, Ripple and Beschta 2003).

Yellowstone National Park (YNP) is no exception, as there has been a noted decline in willow abundance, distribution, and stature on the Northern Elk Winter Range (NEWR) over the past century with the most dramatic declines occurring between the

1920's and 1940's. Four percent of the 800 km² NEWR is dominated by willow communities that include Geyer willow (*Salix geyeriana*), Bebb willow (*Salix bebbiana*), false mountain willow (*Salix pseudomonticola*), Booth willow (*Salix boothii*), Wolf's willow (*Salix wolfii*), and narrow-leafed willows like sandbar willow (*Salix exigua nutt.*) (Singer et al. 1994). The diminished growth and establishment of willows has been attributed to both biophysical and human factors (Chadde and Kay 1996, Beschta 2003). For example, some scientists believe the decline to be a result of climate change or changes in weather patterns and seasonal precipitation (Singer et al. 1994, Romme et al. 1997, Beschta 2003) while others argue that climate alone isn't sufficient to have influenced this species (Wagner et al. 1995, Chadde and Kay 1996, Kay 1997, Ripple and Larsen 2000, Larsen and Ripple 2003). Other suggested mechanisms deterring willow sustainability are fire suppression, overgrazing (predominantly during winter months), natural plant community dynamics, declines in beaver and therefore declining water tables, and reduced secondary compounds from chronic browsing (Singer et al. 1994, Wagner et al. 1995, Ripple and Beschta 2003).

However, given the potential physical and biological factors causing suppression of these plants, they remain resilient and continue to add new growth each season. A review of what is known about willow structure and growth following winter herbivory, and how hydrologic regimes influence willow persistence has led to the pertinent questions about dynamics of willow communities.

Willow Water Sources

Willow species can be either obligate or facultative wetland species. Persistence of obligate riparian species along waterways is a function of both surface and groundwater regimes, while facultative species rely on unsaturated zone soil water (Patten 1998, Shafroth et al. 2000, Beschta 2003). While species differ in their tolerance for water table levels, magnitude of water table fluctuations relative to a previous groundwater depth, for example, in flood events, is more important to willow survival than water table depth (Casanova and Brock 2000, Shafroth et al. 2000). Willow habitat usually encompasses areas with multiple potential water sources. Early in the growing season, rooting zone water can come from high levels of snowmelt and early season precipitation. These result in increased availability of groundwater, soil moisture, and surface water for plant communities. However, as the growing season progresses, these water sources begin to diminish becoming less available to plants which must then adjust to other available water sources.

As the growing season progresses, plant communities access water from three main water sources riparian plants rely on throughout the growing season: alluvial groundwater, capillary fringe soil water, and unsaturated zone soil water (Shafroth et al. 2000). Busch et al. (1992) showed that some riparian plants exhibit shifts in water sources throughout the growing season from soil moisture, to surface runoff, to groundwater. Other studies show that some plants tend to utilize only specific water sources at certain times of the growing season, while others are more opportunistic and

use moisture whenever and wherever it's available (Dawson and Ehleringer 1991, Schwinning and Ehleringer 2001).

Willow and Compensatory Growth

Large herbivores have been blamed for the increased browse on both willow and aspen in the NEWR (Brookshire et al. 2002). Specifically elk (*Cervus canadensis*) are considered the primary forager on willow, although deer (*Odocoileus spp.*), antelope (*Antilocapra americana*), moose (*Alces alces*), and in some instances bison (*Bison bison*) may also utilize willow. Browsing decreases aboveground biomass, altering the stature of the plant and thereby its photosynthetic gains and reproductive capabilities. Browsing has also been shown to stimulate lateral and adventitious buds below the browse level, resulting in rapid, compensatory growth. However, in situations where browsing is chronic for woody plants, such as in the NEWR, belowground carbon reserves are depleted, limiting the plants ability to produce secondary chemicals (Brookshire et al. 2002). The decline in secondary chemicals is thought to aid in perpetuating the browse, as the plants are then preferentially sought out by herbivores (Singer et al. 1994, Wagner et al. 1995, Brookshire et al. 2002). This type of browsing produces long-term growth suppression and reduces the compensatory response (Brookshire et al. 2002).

Riparian Zone Hydrologic Regimes

Different hydrologic systems produce different flow regimes and consequently variation between the physical and biological environments of each. (Baker 1990).

Hydrologic characteristics of a site can alter soil moisture availability as well as soil morphology, and physical and chemical properties, and in effect, the distribution of plant species (Castelli et al. 2000). Riparian systems are generally influenced by surface water, groundwater, and the hyporheic zone, which mediates the exchanges (e.g., water mass transfer, nutrients, organic matter, and nutrient transformations) that occur between the two on spatial (i.e., longitudinal, lateral, vertical (e.g., surface, groundwater, aquifer)), and temporal (e.g., annual and historical) scales (Brunke and Gonser 1997, Amoros and Bornette 2002). This hyporheic connectivity can occur for up to 3 kilometers from the main channel; however, the size of the zone varies based on channel type (Boulton et al. 1998). Increased connectivity increases dissolved nutrient availability in both water and soil substrates (Amoros and Bornette 2002). The most developed hyporheic zones occur in intermediate reaches, are less developed in lowland rivers, and are least developed in headwater streams (Boulton et al. 1998). It is well known that groundwater influences riparian vegetation composition, but less is known about how groundwater affects riparian ecosystem function (Busch et al. 1992). Riparian biodiversity is a function of fluvial dynamics and is increased by the degree of hydrologic connectivity of the system (Amoros and Bornette 2002).

Objectives

Of particular importance to this study was understanding the growth and maintenance of existing willow stands following winter browsing. Given that different levels of herbivory produce varying levels of compensatory growth, that different channel

types provide different hydrologic conditions for vegetation establishment and maintenance (Patten 1998), and the possibility of willow species being either generalist or specialist in terms of utilization of different water sources, this study has four main objectives. The objectives are to determine, for individual willow communities and particular species within each community (1) whether growth is a function of plant stature at the beginning of each growing season; (2) whether growth is a function of plant water stress, and if so is that water stress related to degrees of water availability; and (3) whether growth is influenced by a particular water source or sources throughout the growing season, and if so, is that source again related to water availability, and (4) how water availability varies between hydrologic systems.

STUDY AREA

Site Descriptions

The study area was within the Greater Yellowstone Ecosystem (GYE) (Figure 2). Four sites were selected: Upper Eagle Creek, Lower Eagle Creek, Crystal Creek, and Sunlight Creek. Three sites were within the NEWR (Figure 3) while one was in the northern part of the Shoshone National Forest, east of YNP. While Upper and Lower Eagle Creek are within the NEWR, they are also on the Gallatin National Forest, north of the Park (Figure 2).

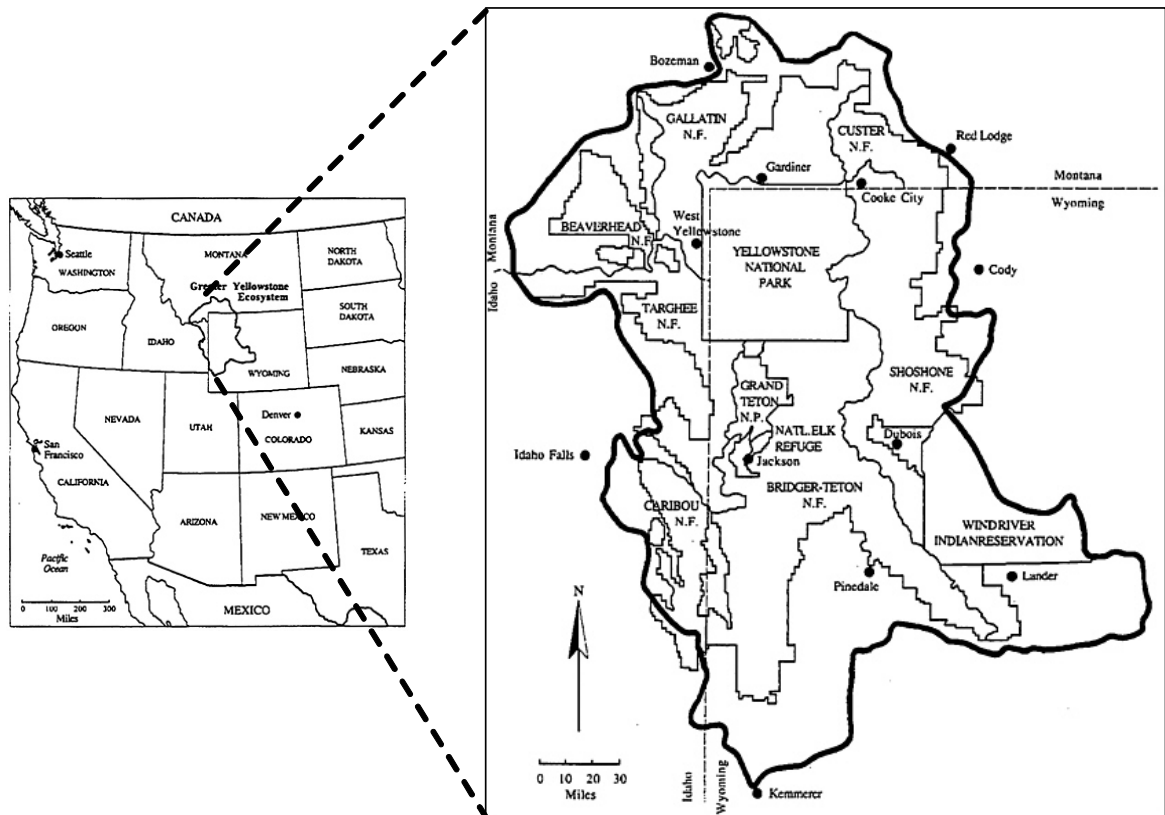


Figure 2: The Greater Yellowstone Ecosystem; figure adapted from Figure 1.1 (Clark et al. 1999). Permissions obtained from Yale University Press 2004.



Figure 3: Yellowstone's NWR outlined in dark gray. Approximate site locations designated with diamond shape (Arthur 2004). Permissions obtained from Montana State University 2004.

Each site is distinctive in its geology, hydrology, and vegetation, although, the surficial geology of all four is largely the result of glacial recession processes. The surficial geology for Upper and Lower Eagle Creek and Crystal Creek is within the Pinedale Formation. Precipitation and average temperatures for each site are slightly different with the Eagle Creek sites having the highest average annual and seasonal temperatures throughout the study period. Crystal had the highest average annual precipitation (16.41 cm), and Eagle Creek (Upper and Lower) the lowest (10.05 cm). Seasonally Eagle Creek sites had the most precipitation in 2003, and Crystal Creek the most in 2004 (Table 1).

Table 1: Annual and growing season precipitation and temperature data. Annual data is compiled from 1971 to 2000, and the seasonal data is from May to August during both study years (NOAA 2003b, a, WRCC 2005). * symbolizes that between one and nine observations were missing from the data. English units for both precipitation and temperature are italicized below metric units in inches and Fahrenheit respectively.

| Climate Characteristics | Site | | |
|--|-------------------------|-------------------------|--------------------------|
| | Upper/Lower Eagle | Crystal | Sunlight |
| Average annual precipitation (cm) | 25.53 <i>(10.05)</i> | 41.69 <i>(16.41)</i> | 38.03# <i>(14.97)</i> |
| Average annual temperature (°C) | 2.63 <i>(45.30)</i> | 2.07 <i>(35.60)</i> | 2.43* <i>(41.90)</i> |
| Average 2003 growing season precipitation (cm) | 2.71 <i>(6.88)</i> | 2.33 <i>(5.92)</i> | 2.34 <i>(5.94)</i> |
| Average 2003 growing season temperature (°C) | 3.82 <i>(65.78)</i> | 3.16 <i>(54.41)</i> | 3.35 <i>(57.69)</i> |
| Average 2004 growing season precipitation (cm) | 3.78 <i>(9.60)</i> | 4.39 <i>(11.15)</i> | 3.62 <i>(9.19)</i> |
| Average 2004 growing season temperature (°C) | 3.47 <i>(59.75)</i> | 2.96 <i>(50.97)</i> | 3.09 <i>(53.21)</i> |
| <i>Station index number</i> | <i>3378</i> | <i>9025</i> | <i>8722</i> |
| | | | <i>Sunlight Basin</i> |
| <i>Station Name</i> | <i>Gardiner</i> | <i>Tower Falls</i> | <i>Crandall (#)</i> |

Upper Eagle Creek, located at 45°03'14"N and 110°40'49"W, is an unnamed spring-fed creek that drains into Eagle Creek. Early in the season, soils are saturated, and the ground surface has intermittent surface saturation. It is a first order stream (Horton 1945). Within the study reach, average maximum stage and bankfull width were 0.04 cm and 4.0 mm. The valley segment type could be classified between a v-shaped moderate-gradient bottom and an alluviated mountain valley (Naiman 1998). The dominant willow at this site is Bebb willow, but Geyer willow is also present. The dominant understory vegetation is graminoid and forb species. Surficial geology of this site is on Kame, well sorted gravels, generally 5-10 cm (2-4 in) in diameter deposited by ice-margined streams.

This deposit is about 30 m (100 ft) deep (Pierce 1973). Bedrock geology consists of Holocene alluvium and some Pleistocene outwash (Fraser et al. 1969).

Lower Eagle Creek (Eagle Creek proper) is located at 45°02'47"N and 110°40'45"W and drains into the Yellowstone River. This channel has beaver (*Castor canadensis*) activity and the study reach has a string of ponds and small side channels. Early in the season, the study area soils were generally saturated and frequently subject to overbank flows. Standing water often occurred in areas throughout the site. It is a third order stream within our study reach, according to the Horton (1945) classification method, and has an average maximum stage and approximate bankful width of 0.13 m and 10 m. The valley segment type is most like an alluviated lowland type (Naiman 1998). Dominant overstory vegetation within the site is composed of Alder (*Alnus glutinosa*) and Bebb willow with both Geyer and sandbar willow also present. The most prevalent understory species are graminoids and forbs. Surficial geology is till with an unsorted, nonstratified compact mixture of rounded stones, sand, silt, and clay and is approximately nine meters (30 ft) thick (Pierce 1973). The bedrock geology consists of glacial deposits of undifferentiated till and glacio-fluvial deposits (Fraser et al. 1969).

Crystal Creek (44°54'19"N and 110°19'13"W) is a tributary of the Lamar River, and according to the Horton classification, a second order stream at the study site (1945). It is in a v-shaped, moderate-gradient valley segment (Naiman 1998), and the average maximum stage is 0.11 m with the average bankful width 1.50 m. Bebb willow is the most common overstory species with Booth and Geyer willows also present, and graminoid and forb species characterizing the understory. Surficial geology is glacial till

with compact rounded stones, sand, silt, and clay and is about nine meters (30 ft) deep. The site is situated just below the Junction Butte ice margin (Pierce 1974) along the border of two bedrock geologies. The northern geology is glacial deposits while the southern geology is the main body of the Sepulcher formation. This formation is composed of volcanic breccia, conglomerate, sandstone, and tuffs. Precambrian metamorphic rocks as well as fossil trees and leaves can also be found in some horizons (Prostka et al. 1975).

The Sunlight Creek site, located at 44°41'46"N and 109°36'47"W, drains into the Clarks Fork of the Yellowstone, and at the study site is a third order stream (Horton 1945). The valley type is most like an alluviated mountain valley (Naiman 1998), and the average maximum stage and bankful width are 0.46 m (1.5 ft) and 12 m (39.4 ft). Booth willow is the dominant overstory species, although both Drummond and Geyer willow are also present. Again, graminoid and forb species make up the majority of the understory vegetation. Surficial geology is unconsolidated alluvium consisting of sand, silt, and gravels within this floodplain. (Pierce et al. 1982), and is part of the Absaroka Volcanic Supergroup (Meyer 2001).

Study Site Selection.

Each of the four study sites was selected, within the study areas described above, based on objectives of the biocomplexity project and the individual goals of this submodel research project. Willow sites were selected based on having the following parameters: willow, wolves, elk, a stream channel or identifiable water source, topography that would collect snow, and potential or actual human impacts. The area also

had to be within elk winter range (predominantly Yellowstone's Northern Elk Winter Range). Four sites were selected, three in the NEWR and one in a GYA winter range east of the NEWR (Figure 4, Figure 5, Figure 6, and Figure 7) (NPS 1997).

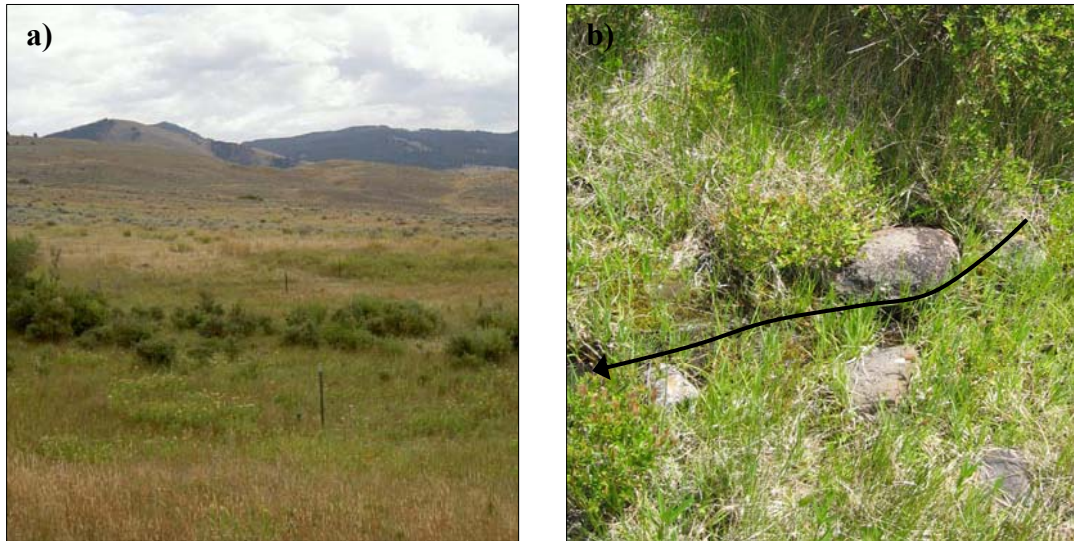


Figure 4: Upper Eagle Creek a) landscape view and b) stream channel.

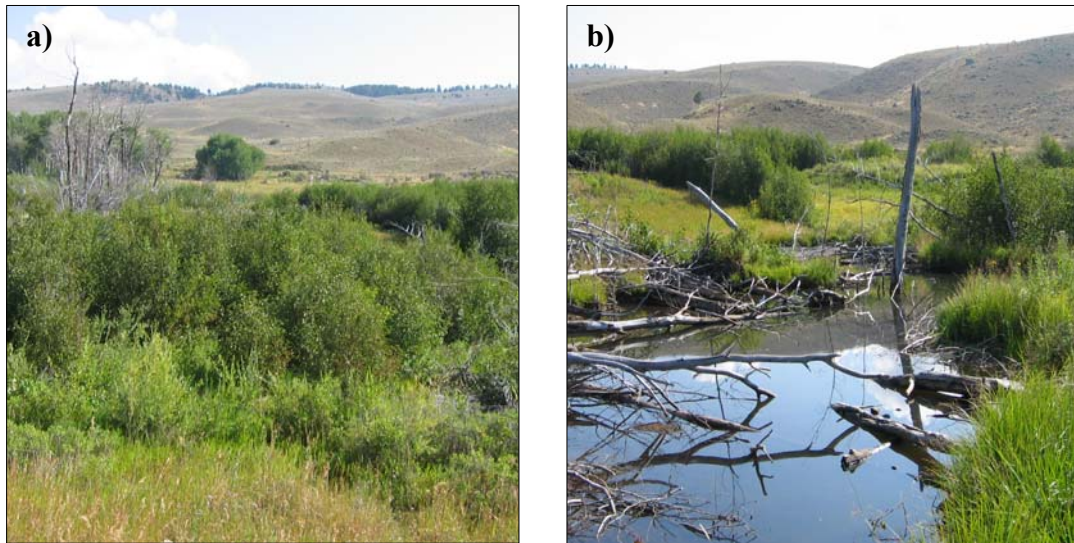


Figure 5: Lower Eagle Creek a) landscaped view and b) stream channel with beaver ponds.



Figure 6: Crystal Creek a) landscape view and b) stream channel.

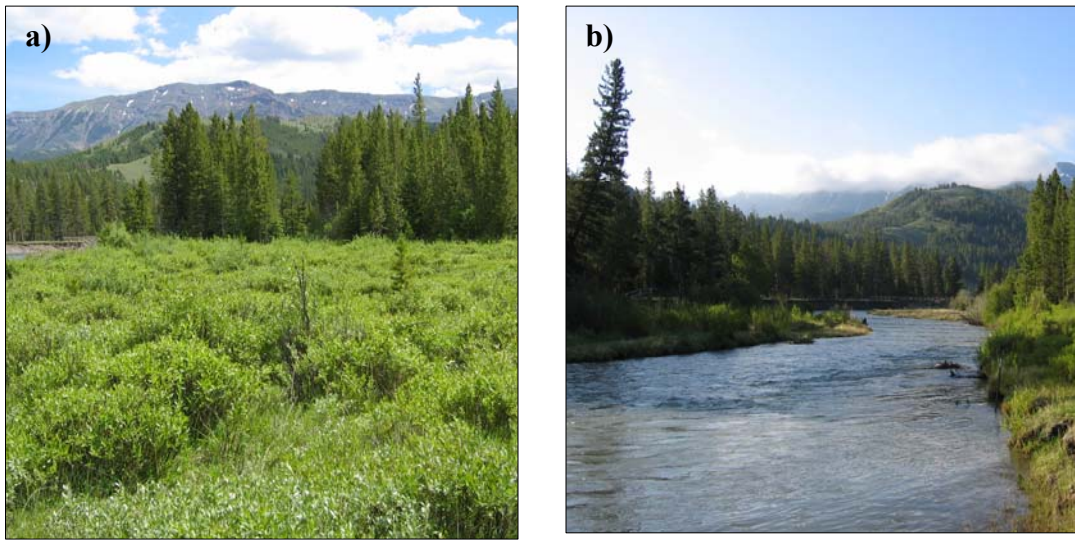


Figure 7: Sunlight Creek a) landscape view and b) stream channel.

METHODS

Data Collection

The study period was from June to September during 2003 and 2004. Preliminary data were collected in 2003, while more extensive, complete data sets were collected in 2004. On average, sample dates were every three weeks starting 1 June. Both site layout and sampling scheme were designed to be able to quantify gradients both within and between sites over time.

Two 5 meter wide belt transects were established at each site. Transects either started at the water source, went through the willow community and ended at the outer edge of the riparian zone or spanned the water source with at least one end at the riparian (defined as: phreatic vegetation, shallow groundwater, high soil moisture areas) outer edge. The research was conducted within a five meter belt perimeter for each transect. Plant community characteristics, biologic attributes, and physical properties were collected for each site (Table 2, Figure 8, Figure 9, Figure 10, and Figure 11).

Table 2: Biotic and physical parameters measured for use in entire biocomplexity vegetation study. Asterisked parameters were used to answer the questions relative to this research.

| <u>BIOTIC</u> | <u>PHYSICAL</u> |
|---|---------------------------------|
| Plant height* | Depth to water table* |
| Plant width on two axis | Relative percent soil moisture* |
| Plant volume | Soil texture* |
| Individual plant stem length | Soil nutrients* |
| Individual plant stem base diameter | Stream stage* |
| Individual plant stem tip diameter | Snow depth |
| Predawn water potential (ψ_{pre})* | Snow water equivalent (SWE) |
| Midday water potential (ψ_{mid})* | Isotopes* |
| Percent browse | |
| Water source* | |

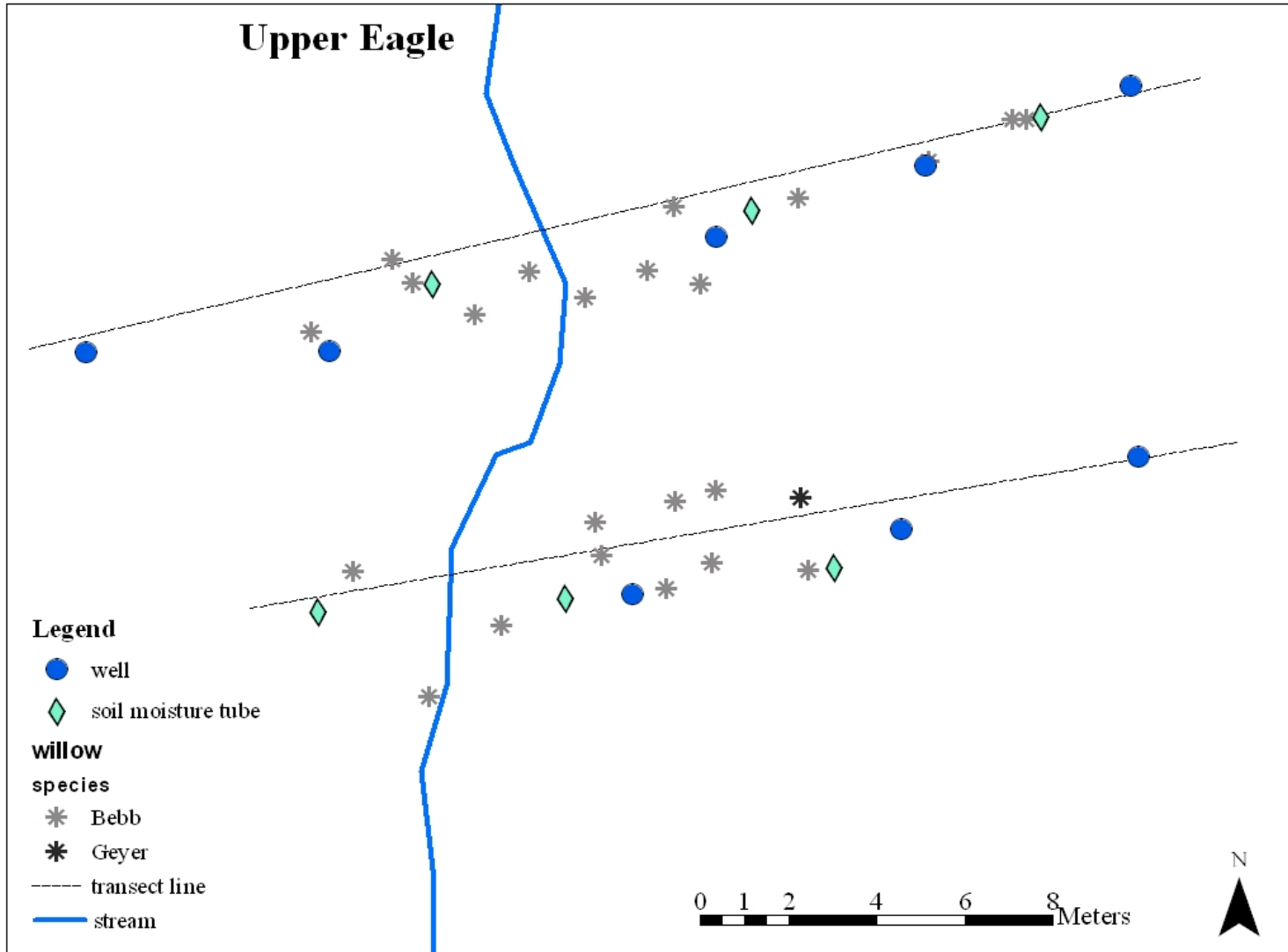


Figure 8: Upper Eagle general site layout

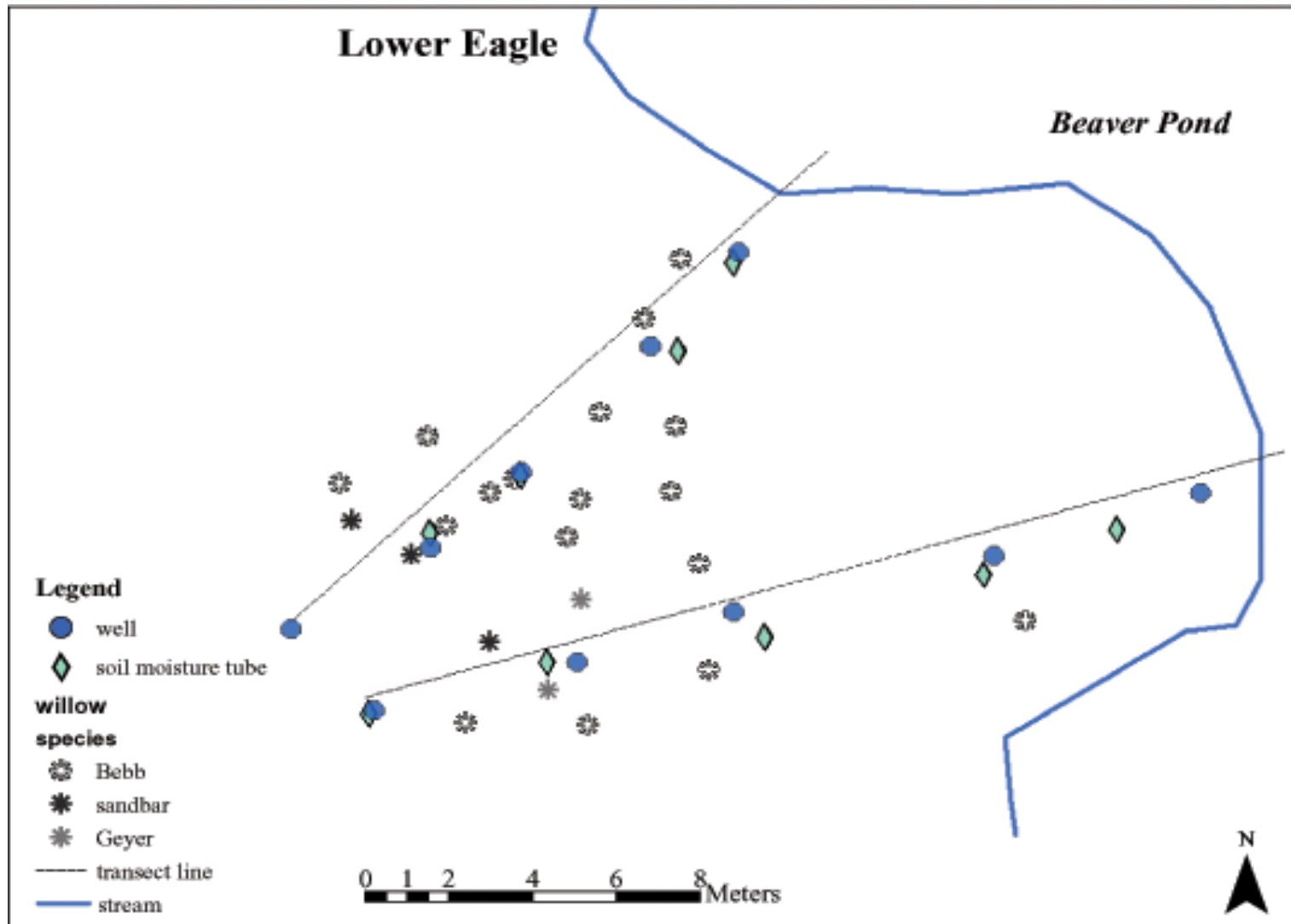


Figure 9: Lower Eagle general site layout.

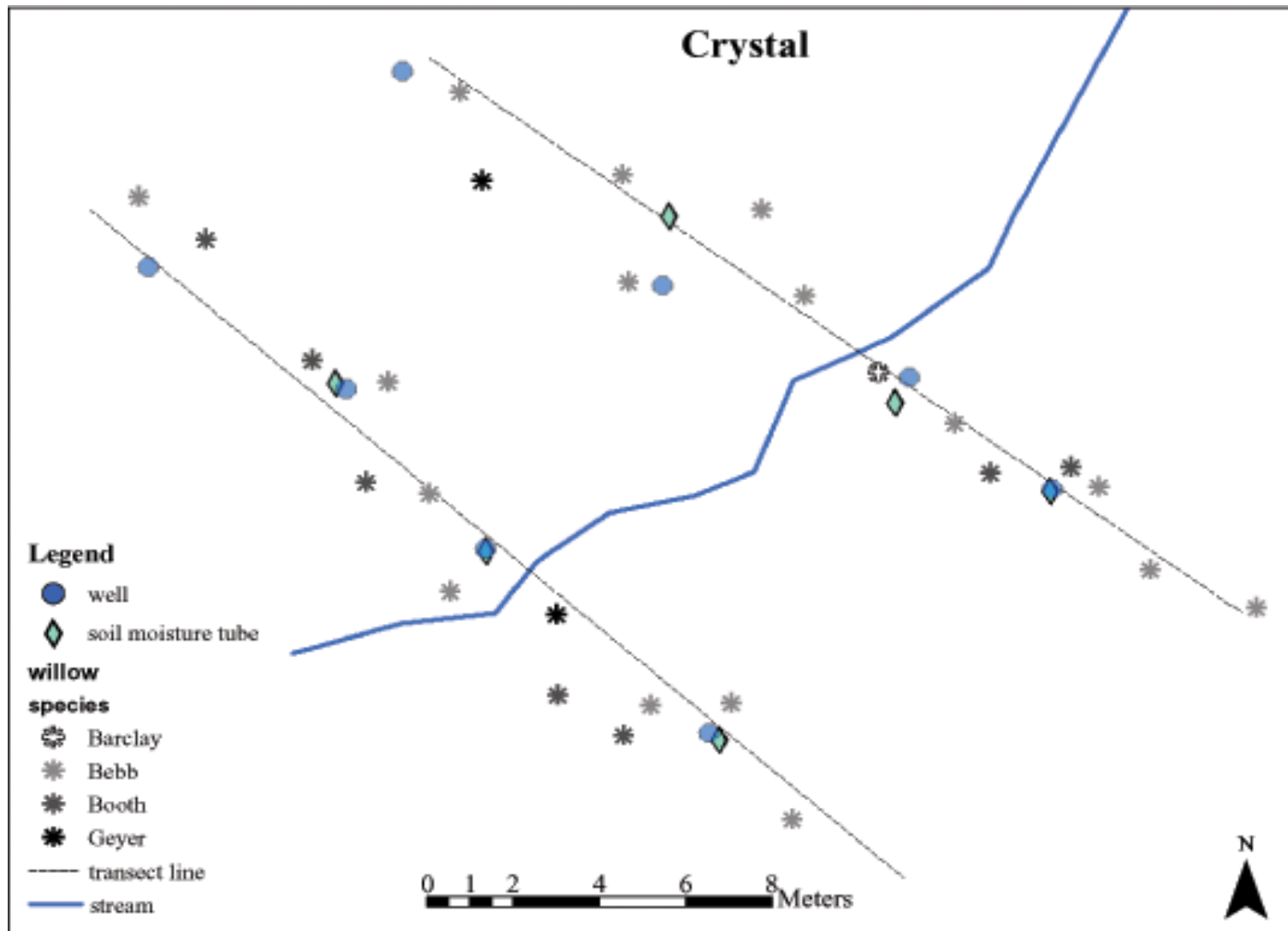


Figure 10: Crystal general site layout.

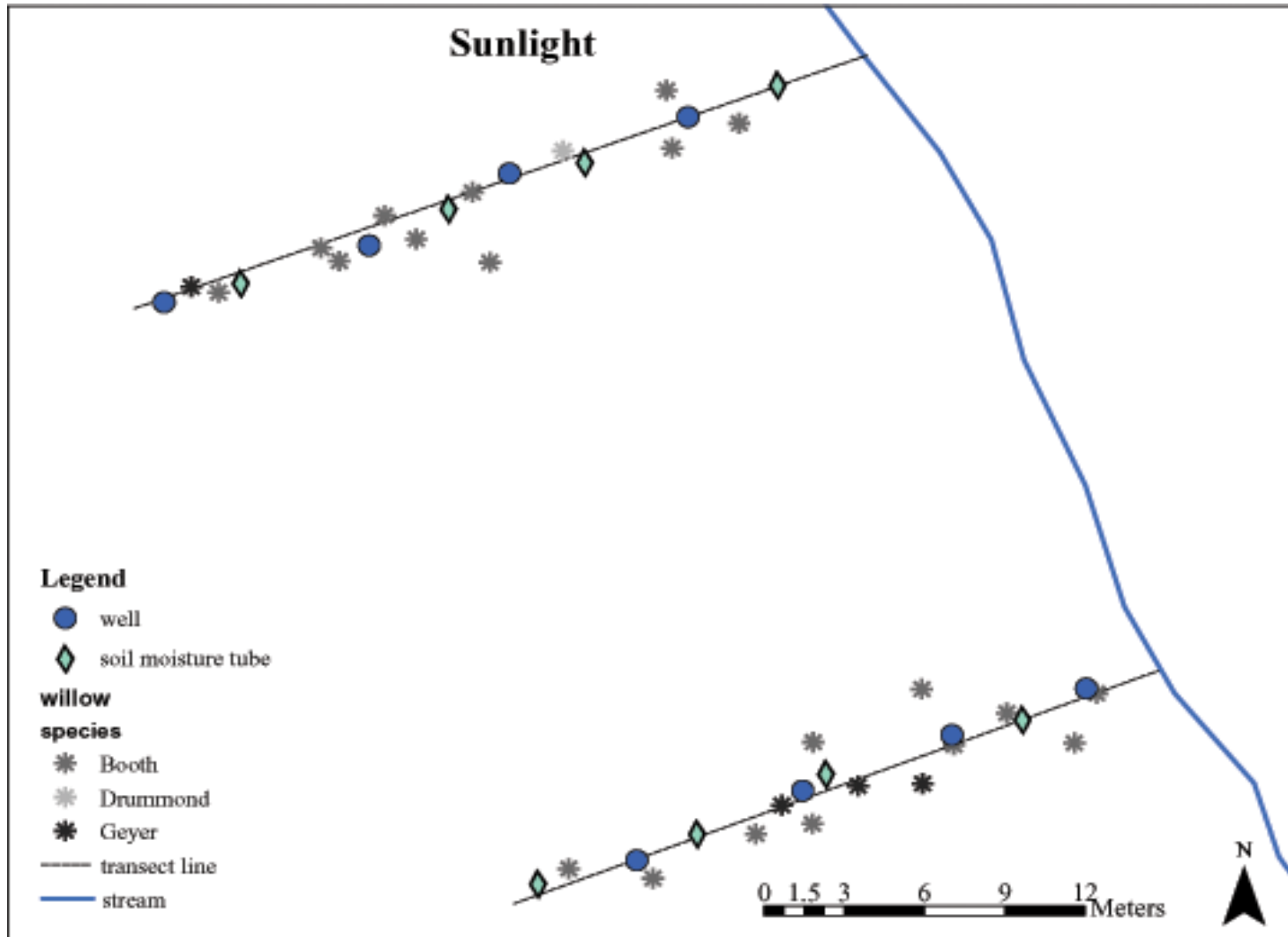


Figure 11: Sunlight general site layout.

Plant Community Characterization

To analyze the entire willow community, transects were divided into three sections, and within each section, at least one of every willow species was permanently marked with a numbered metal tag. An average of 12 plants were tagged per transect. Willow species were identified both in the field and verified by the Montana State University Herbarium¹ using collected, pressed stem and catkin samples. Community cover was determined for each transect segment using areal cover estimates (total = 100%) and total cover estimates (total \geq 100%).

Biologic Attributes

Willow height was used to quantify growth. On the first visit of each growing season, the maximum height of what remained of the previous year's growth was measured to show how much terminal growth from the previous season existed following winter browse. This metric was called "previous year's growth". On every visit, the maximum height of each plant was measured. From this, a daily growth rate was calculated for the period between each measurement date, and is referred to as "growth rate". A growth ratio was also calculated based on the end of season height of the plant relative to its previous year's growth starting height.

Plant water potential (total water potential) was used as an indicator for plant water stress. Predawn ψ_{pd} and midday ψ_{md} water potential readings were taken with a Scholander pressure chamber (Alstad et al. 1999, Cochard et al. 2001) to represent the water stress following rehydration (ψ_{pd} or minimum stress or increasing ψ) and a time of

¹ Plant species verification by Montana State University Herbarium Collection Manager, Cathy Seibert.

day when the plant is actively transpiring (ψ_{md} or maximum water stress or decreasing ψ) (Stromberg et al. 1993). Three plants per transect section were randomly selected (18 plants per site). For both times of day, two new growth shoots were again randomly chosen and clipped. Plant cuttings were immediately placed in plastic bags and kept in a cooler. Water potential measurements were collected within 20 minutes of harvesting.

Physical Properties

Stream stage measurements were collected for each transect. When the deepest part of the channel could not be reached, this measurement was collected at a permanent marker (T-post) along the channel edge. Groundwater monitoring wells were installed at approximately 5 meter intervals along transect lines (Figure 8, Figure 9, Figure 10, and Figure 11). Wells were approximately five cm (2 in) diameter, slotted PVC pipe. Well holes were hand augured, the monitoring wells were put in place, and sterilized sand was poured around the pipe to prevent fine sediments from blocking the perforations. In instances, where gravel soils prevented use of an augur, sandpoints (screened for the lower 75 cm (2.5 ft)) were driven into the ground. While sandpoints are considered piezometers, stream depth and other water levels were used to estimate the appropriate installation depth so water fluctuations would fall within the screened portion. The sandpoints therefore acted as monitoring wells instead of piezometers. Stage and groundwater measurements provided a means to map summer season flow paths.

Soil moisture tubes (AquaPro) were used to measure percent soil moisture at a maximum of six depths (approximately 15, 25, 30, 45, 60, and 75 cm. or 6.0, 9.8, 11.8, 17.7, 23.6, 29.5 in). Holes were augured to 0.75 m (2.5 ft), the soil removed and made

into a slurry which was then poured back into the hole around the tube. Readings were percent soil moisture at saturation.

Composite soil samples at 5, 30, and 55 cm were collected at the beginning of the growing season for textural and nutrient analysis. Three composite samples for each depth were collected from each transect section. These samples were sent to MDS Harris Laboratories and analyzed for percent organic matter (%OM), total and available nitrogen (N_T and N) (organic and ammonia (NH_4)), phosphorus (P), and potassium (K). Organic matter was determined by loss on ignition, N by the cadmium reduction method, N_T by Kjeldahl Digestion, P by either Bray I or Olson extraction methods, and K by a modified Ammonium Acetate Method (Frack 2004).

Isotopic Study of Biological and Physical Parameters

Oxygen and hydrogen isotopes are ideal tracers of water sources because they are integral constituents of water molecules (Kendall and McDonnell 1998). As environmental isotopes, oxygen-18 ($\delta^{18}O$) and deuterium (δD) are used individually and in combination to determine water sources as one or a mixture of the following end members (for example): rainwater, snow water, stream water, groundwater, and soil water. Quantification of water sources is possible in many systems because summer rain and groundwater may have significantly different isotopic signatures because groundwater derived primarily from snowmelt water is isotopically depleted as compared to summer rain (Welker 2000). For instance, in the Northern Rocky Mountain region, snow melt water has $\delta^{18}O$ values of approximately -25 per mil while summer rain has values of approximately -5 to -10 per mil. (Ehleringer and Dawson 1992, Alstad et al.

1999). The magnitude of water sources is reflected in the ψ_{pd} of plants. Under water stress, the proportion of water from soil (rain) is greater than when plants have high water potentials and may be using a more reliable source of water, such as groundwater (Dawson and Ehleringer 1998).

At the Crystal Creek site, limited isotopic research was conducted along one transect to determine seasonal plant water source. In riparian communities, understanding plant water sources is complicated by the dynamic hydrology of alluvial systems. In certain instances trees use soil water even when groundwater is readily available. By using the stable isotopes of water, plant water source can be characterized (Busch et al. 1992). For this study, the environmental isotope oxygen-18 ($\delta^{18}\text{O}$) was used to determine willow water sources, and if only one isotope is being used, $\delta^{18}\text{O}$ is generally the better choice due to the complexity of laboratory analysis of deuterium ($\delta^2\text{H}$), which, in addition, is generally analyzed (Kendall and Caldwell 1998). Although snow and rainfall are also potential source waters, this study did not evaluate which source recharges ground, stream and soil water. Snowmelt and rainfall will either infiltrate into the vadose and phreatic zones or runoff directly into the stream incorporating their isotopic signatures with those of the three water sources most available for root uptake. Once water is extracted from soils by roots, it is in a continuous system to leaf surfaces (Busch et al. 1992), and no fractionation occurs during the transfer of water from the soil to the plant (Dawson and Ehleringer 1991, Brunel et al. 1995). Xylem water, therefore, can be used to identify which water source the plant is using (Busch et al. 1992, Brunel et al. 1995).

Three potential source waters were analyzed: soil water, stream water, and groundwater. Soil samples were collected in the early morning, while stream, groundwater, and plant samples were collected predawn in conjunction with water potential, hydrology, and soil moisture measurements.

Soil Water. Within each transect segment, and next to each soil moisture tube, three composite samples were taken at 30 and 60 cm to quantify the isotopic variability prevalent in riparian areas and slope bottoms (Genereux and Hooper 1998). Total water was measured, as this is an integrated value of water in soil, and is necessary to avoid fractionation between extracted water and water remaining in the soil or plant tissue (Revesz 1990).

Groundwater & Stream Water. Groundwater and stream water samples were collected from existing groundwater wells and nearby streams. Samples were collected in 7 ml scintillation vials. The vials were rinsed twice with the particular source water, filled, and sealed. Groundwater wells were drained the day before samples were collected to ensure that only recharge water was collected and not standing groundwater that had been subject to evaporation. A well pump was used to remove water from the wells. Stream water samples were taken by submerging the vial to half of the stream depth. Plant tissue samples from designated plants representing all willow species at the site were used. One sample of each willow species was collected, when present, within each transect segment. Five new growth samples, each approximately 10 cm long (4.0 in), were collected from the plant canopy and stripped of leaves. Tissue samples were put into glass vials and sealed. All samples were put on ice during transport from the

field and at the laboratory, plant and soil samples were frozen and water samples were kept refrigerated until analysis.

The composition of water is reported with reference to the Standard Mean Ocean Water (V-SMOW/V-SLAP), in parts per thousand. The definition for the stable isotope oxygen is noted in Equation 1 (Lamb 2000). Plant xylem water was extracted using a cryogenic vacuum distillation line (Dawson and Ehleringer 1991, Dodd et al. 1998) by cutting the stem segments into small units, placing them in vials, heating the vials and

$$\text{Equation 1: } \delta^{18}\text{O}_{\text{V-SMOW}}(\text{‰}) = \left(\frac{{}^{18}\text{O}/{}^{16}\text{O}_{\text{sample}}}{{}^{18}\text{O}/{}^{16}\text{O}_{\text{standard}}} - 1 \right) * 1000$$

trapping the water in adjacent vials submerged in liquid nitrogen under a vacuum of $\sim 10^{-3}$ torr. Liquid water samples were analyzed, and the values were reported relative to VSMOW (Kendall and Caldwell 1998).

Data Analysis

Figure 12 depicts the template for analyses used in this study. Growth was tested as a function of water availability, plant water stress, and plant stature. Water availability and water sources were compared with weather patterns, and plant water stress was analyzed as a function of water availability, plant height, and early season plant stature.

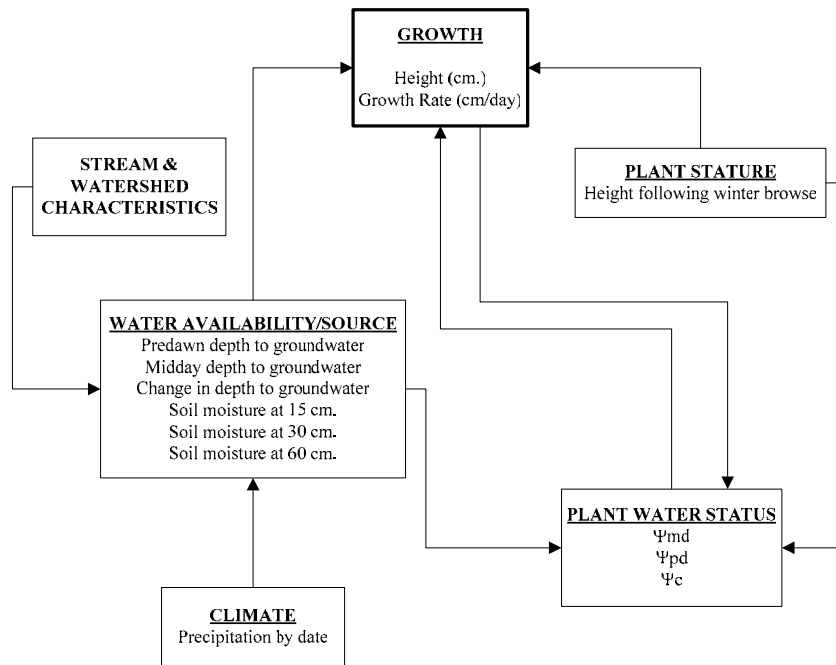


Figure 12: Diagram of relationships being analyzed.

Community characteristics or similarities between the different sites were characterized by calculating Sorensen's Coefficient of Similarity or Quotient of Similarity (Equation 2).

$$\text{Equation 2: } QS = (c/(a+b/2)) * 100$$

In the equation, QS is the similarity between two populations, a is the number of species in one population, b the number of species within another population, and c the number of species common to both, and the resultant is the percentagewise similarity of species between two populations in proportion to the similarity possible based on number of species preset (Sorenson 1948).

Two coefficients were calculated; one for the total number of species at each site and for only willow species.

Kruskal-Wallis tests were used, due to the nonparametric nature of the data, to test for physical and biological differences between willow groups at individual sites (Figure 12). Specifically, differences were compared between species relative to depth to groundwater, soil moisture, growth rate, height, and water potential at a site. Alpha levels were of 0.10 or less were accepted to determine significance. Kruskal-Wallis was not used at Upper Eagle, as only one species was abundant enough for analysis.

Simple linear regression was used to determine whether variation in height of the plant later in the season (dependent variable) was explained by plant stature of prior year's growth. Simple and multiple regressions were used to show the relationships between height, growth, water availability, plant water status, and plant stature (Figure 12). In most cases, height and growth rate were used as dependent variables. Prior to regressions, correlations between the parameters were established. All possible regressions were computed, however, similar parameter groups such as predawn and midday groundwater, water potentials, or soil moisture depths that were highly correlated were not used in the same regression analysis. Regressions were run for all willows at each site as a community and for individual willow species at each site. Regressions were considered significant based on the following criteria.

1. R^2 value must exceed 0.25
2. A p-value of ≤ 0.1 . Of those values meeting criteria one and two, the parameter with the smallest p-value was chosen.

3. If parameters have p-values of the same value, the one with the larger R^2 was chosen.
4. If p-values and R^2 were equal, both were accepted.

Isotope end member comparisons were used to determine water sources. Climate data from National Oceanic and Atmospheric Administration (NOAA) and the Western Regional Climate Center (WRCC) were used to determine whether precipitation prior to water measurements and collection of samples for isotopic analyses would explain any of the water availability and water source information.

Boxplots and means (crosshairs symbol) were used to analyze differences between species across dates for individual sites. Boxplots consist of a box and two whiskers. The box summarizes the shape, dispersion, and median of the data, and outliers are signified by an asterisk symbol. In addition, the box and whiskers represent the quartile ranges with 50% of the observations falling within the box itself (interquartile range). The whiskers indicate the highest and lowest values.

RESULTS

The study sites were quite variable in vegetation assemblages. We purposely selected sites with different hydrological settings and expected different vegetation and ecological processes. One common theme had to be that the sites included willow species and that there was evidence of browsing. The following results demonstrate the heterogeneity of the study sites and yet also show some similarities. The results first describe and compare biological attributes such as cover, growth, water potential and browse and then look at physical/chemical attributes such as climatic data, soil characteristics and groundwater at each site. Regression analyses are then used to discover relationships among biotic and physical factors.

Biologic Attributes

Vegetative Cover

Sunlight Creek had the highest cover percentage of willow, with a willow canopy so dense that few other species were able to grow in the understory. Upper Eagle had the highest cover percentages for graminoids and forbs and least for willows. Both Eagle sites had low cover percentages of willow, and higher percentages of graminoids, forbs, and other shrub and tree species (Table 3).

Willow species sampled within each transect are noted in Table 4. While percentages of each species were not counted within the aerial cover, the numbers of each are still representative of the willow cover for each site. Bebb willow was most dominant at all three sites within the NEWR while Sunlight, east of the Park, is dominated by Booth willow. Booth willow was found at both Crystal and Sunlight, Bebb willow at all but Sunlight, and Geyer's willow at all NEWR sites (Table 4).

Table 3: Total cover (in italics) and percent aerial cover for each study site. Trace (T) represents less than one percent of a species.

| SPECIES | | SITES | | | | | | | |
|--------------------|--|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|
| Common name | Latin name | Upper Eagle | | Lower Eagle | | Crystal | | Sunlight | |
| willow | <i>Salix spp.</i> | <i>24.2%</i> | <i>24.2%</i> | <i>26.7%</i> | <i>26.2%</i> | <i>47.5%</i> | <i>47.5%</i> | <i>62.5%</i> | <i>62.5%</i> |
| graminoids/forbs | <i>N/A</i> | <i>96.3%</i> | <i>71.8%</i> | <i>90.5%</i> | <i>55.0%</i> | <i>78.3%</i> | <i>44.5%</i> | <i>92.5%</i> | <i>33.5%</i> |
| Wood's rose | <i>Rosa woodsii Lindl. var. glabrata</i> | <i>1.7%</i> | <i>1.7%</i> | <i>4.2%</i> | <i>2.0%</i> | <i>5.0%</i> | <i>4.2%</i> | – | – |
| shrubby cinquefoil | <i>Dasiphora floribunda</i> | – | – | – | – | <i>1.7%</i> | <i>1.7%</i> | <i>30.8%</i> | T |
| stream | <i>N/A</i> | – | – | – | – | <i>3.3%</i> | <i>2.2%</i> | – | – |
| bare ground | <i>N/A</i> | <i>3.3%</i> | <i>2.0%</i> | – | – | – | – | <i>4.2%</i> | <i>4.0%</i> |
| mountain alder | <i>Alnus viridis</i> | <i>0.3%</i> | <i>0.3%</i> | <i>14.2%</i> | <i>13.3%</i> | – | – | – | – |
| common snowberry | <i>Symphoricarpos albus</i> | – | – | <i>2.5%</i> | <i>1.2%</i> | – | – | – | – |
| lodgepole pine | <i>Pinus contorta</i> | – | – | – | – | – | – | <i>56.7%</i> | T |
| spruce | <i>Picea A. Dietr.</i> | – | – | – | – | – | – | <i>28.0%</i> | T |

Table 4: The number of willow species at each site.

| SPECIES | | SITES | | | |
|-------------------|---------------------------------|-------------|-------------|---------|----------|
| Common name | Latin name | Upper Eagle | Lower Eagle | Crystal | Sunlight |
| Bebb willow | <i>Salix bebbiana</i> | 19 | 14 | 16 | – |
| Booth's willow | <i>Salix boothii</i> | – | – | 7 | 20 |
| Barclay willow | <i>Salix barclayi</i> | – | – | 1 | – |
| Geyer's willow | <i>Salix geyeriana</i> | 1 | 2 | 2 | 4 |
| sandbar willow | <i>Salix exigua var. exigua</i> | – | 3 | – | – |
| Drummond's willow | <i>Salix drummondiana</i> | – | – | – | 1 |

Community Similarity Between Sites

Using Sorenson's Coefficient of similarity to compare all sites shows community similarity between sites with 100% being most similar and zero being least (Sorenson 1948). Upper and Lower Eagle sites are most similar for both total species composition and willow composition, and Lower Eagle and Sunlight are least alike for both (Table 5). However plant communities appear to be distinct among sites when comparing both similarity indexes between them, all of which are low.

Table 5: Comparison between sites using Sorenson's percentagewise similarity for all species and only willow at each of the four sites.

| <i>Sites</i> | QS_{all} | | | | QS_{willow} | | | |
|--------------|-------------|-------------|---------|----------|---------------|-------------|---------|----------|
| | Upper Eagle | Lower Eagle | Crystal | Sunlight | Upper Eagle | Lower Eagle | Crystal | Sunlight |
| Upper Eagle | --- | 36 | 30 | 27 | --- | 40 | 33 | 20 |
| Lower Eagle | 36 | --- | 27 | 17 | 40 | --- | 29 | 17 |
| Crystal | 30 | 27 | --- | 27 | 33 | 29 | --- | 29 |
| Sunlight | 27 | 17 | 27 | --- | 20 | 17 | 29 | --- |

Height, Growth Rates, Water Status

General Trends. Although height of all willow increased throughout the season at all sites, the timing of peak growth rates varied by species. For example, growth rate for Bebb willow is greatest at the beginning of the season while for sandbar willow, Booth, and Geyer it is the middle of the season. Midday water potential (ψ_{md}) tends to decrease (more plant water stress) throughout the season, and predawn water potential (ψ_{pd}) increases (less plant water stress). For all species, (ψ_{pd}) increases, and (ψ_{md}) tend to decrease throughout the season. For ψ_{pd} and ψ_{md} , September is the exception, to the above findings, with much less variability between the two (Figure 13).

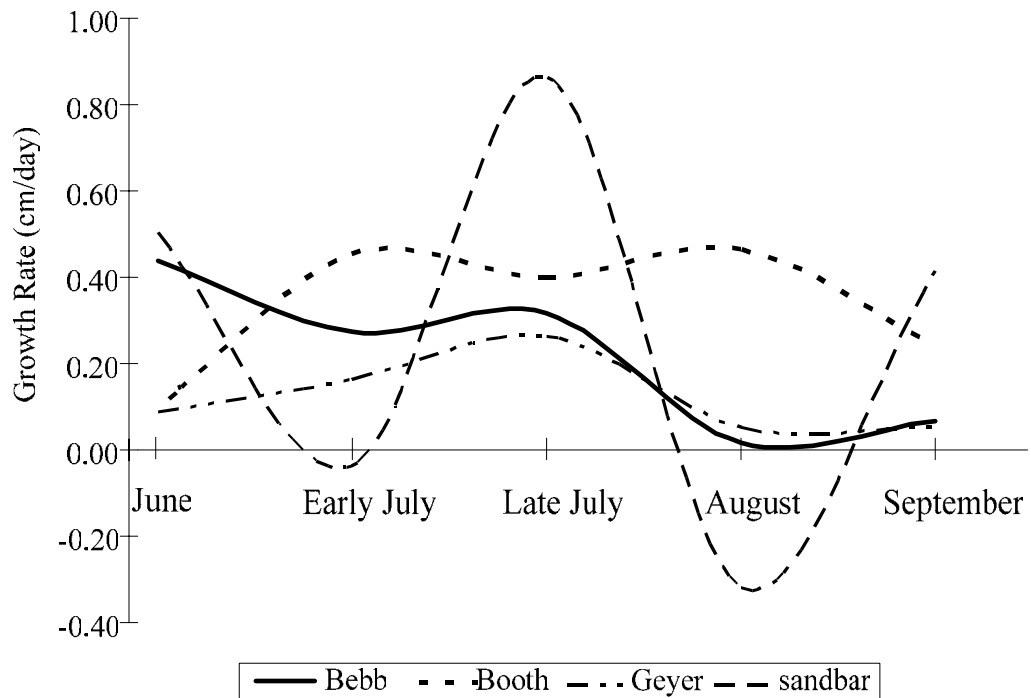


Figure 13: Growth trends by species across all sites for the 2004 growing season.

Data by Site. Upper Eagle had the least willow growth throughout the season.

Height increased slightly in the early season and remained static for the rest of the season (Figure 14). This was a function of growth rate which showed almost no growth following the initial burst (Figure 15). Midday water potential showed significant decreases between July and August, while ψ_{pd} is elevated in the early season, and continues to increase through August. In September, there was little difference between ψ_{pd} and ψ_{md} , as ψ_{pd} values decreased and midday values increased (Figure 16).

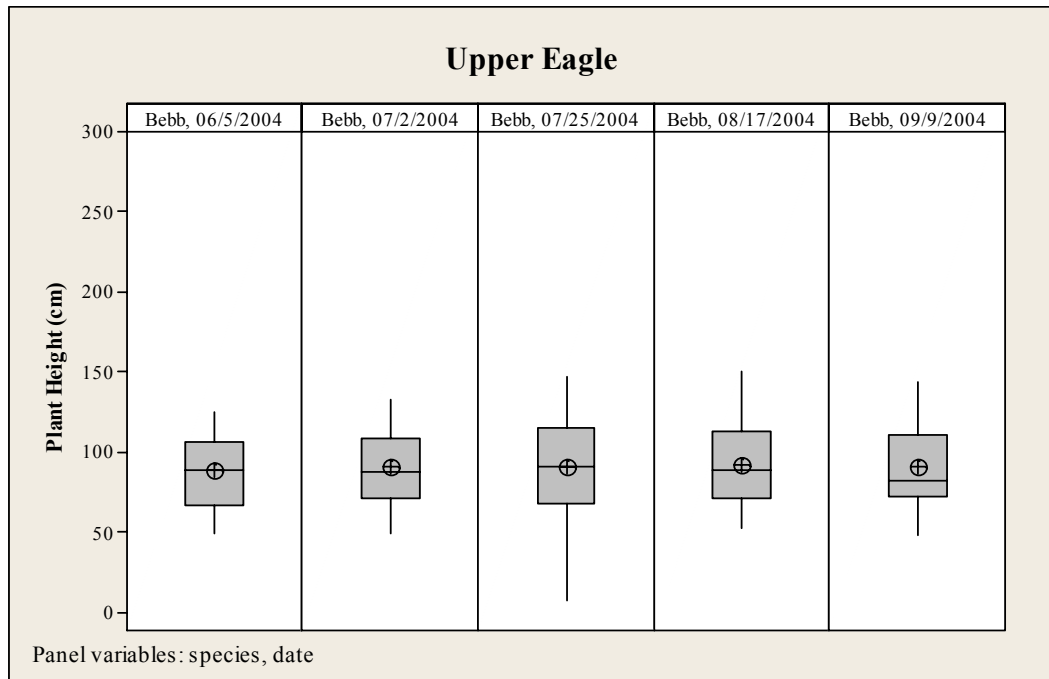


Figure 14: Boxplots and means of plant height at Upper Eagle.

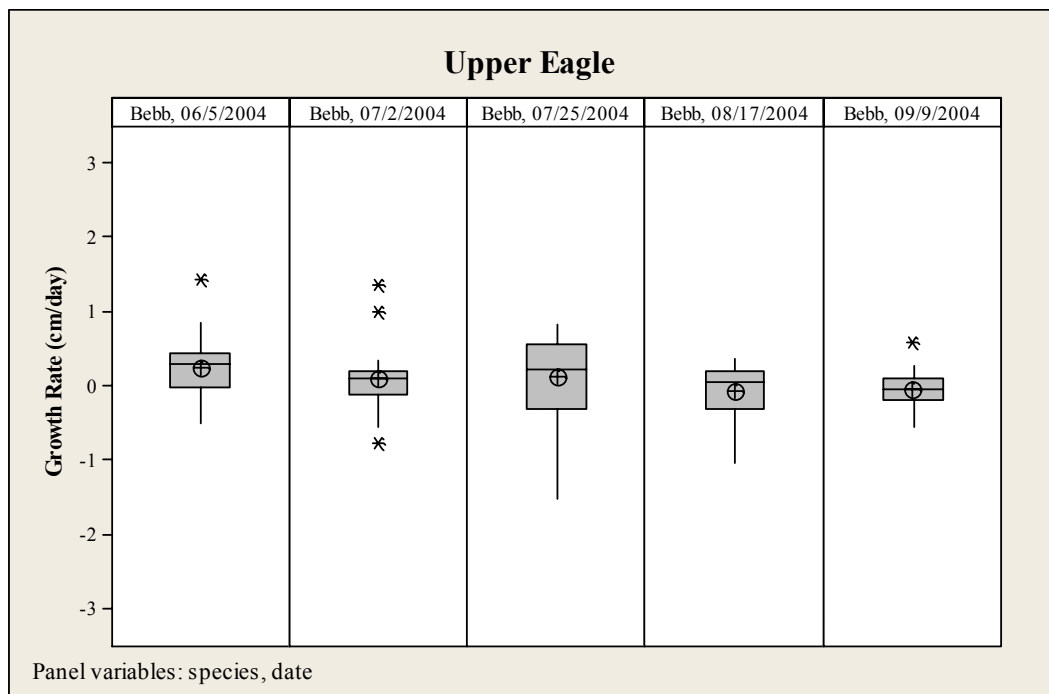


Figure 15: Boxplots and means for growth rate at Upper Eagle.

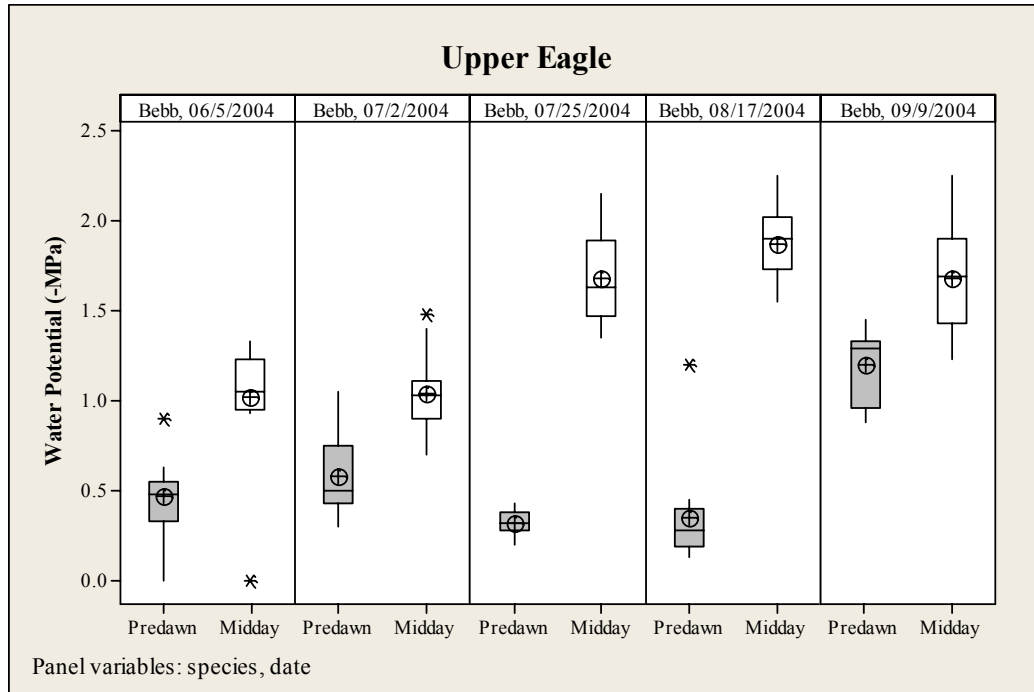


Figure 16: Boxplots and means of water potential by time of day at Upper Eagle.

Lower Eagle willows increased in height throughout the summer (Figure 17). Growth rates for Bebb willow were greatest in June, and quickly declined, while for sandbar willow, the greatest growth rates occurred in late July, although it had low growth rates throughout the season (Figure 18). Water potential patterns were much more variable at Lower Eagle than the other sites. In general, it had the least plant water stress of all four sites and smaller changes in water potential (ψ_c), with the exception of June and late July. The September water potential readings also varied from general trends at the other sites. Predawn didn't show the significant September decrease found at other sites. This pattern exists for both species at Lower Eagle, although in August, for sandbar willow, predawn readings are lower than midday readings (Figure 19).

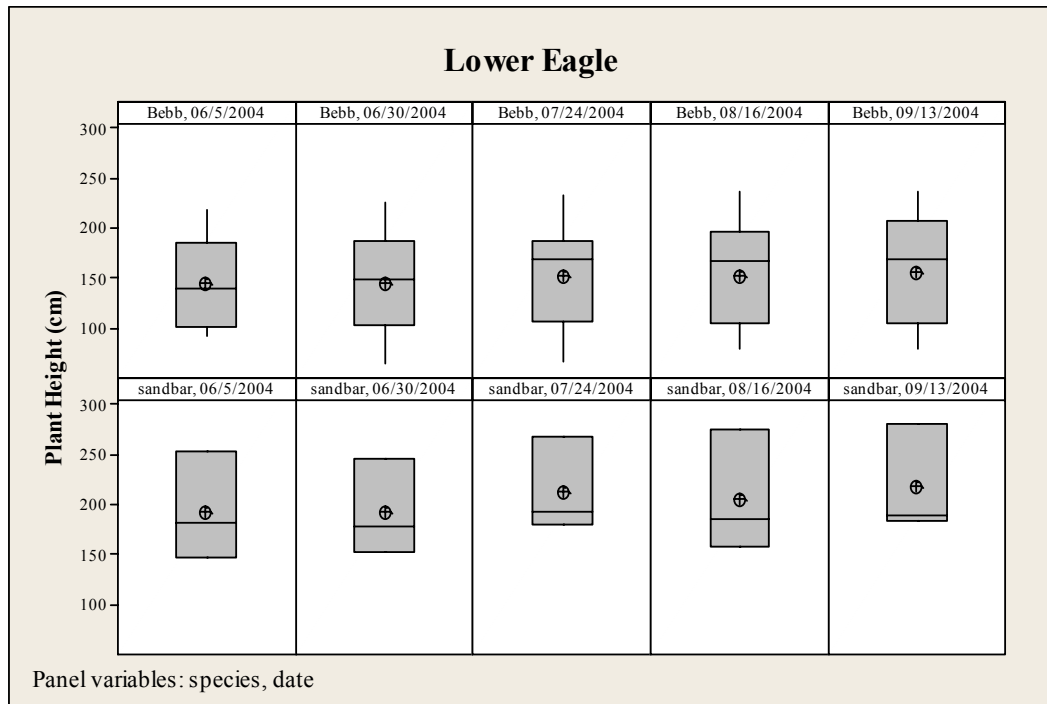


Figure 17: Boxplots and means of plant height at Lower Eagle.

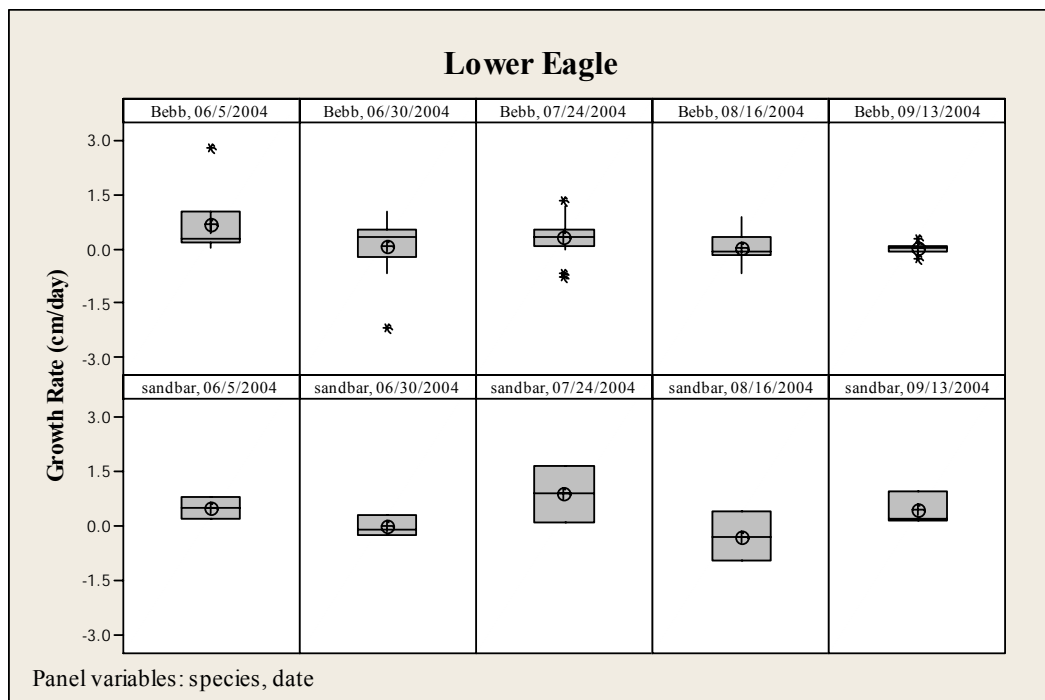


Figure 18: Boxplots and means for growth rate at Lower Eagle

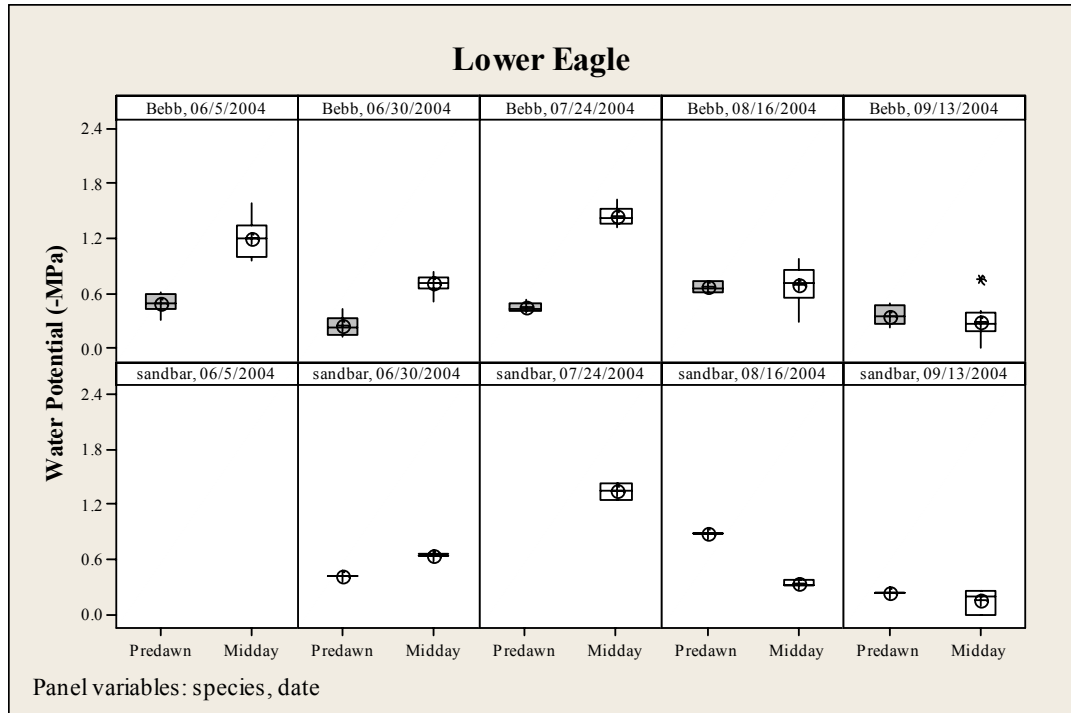


Figure 19: Boxplots and means of water potential by time of day at Lower Eagle.

Willows at Crystal Creek showed consistent gradual height increases during the growing season and the highest growth rates (Figure 20). For Bebb willow, the growth rate was greatest in early July with little or no growth in June, and a gradual decline following the early July spurt. Booth willow had the greatest growth rate in late July, with a substantial increase in early July leading to this maximum. Growth rate declined following the July burst, but growth still remained constant (Figure 21). Predawn water potential was less variable at Crystal than other sites throughout the season and stayed fairly constant. In September, ψ_{md} reached early season levels with the lowest readings in September (Figure 22).

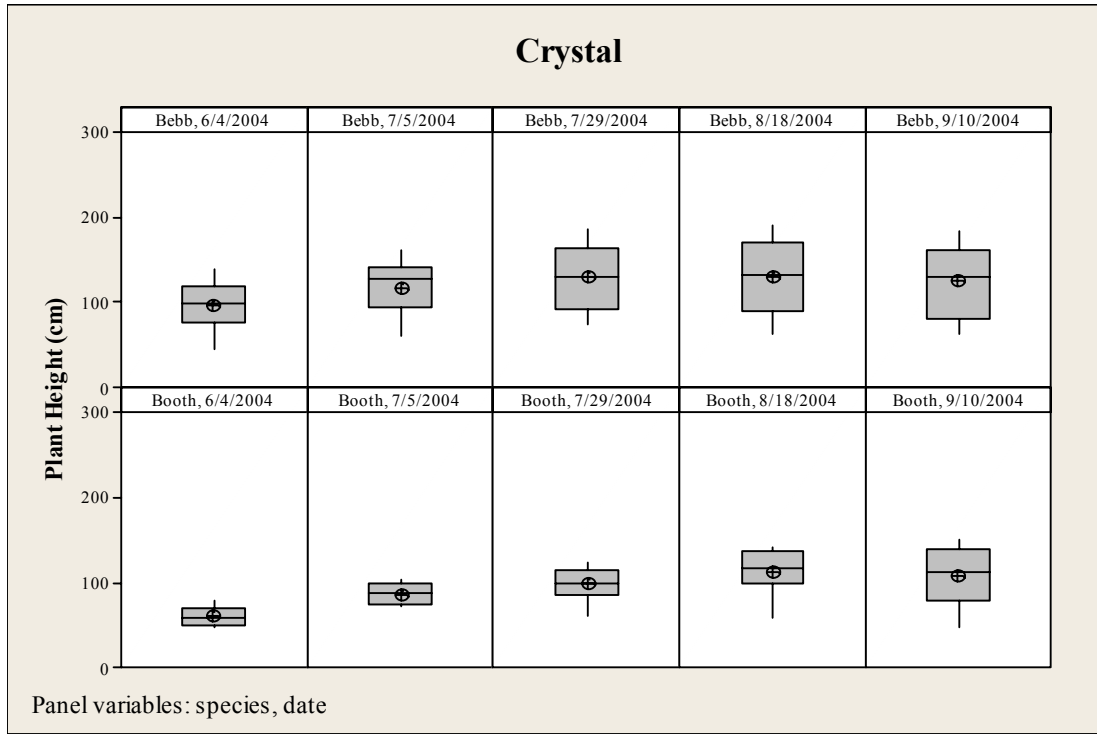


Figure 20: Boxplots and means of plant height at Crystal.

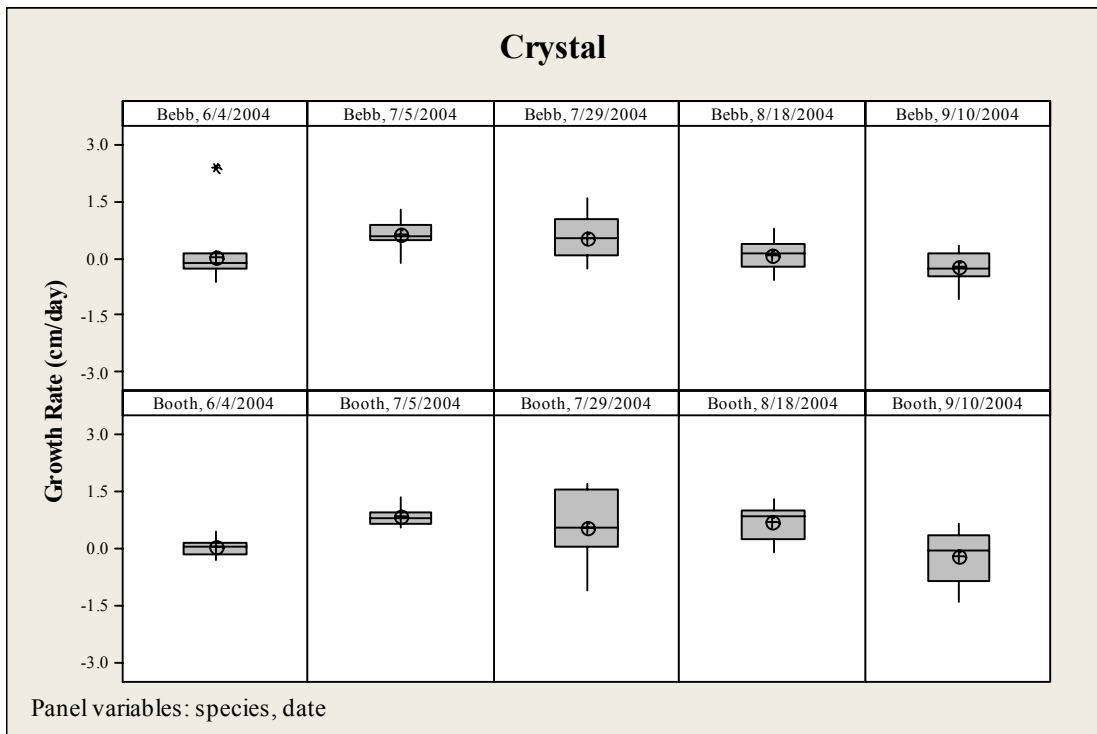


Figure 21: Boxplots and means for growth rate at Crystal.

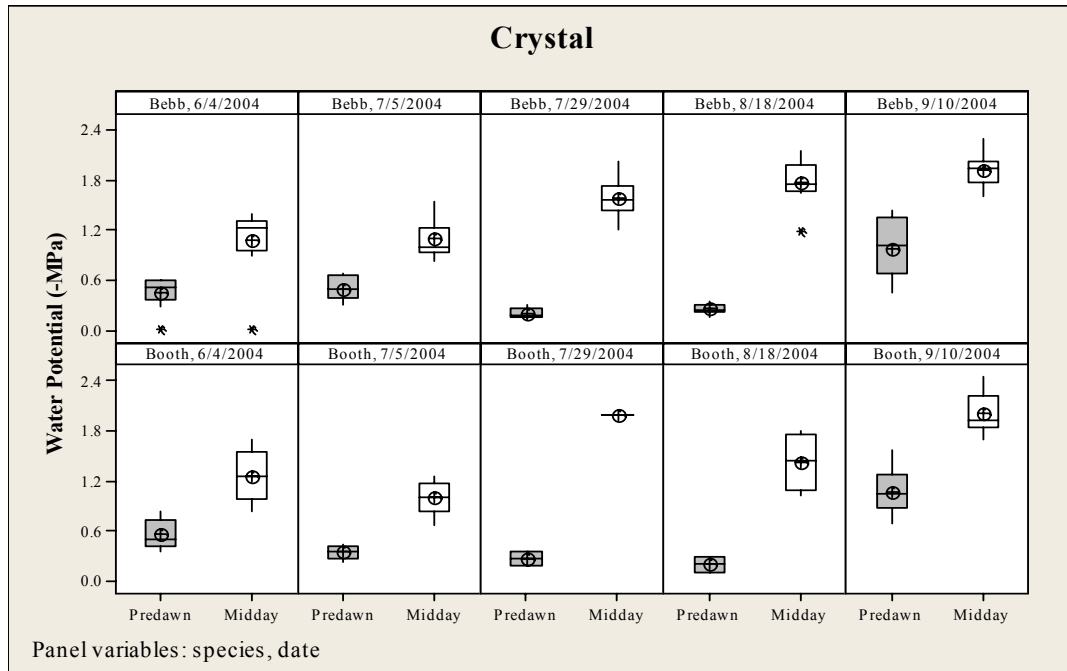


Figure 22: Boxplots and means of water potential by time of day at Crystal.

Willow height at Sunlight Creek gradually increased throughout the season (Figure 23). Growth rates for both species were the lowest of all sites and species. Booth had a slight increase in late July and maintained that rate for the rest of the season. This was opposite from Geyer; which maintained a higher initial rate for June and early July and reached its maximum in late July with essentially no growth the remainder of the season (Figure 24). Predawn water potentials were low in the early season and reached almost no water stress in August. Midday readings for Booth decreased in late July. Readings were consistent for June and early July, decreased in late July and maintained this low level through August. For Geyer, midday readings decreased through late July and increased through September. In September, predawn readings decreased drastically and showed almost no variation from the midday readings (Figure 25).

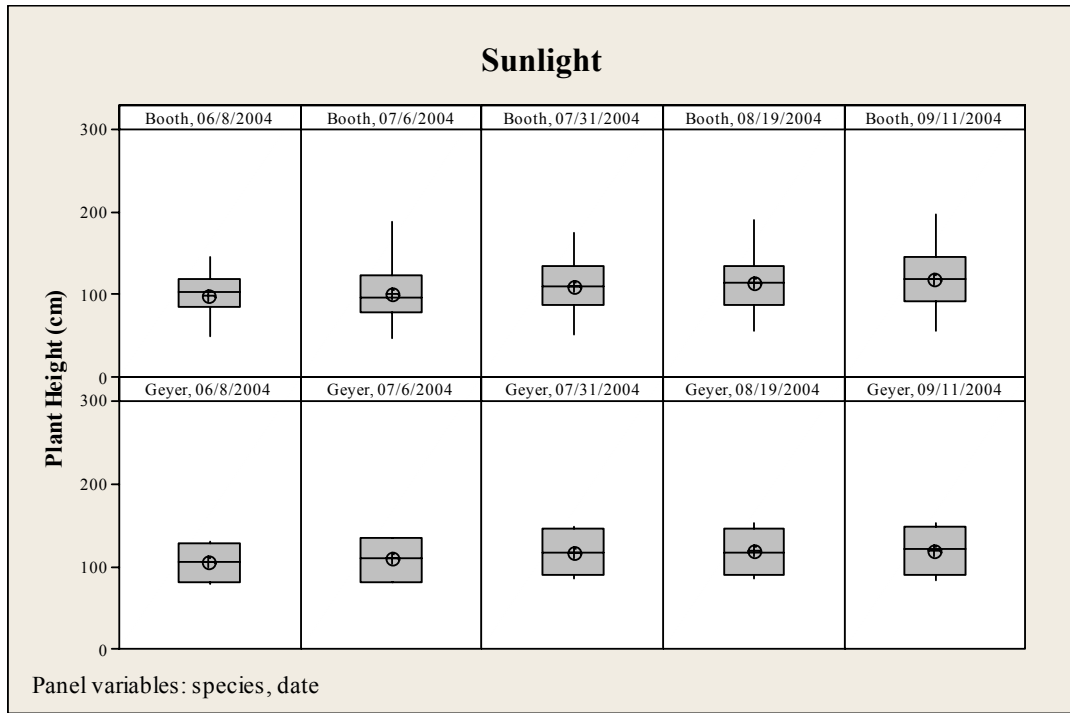


Figure 23: Boxplots and means of plant height at Sunlight.

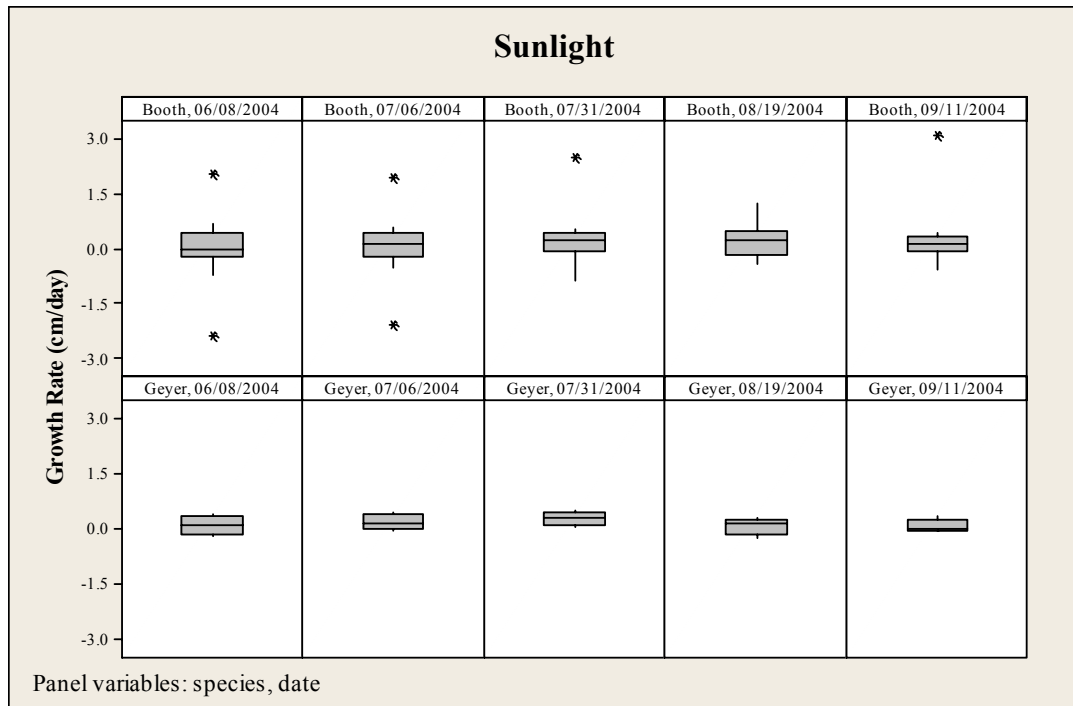


Figure 24: Boxplots and means of growth rate at Sunlight.

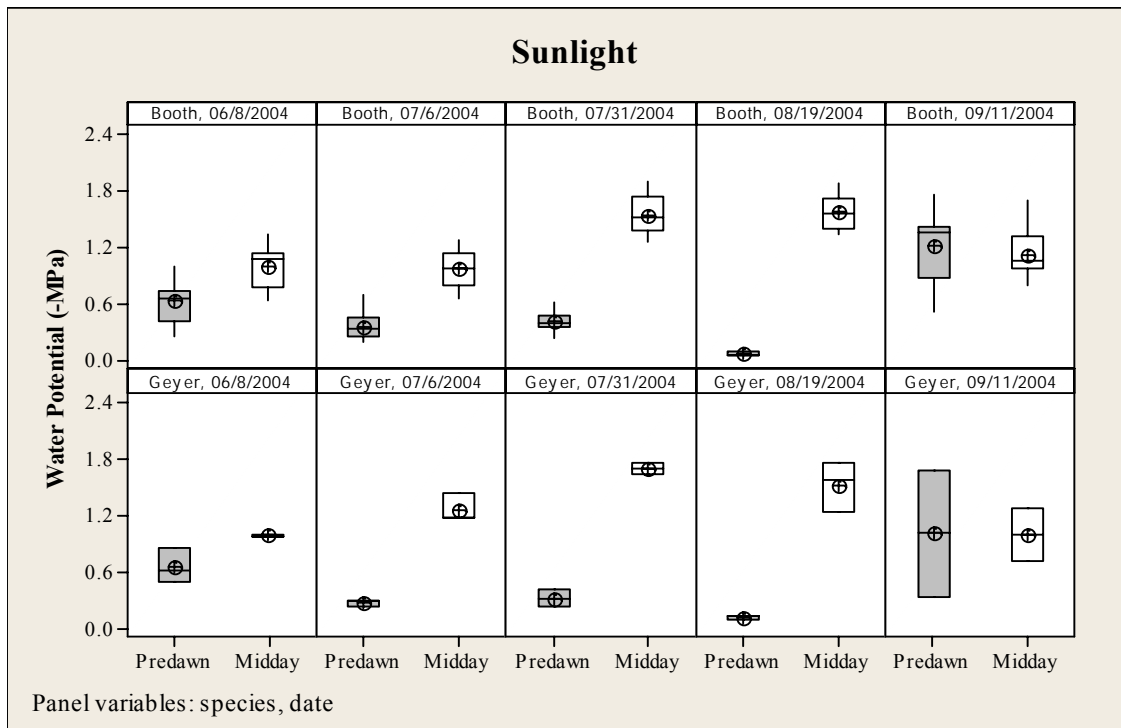


Figure 25: Boxplots and means of water potential by time of day at Sunlight.

Site Browse & Growth

Crystal Creek was subject to the most winter browsing (twice as much as any other site) followed by Lower Eagle, Sunlight, and Upper Eagle (Figure 26). A comparison of browse of species at each site shows that Booth had almost twice the browse pressure as Bebb at Crystal. At Lower Eagle, Bebb was browsed more than sandbar willow, and there were similar amounts of winter browsing of the two species at Sunlight (Booth and Geyer) and Upper Eagle (Bebb and Geyer) (Figure 27).

A comparison of plant growth between sites shows that the most browsed willows (Crystal site) exhibited the most growth, and willows at the least browsed site, Lower Eagle, had the least amount of growth (Figure 28).

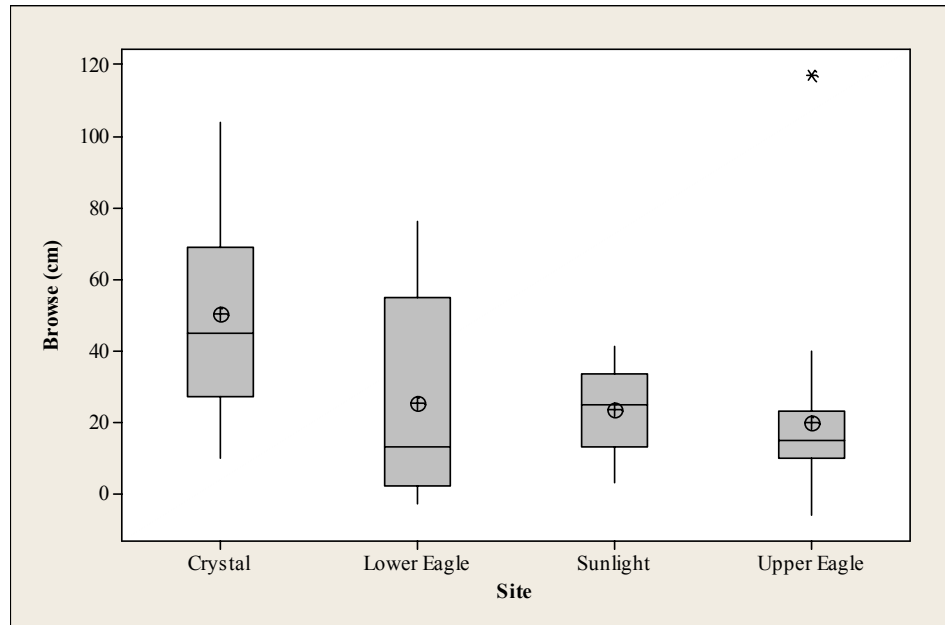


Figure 26: The amount of vertical plant tissue (height) removed during winter by site.

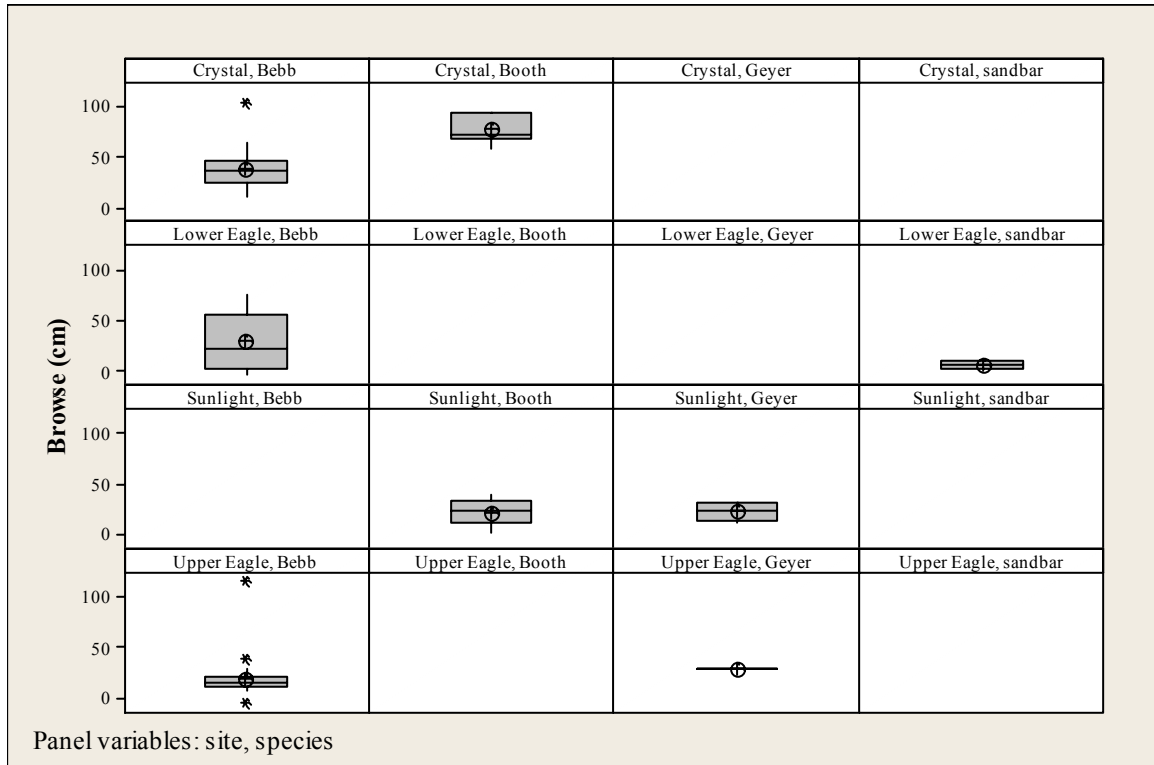


Figure 27: The amount of vertical plant tissue (height) removed during winter for individual species at each site.

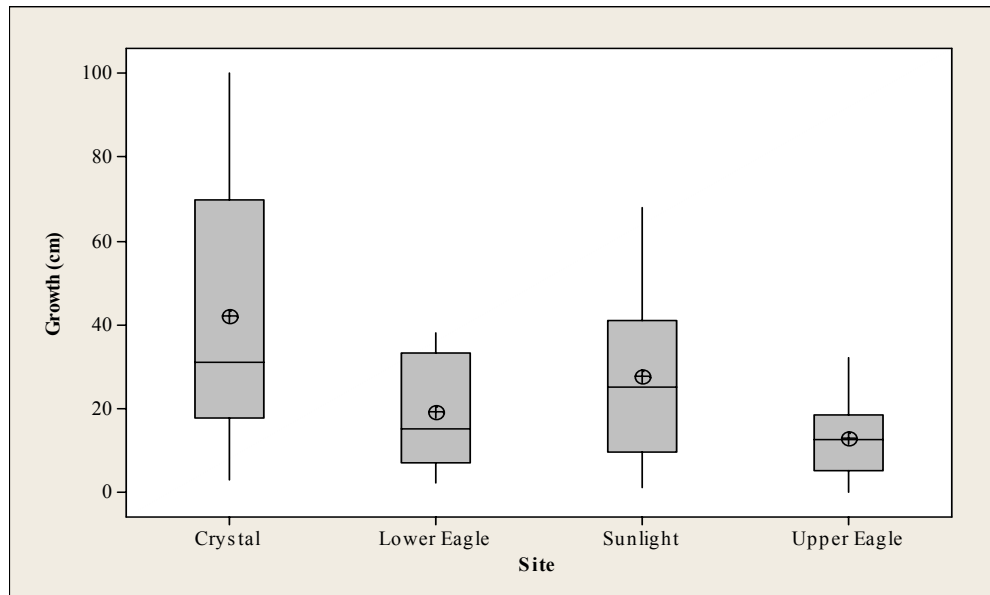


Figure 28: Average total plant growth (height) per site following winter browse.

Plant Stature

The importance of initial plant stature to seasonal growth did not show consistent trends by species but instead by site and then species (Table 6, Table 7, Table 8, and Table 9). Growth ratios (end of season height/ pre-growing season ht) based on height classes of >120-150, >150-180, and >180-210 show Bebb at Upper and Lower Eagle had the most growth. Growth ratios above and below these height classes were much lower. At Crystal, the Bebb that grew most was in the >60-90 class. At Lower Eagle, sandbar willow plants in the >210-240 range exhibited the most growth relative to pre-season height, but this growth was not much different from those plants two height classes lower. Booth at Crystal and Sunlight did not have the same distribution of height classes as the previous two NEWR sites making the ratios between sites difficult to compare. At Crystal, the >60-90 pre-season height range for Booth had the highest growth ratios while at Sunlight, it was the >90-120 range. Geyer willow at the Sunlight site had smaller

plants showing the most growth, >60-90 range. Geyer willow, only analyzed at Sunlight, had smaller plants (>60-90 range) showing the most growth.

Table 6: Ratio of end of season height to beginning of the season height.

| Site: Upper Eagle Creek | |
|---------------------------------------|------|
| Beginning of Season Height Class (cm) | Bebb |
| 30.10 - 60.00 | 1.11 |
| 60.10 - 90.00 | 1.12 |
| 90.10 - 120.00 | 1.05 |
| 120.10 - 150.00 | 1.15 |

Table 7: Ratio of end of season height to beginning of the season height.

| Site: Lower Eagle Creek | | |
|---------------------------------------|------|---------|
| Beginning of Season Height Class (cm) | Bebb | sandbar |
| 60.10 - 90.00 | 0.88 | --- |
| 90.10 - 120.00 | 1.03 | --- |
| 120.10 - 150.00 | 0.95 | --- |
| 150.10 - 180.00 | 1.17 | 1.15 |
| 180.10 - 210.00 | 1.17 | --- |
| 210.10 - 240.00 | 0.98 | 1.19 |

Table 8: Ratio of end of season height to beginning of the season height.

| Site: Crystal Creek | | |
|---------------------------------------|------|-------|
| Beginning of Season Height Class (cm) | Bebb | Booth |
| 30.10 - 60.00 | 1.22 | 1.54 |
| 60.10 - 90.00 | 1.37 | 1.93 |
| 90.10 - 120.00 | 1.35 | --- |
| 120.10 - 150.00 | 1.18 | --- |

Table 9: Ratio of end of season height to beginning of the season height.

| Site: Sunlight Creek | | |
|---------------------------------------|-------|-------|
| Beginning of Season Height Class (cm) | Booth | Geyer |
| 30.10 - 60.00 | --- | --- |
| 60.10 - 90.00 | 1.15 | 1.22 |
| 90.10 - 120.00 | 1.21 | --- |
| 120.10 - 150.00 | 1.11 | 1.12 |

However, ratios developed based on amount of summer growth and winter browse (new growth/ amount of winter browse in terms of height) do show some distinct growth patterns (Figure 29). Each species shows different response levels with sandbar and Booth willow putting on the most growth followed by Bebb and then Geyer. Plants browsed up to 20 cm responded with the most growth (up to three times the amount of tissue browsed), followed by the >20-40 cm browse class, while anything greater than this shows less and fairly equal amounts of growth. Willows browsed between 20 and 40 cm. showed a much smaller growth response and pattern between sites; Bebb responded with the most growth at Lower Eagle and the least at Crystal. Booth, common to two sites, showed Crystal plants responding with more growth than Sunlight for this browse class.

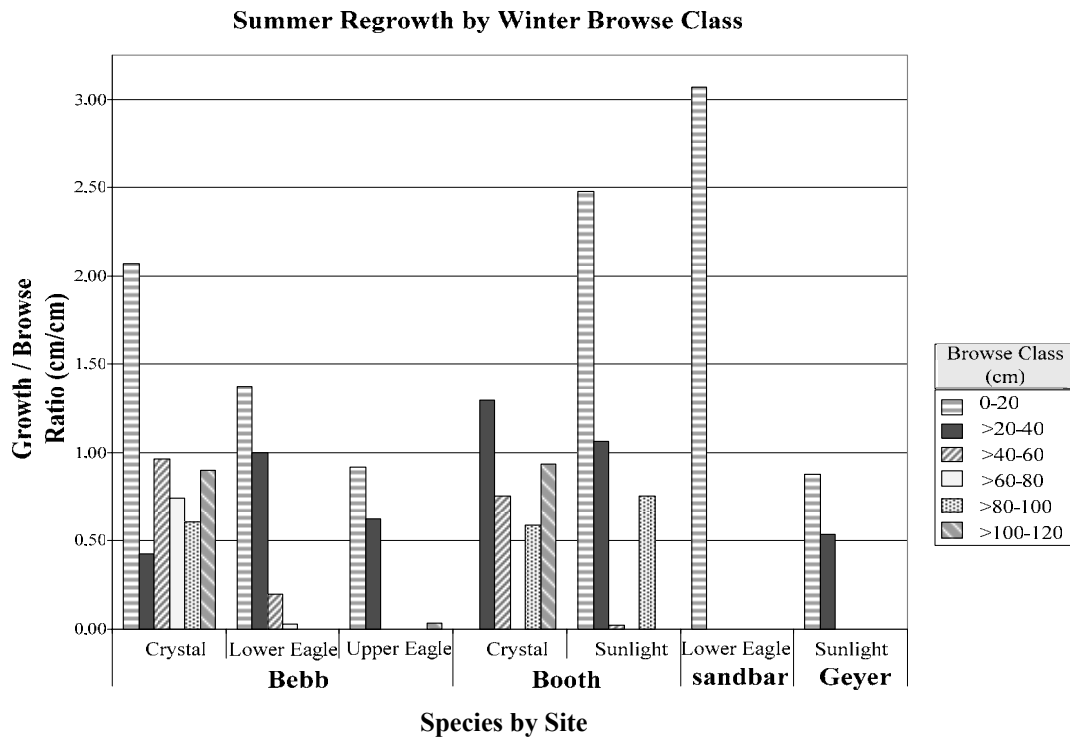


Figure 29: Willow growth ratio formulated by dividing summer plant growth increase (height) by amount of winter browse (browse class).

Physical Attributes

Flowpaths & Water Tables

Water table diagrams throughout the growing season for each site showed Upper Eagle and Crystal to be gaining in the early season and losing by mid season. Sunlight Creek was gaining all season, and Lower Eagle losing all season. Groundwater tables dropped throughout the season, and diurnal fluctuations generally showed midday groundwater levels below predawn levels (Figure 30, Figure 31, Figure 32, and Figure 33). However, in some instances midday water tables were elevated above predawn

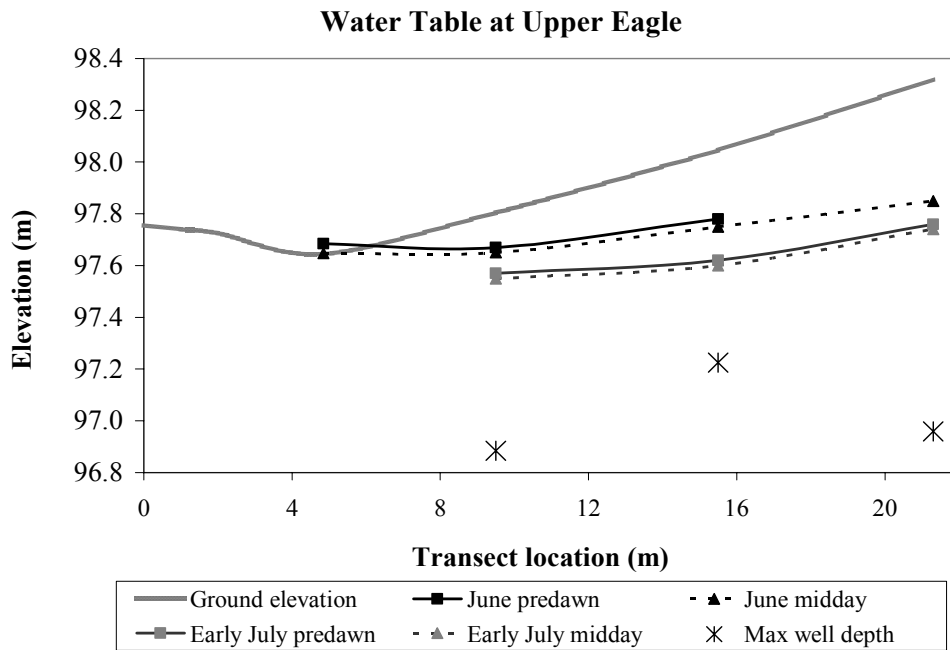


Figure 30: Upper Eagle groundwater table seasonal changes as compared to relative ground elevation.

depths. Sunlight had the most level water table (in respect to ground surface topography) that elevated slightly with increased distance from the stream perhaps as a result of

shallow hyporheic flows from upstream meander bends and hillslope runoff/drainage (Figure 33). In contrast, Lower Eagle showed the sharpest decline with increased distance from the beaver ponds (Figure 31).

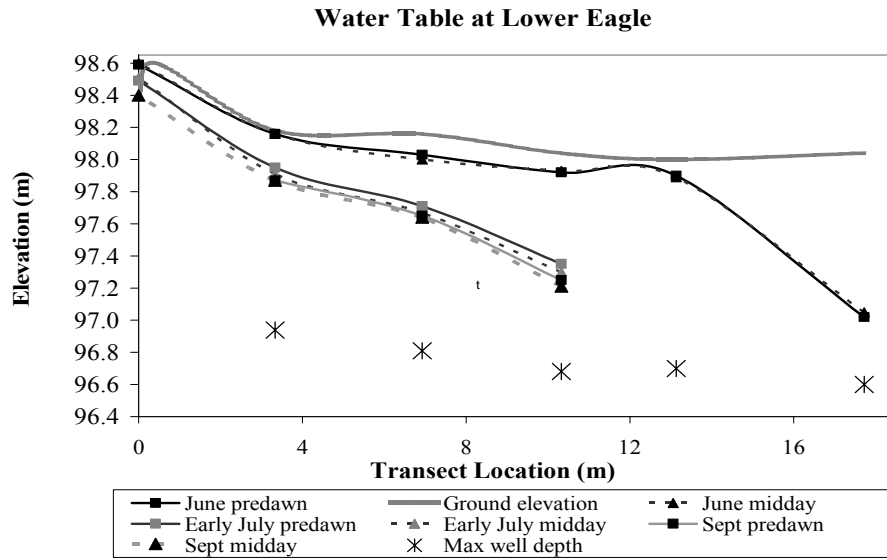


Figure 31: Lower Eagle groundwater table seasonal changes as compared to relative ground elevation.

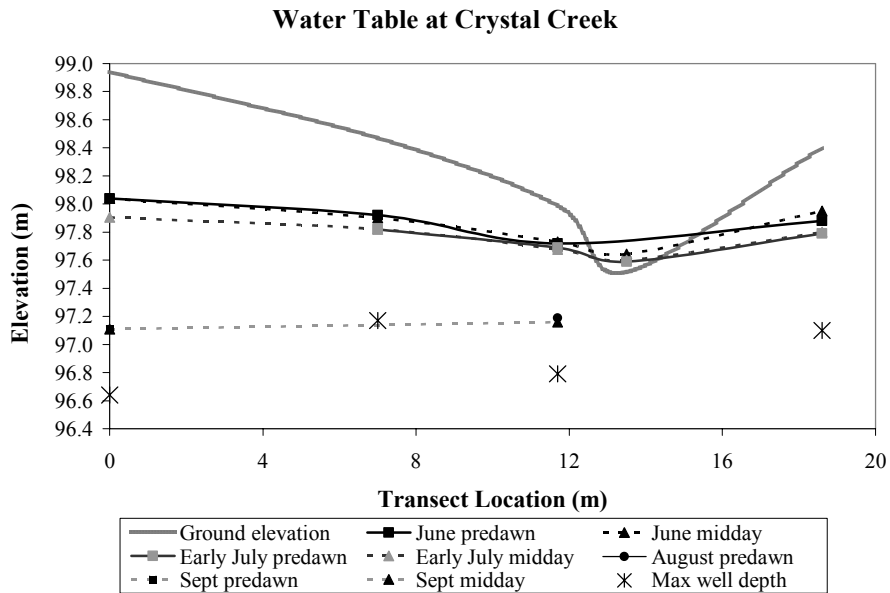


Figure 32: Crystal groundwater table seasonal changes as compared to relative ground elevation.

Water Table at Sunlight Creek

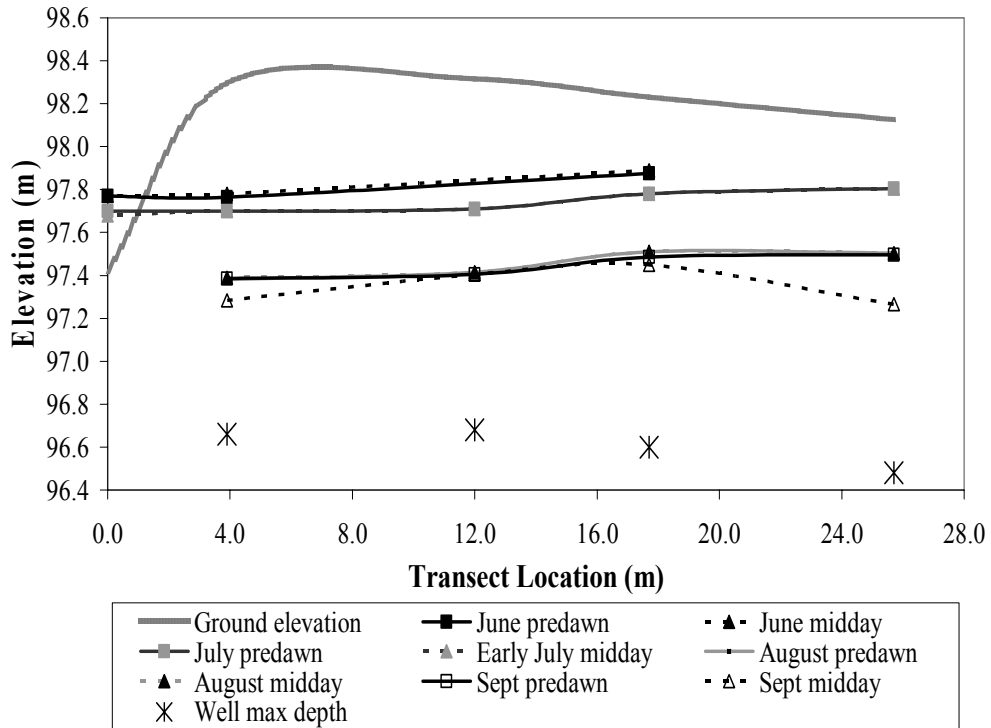


Figure 33: Sunlight groundwater table seasonal changes as compared to relative ground elevation.

Groundwater & Soil Moisture

General trends for groundwater depth and soil moisture are not as straight forward as the biologic characteristics. Overall, groundwater was deepest at Sunlight and most shallow or available at Lower Eagle while Sunlight had least soil water and Crystal the most (Figure 34). Through the growing season, depth to groundwater and percent soil moisture at Upper and Lower Eagle generally increased; while at Crystal and Sunlight depth to groundwater also increased, but soil moisture was initially high and decreased later in the season. Soil moisture data represents only one of the diurnal measurements, as there was no changes between predawn and midday readings.

Depth to Groundwater

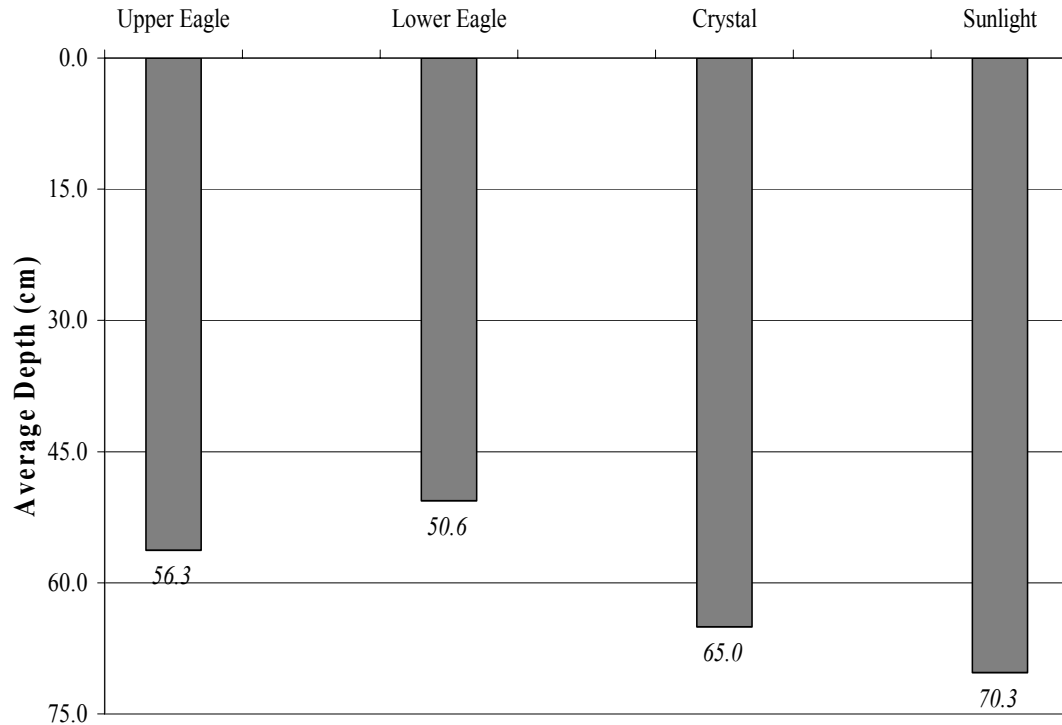


Figure 34: Average depth to groundwater for each site during the 2004 growing season.

Upper Eagle showed a consistently declining water table, and in August, the depth dropped below the depth of the monitoring wells (Figure 35). In contrast, soil moisture levels in June and early July showed the most variability between each of the three depths (15, 30, & 60 cm). The 60 cm depth had the highest moisture content with 15 cm being the driest of the season. Late July through September readings showed little variability in soil moisture between depths. The 15 and 30 cm readings increased to almost equal to the 60 cm depth moisture levels (Figure 36).

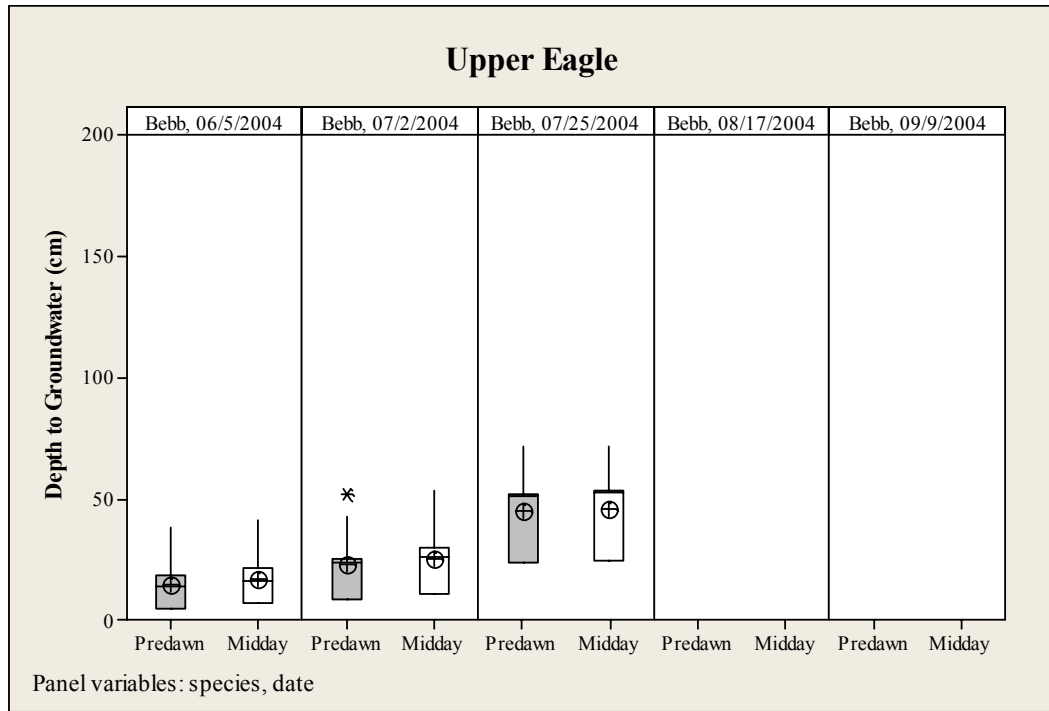


Figure 35: Boxplots and means of depth to groundwater by time of day at Upper Eagle.

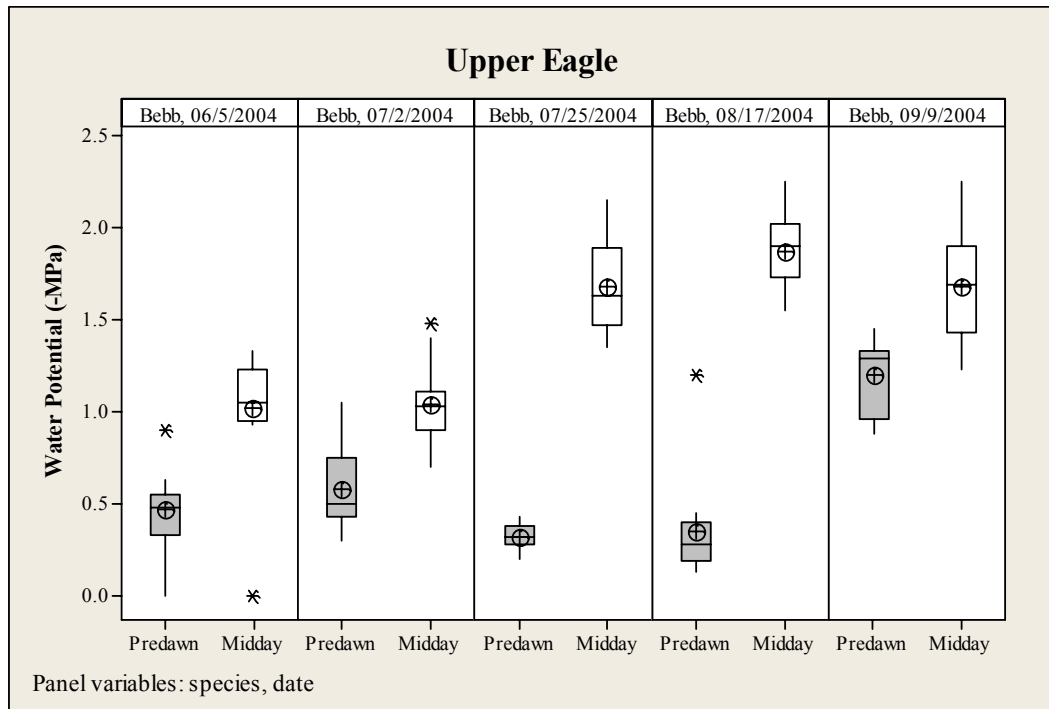


Figure 36: Boxplots and means of soil moisture at depth for Upper Eagle.

Groundwater readings at Lower Eagle were only at Bebb locations throughout the season. Groundwater depths at this site declined through late July, but less so than the other sites. In August, only one well remained with water, and average depth was shallower than the late July average. In September, average depth was shallower than in early July. Wells next to sandbar willows had water through June, and this depth to groundwater was much shallower than in wells near Bebb plants (Figure 36). Soil

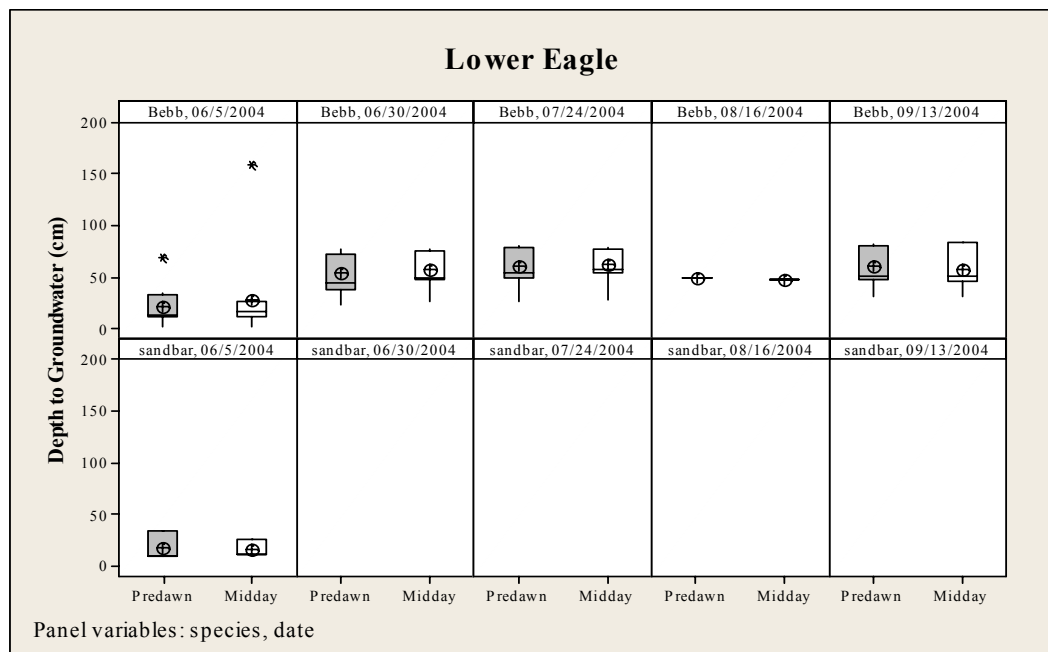


Figure 37: Boxplots and means of depth to groundwater by time of day at Lower Eagle

moisture at Lower Eagle near Bebb plants was greater than at the above Upper Eagle site, but does follow the same trend as the Upper site with readings between depths becoming less variable and soil moisture increasing through the season. A slight drop in moisture at 15 and 30 cm depths is noted in September. Soil moisture near sandbar willow was much

lower than near Bebb at 15 and 30 cm. early in the season, but had similar soil moisture trends for late July and August. However, the September decrease in moisture content is more evident at sandbar willow locations (Figure 38).

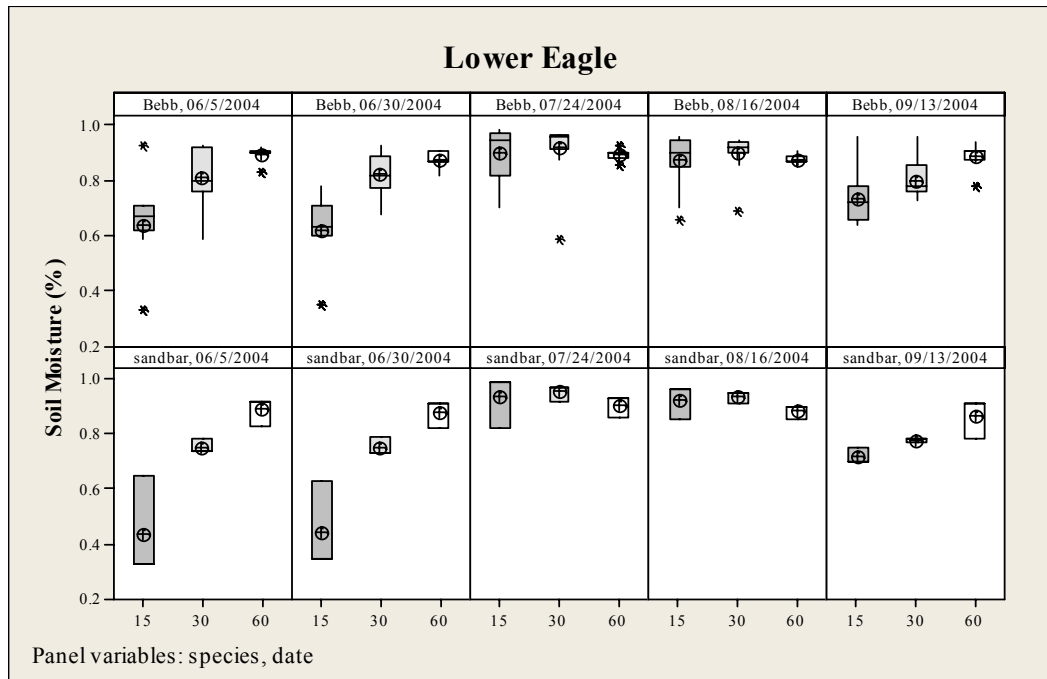


Figure 38: Boxplots and means for soil moisture by depth at Lower Eagle.

At Crystal Creek, depth to groundwater increased through late July for both Bebb and Booth, and predawn and midday values were similar between species at each reading (Figure 39). The late July reading was unchanged through August for Bebb, and for the predawn Booth reading. In September, depths to groundwater increased for each species, but more so for Booth willows. Soil moisture was close to 100% for both species through early July. In late July, a gradual decline at the two shallower depths became evident, and by late July there was a sharp decline. This decline was noted only for the

two shallower depths near Bebb willows and for all three depths near Booth willows.

Again in August the decline continued, being more evident for Booth (Figure 40).

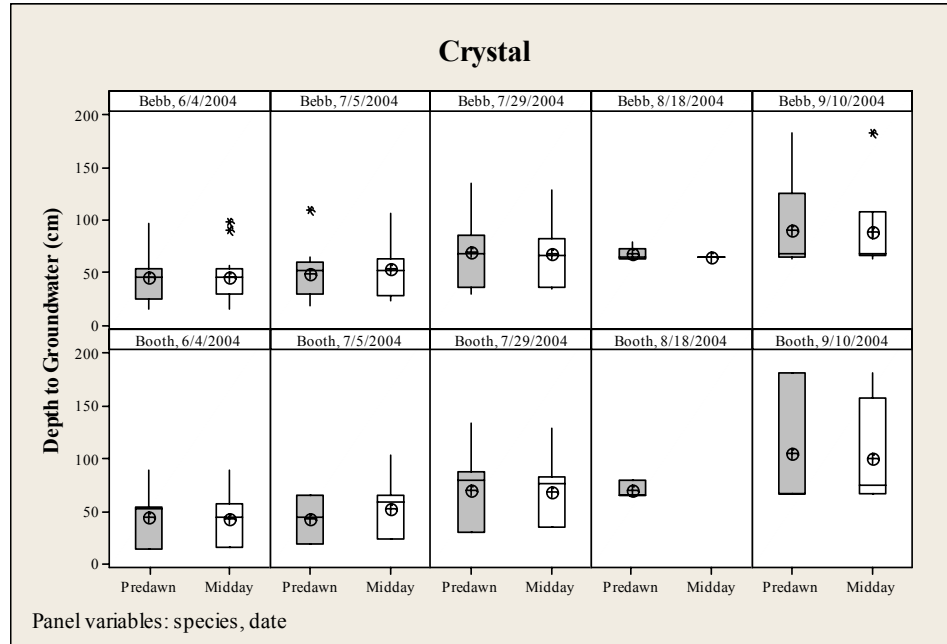


Figure 39: Boxplots and means of depth to groundwater by time of day at Crystal.

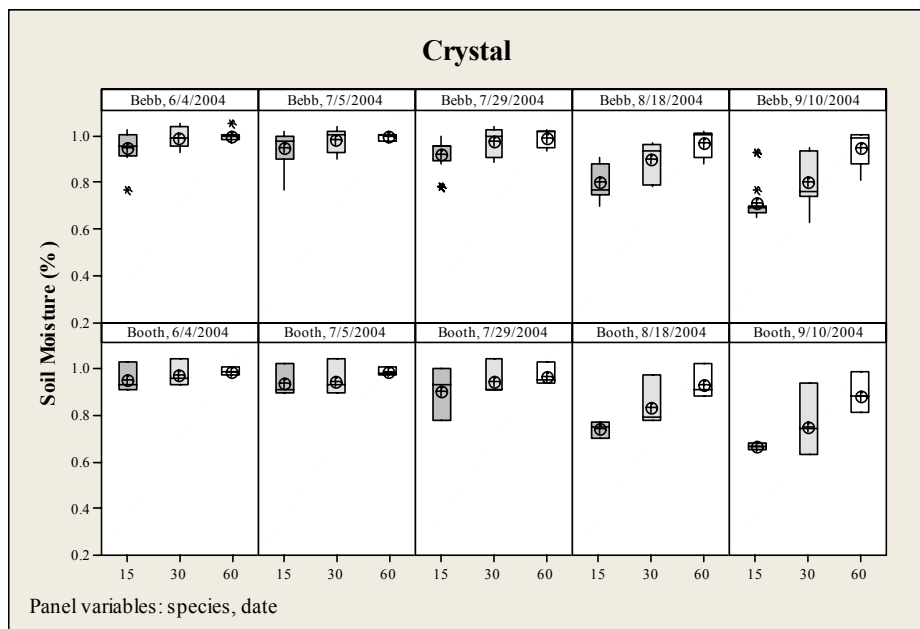


Figure 40: Boxplots and means of soil moisture by depth at Crystal.

Sunlight showed a consistent gradual decline in groundwater. This trend and depths to the groundwater table were similar for both species, Booth and Geyer willow. August groundwater remained static through September (Figure 41, Figure 46). Soil moisture differed between species. Near Booth willows there was little variation between

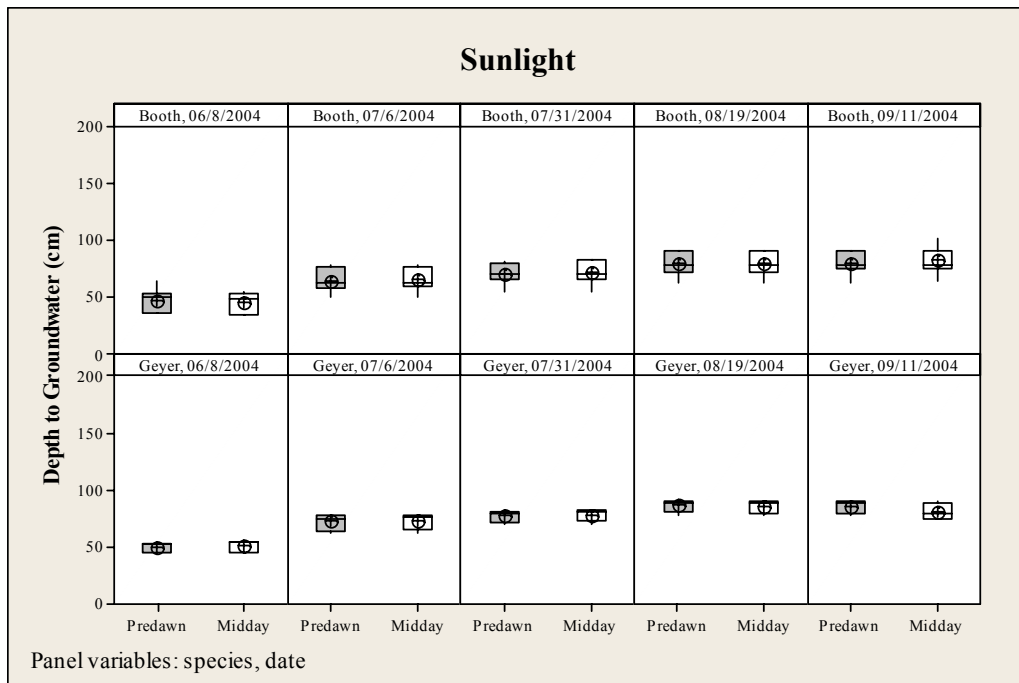


Figure 41: Boxplots and means of depth to groundwater by time of day at Sunlight.

the three depths throughout the season. There was, however, a small increase in soil moisture at 15 cm in July. Slight drops in all depths occurred in August and September. Soil moisture near Geyer willows showed much variation in soil moisture among depths and seasonal readings. In general, soil moisture content was high, but June and early July readings at 30 cm were considerably lower than the 15 and 60 cm. readings. In late July through September, soils became much drier for all levels. This site, however, differed

from the others in that the 15 cm depth maintained a higher soil moisture content than the 60 cm depth (Figure 42).

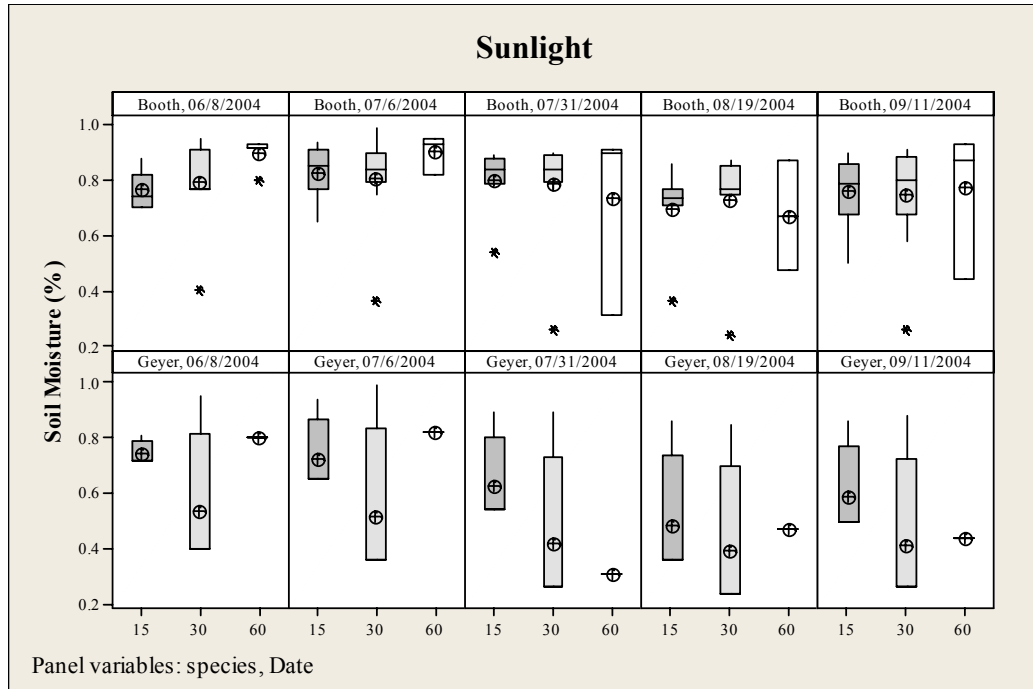


Figure 42: Boxplots and means of soil moisture by depth at Sunlight.

Precipitation

Because precipitation might play an important role in groundwater depth and soil moisture, precipitation was assessed relative to sampling dates. Weather stations used relative to each site were the Gardiner, Montana station for both Upper and Lower Eagle, Tower Junction, YNP, Wyoming for Crystal Creek, and Sunlight Basin, Wyoming for the Sunlight site. Precipitation prior to sampling dates showed Lower Eagle having the most precipitation during the total ten days prior to site visits followed by Sunlight, Crystal, and then Upper Eagle. In general, in the 6-10 day pre-sampling period, most

precipitation occurred at Sunlight followed by Upper Eagle, Crystal, and Lower Eagle. The order for the 3-5 day pre-sampling period was Lower Eagle, Crystal, Sunlight, and Upper Eagle, and two days prior to sampling was Lower Eagle, Sunlight, Crystal, and then Upper Eagle (Table 10).

Upper Eagle received the most precipitation in the days preceding the late July visit. June, however, had a fair amount of rain with most of it occurring 6-10 days before the visit and a small amount in the 2 day period. Early July had even distributions between 3 and 10 days and a minute amount again occurring in the 2 day pre-sample period. In late July, almost all the rain occurred 6-10 days before the visit, and in August there was only a small amount of precipitation which occurred in the two day pre-sample period. In September, there was no precipitation during the 10 day period prior to a site visit.

Lower Eagle also experienced the most rain in late July, but June and September also had high amounts. In June most of the rain occurred 6-10 days before the site visit, and small amounts occurred two days prior. Early July had most of its rain two days prior, but earlier small storms were noted in the ten days leading up to the site visit. In late July, there were larger amounts of rain between 3 and 10 days prior. There were no storms in the days leading up to the August visit, and in September, approximately 2 cm of rain occurred in the 2-5 day pre-sampling period.

At Crystal, the most precipitation occurred in June; however, it occurred 6-10 days before field measurements. In early July most of the rain occurred between 3 and five days prior to the visit. Late July had most of its rain in the latter part of the 10 day

period, however, in August, most of the rain occurred two days before the site visit.

There was much less rain in September; it was, however, split almost evenly between 3-5 and 6-10 days prior to sampling.

At Sunlight, the least amount of rain occurred in June and August and the most in late July. In June, most of the rain was in the 6-10 day pre-sample period. In early July, most of the rain occurred in the 6-10 and 2 day pre-sample period. In late July, there were storms leading up to the site visit, but most of the rain occurred 6-10 days before. In August, there was a minute amount of precipitation within the 3-5 and two day periods. In September, the rain events were 6-10 days before a site visit.

Table 10: Precipitation data for two, three to five, and six to ten days prior to site visits. The day of measurement collection is included in the number of days (NCDC 2005).

| Site | Time Period | Precipitation (cm) | | | | |
|----------|--------------|--------------------|------------|-----------|--------|-----------|
| | | June | Early July | Late July | August | September |
| Upper | 0-2 days | 0.30 | 0.13 | 0.00 | 0.36 | 0.00 |
| | 3-5 days | 0.08 | 0.40 | 0.10 | 0.00 | 0.00 |
| | 6-10 days | 0.97 | 0.44 | 2.26 | 0.00 | 0.00 |
| | 10 day total | 1.35 | 0.97 | 2.36 | 0.36 | 0.00 |
| Lower | 0-2 days | 0.30 | 0.41 | 0.00 | 0.00 | 0.91 |
| | 3-5 days | 0.08 | 0.20 | 0.91 | 0.00 | 0.92 |
| | 6-10 days | 0.97 | 0.23 | 1.45 | 0.00 | 0.00 |
| | 10 day total | 1.35 | 0.84 | 2.36 | 0.00 | 1.83 |
| Crystal | 0-2 days | 0.00 | 0.00 | 0.03 | 1.14 | 0.00 |
| | 3-5 days | 0.03 | 0.86 | 0.05 | 0.00 | 0.15 |
| | 6-10 days | 1.44 | 0.49 | 0.99 | 0.00 | 0.13 |
| | 10 day total | 1.47 | 1.35 | 1.07 | 1.14 | 0.28 |
| Sunlight | 0-2 days | 0.00 | 0.64 | 0.51 | 0.10 | 0.00 |
| | 3-5 days | 0.08 | 0.27 | 0.28 | 0.10 | 0.00 |
| | 6-10 days | 0.12 | 0.69 | 1.52 | 0.00 | 1.45 |
| | 10 day total | 0.20 | 1.60 | 2.31 | 0.20 | 1.45 |

Soil Characteristics

Soil textures at each of the sites were predominately loam at all three soil moisture depths. The exceptions were Upper Eagle and Sunlight. Upper Eagle at 30 cm was separated evenly into silt and clay loams. At Sunlight, soils were silt loam in the upper 15 cm and silty and sandy loams at 30 cm. The 60 cm depth was a sandy loam.

Overall, nutrients were most available (nutrients in ppm) at Lower Eagle, and least available at Sunlight and Crystal; however, total nutrients between sites showed Crystal having more potential nutrient availability (% nutrients) for nitrogen (N) and organic matter (OM). Average potentially available soil nutrients in late May showed Crystal having the highest N_T and OM levels and Lower Eagle the most total potassium (K). Crystal Creek also had the most available nitrogen (N) and Lower Eagle far

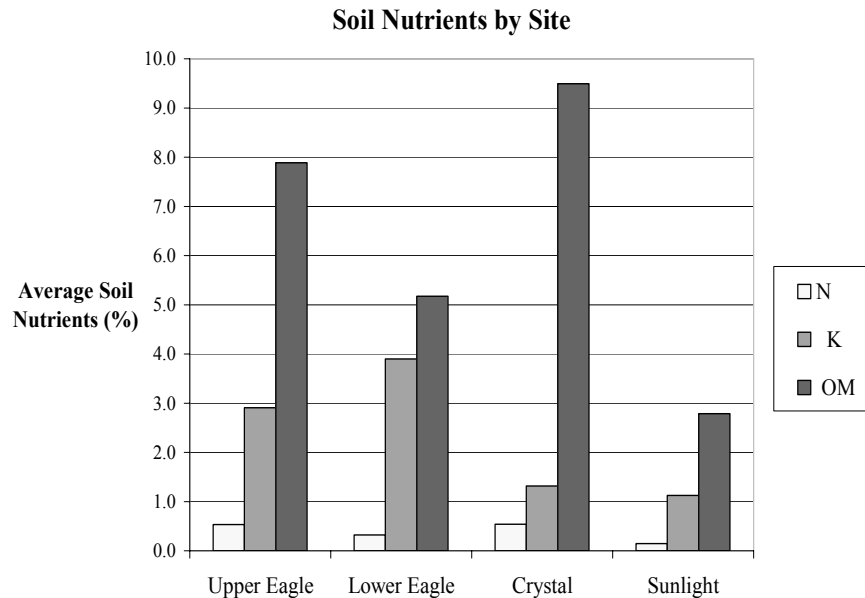


Figure 43: Total (potentially available) soil nutrients per site.

exceeded the other sites in available phosphorus (P). Available K is greatest at Upper and Lower Eagle and lowest at Crystal and Sunlight (Figure 43, Figure 45).

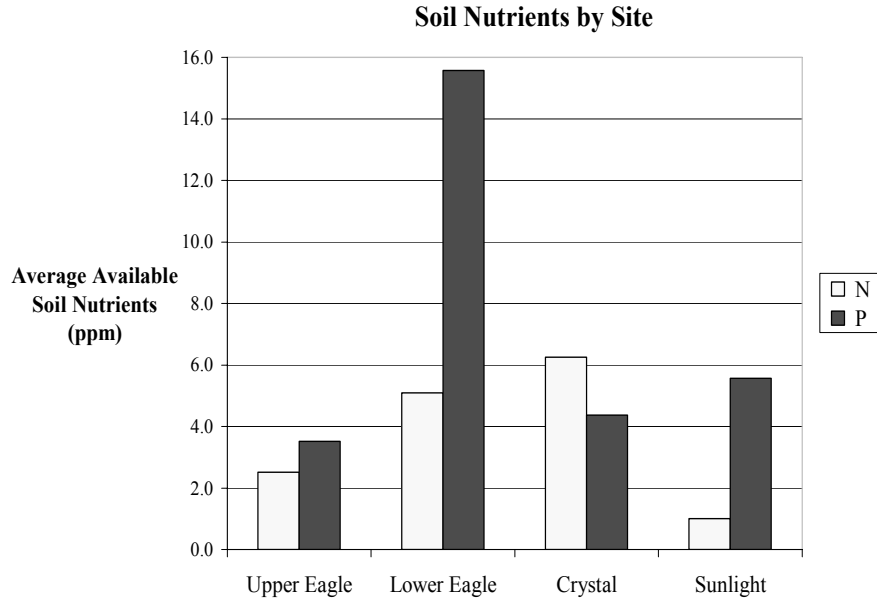


Figure 44: Available nitrogen and phosphorous per site.

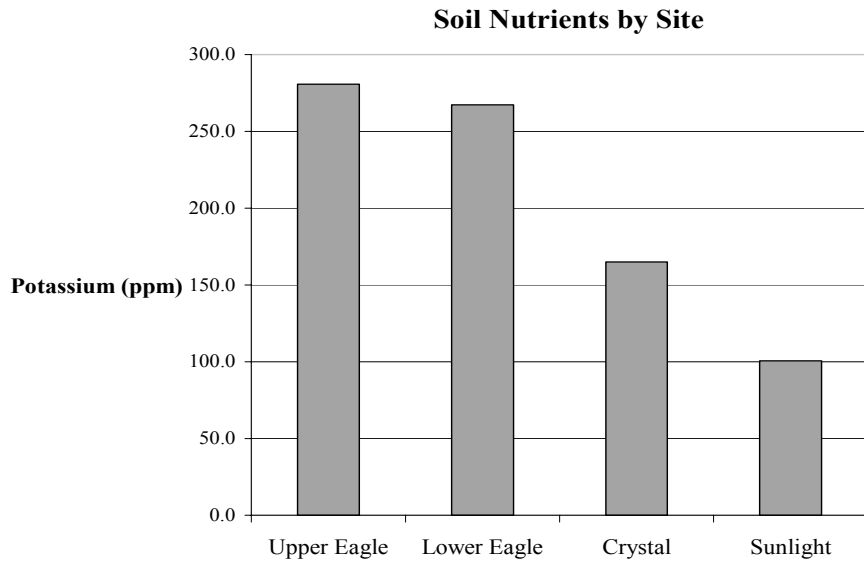


Figure 45: Available potassium per site.

Cross-Species Comparisons

Kruskal-Wallis was used to test whether significant differences between willow groups or populations existed for both the physical and biological parameters (Figure 12). At the Lower Eagle site, the only difference between species occurred in August with the midday water potential readings. At Crystal, in early July there were differences in ψ_{md} and in August for ψ_{md} and growth rates between species. In September at Crystal, soil moisture at 60 cm varied between species. For Sunlight, a number of seasonal differences between species were found. In June, differences existed between species for soil moisture at 60cm. and change in depth to groundwater. In early July, there were differences in ψ_c , ψ_{md} , and again soil moisture at 60cm. Late July showed differences between populations of willow species at both 30 and 60 cm soil moisture which remained through August. Differences in ψ_{pd} between species also occurred in August.

Water Sources

Regression Analyses

Regressions were used to determine the significant factors influencing separate biological parameters: height, growth rate, change in water potential, predawn water potential, and midday water potential (Figure 12). This was done for all willows at each site as a community and for individual willow species at each site (Appendices A & B).

Willow Community. When the regression analysis used all willow species at each site together, height was primarily a function of the depth to groundwater and plant water potential (Table 11). The variability in water potentials were more evenly

explained by predawn and midday groundwater depths and soil moisture at the 30 and 60 cm depths.

Regressions by site and individual species at each site showed a greater number of significant relationships than when all willow species were considered together at each site (Table 12).

Individual Willow Species, Upper Eagle. In June, for Bebb, variability in plant height was explained most by diurnal change in depths to groundwater, and soil moisture at 60 cm (Table 12). Soil moisture at this depth was the highest and the minor fluctuations were apparently enough to explain variability in plant height (Figure 46). So, plants increased in height, with increased soil moisture at 60 cm and change in groundwater depth (midday versus predawn). In addition, this soil moisture depth also explains the variability in ψ_c in June. The plants apparently were using shallow groundwater and deep soil moisture or vadose water, and that deep soil moisture was affecting the change in plant water potential.

During early July, variability in growth rate was explained by ψ_{pd} and ψ_{md} , both of which are slightly more negative than the June readings (Figure 46). Variability in soil moisture at 15 cm best explains the changes in ψ_{pd} indicating this water source continued to be important to plant functions; although soil moisture at this depth was much drier than the other depths. In addition, for this time period, soil moisture at 15 cm was also the driving factor for ψ_{pd} . Height variability is best explained by soil moisture at 30 cm and midday groundwater. As the growth rate increased at this date, ψ_{pd} and ψ_{md}

decreased, and as height increased, there was more moisture at 30 cm and greater depths to midday groundwater (Table 12, Figure 46).

Readings in late July showed ψ_{md} to be linearly related to soil moisture at 15 and 60 cm while there is more moisture available at 30 cm (Table 12, Figure 46). As the moisture readings at 15 and 60 cm increased, growth rates also increased.

Analysis in August showed the growth rate to be related to ψ_m which was more negative than any other readings up to this point in the summer. This was a negative relationship, and showed increased growth rates for those plants with less negative ψ_{md} (i.e., less water stress) (Table 12).

Growth rate was negatively related to soil moisture at 30 cm in September meaning that locations with higher soil moisture had lower growth rates.

Individual Willow Species, Lower Eagle. While Bebb and sandbar willow were both present at this site, there were no significant plant function to environment relationships for sandbar willow until September.

In June, variability in growth rate of Bebb was related to soil moisture at 15 cm which was drier than any other depths at this point (Table 12, Figure 46). The relationship was negative showing decreased soil moisture readings with increased growth rates.

Many relationships were significant in early July. Height variability was explained by soil moisture at 30 and 60 cm. These soil moisture values were drier than the rest of the season's readings. Plants that are taller, at that point, were associated with elevated soil moisture readings at 30 and 60 cm. Growth rate variability was explained by

soil moisture at 60 cm and midday groundwater. Increased growth rates were related to shallow midday groundwater depths, and less soil moisture at 60 cm. Variability in ψ_{pd} was best explained by variability in predawn groundwater and soil moisture at 60 cm. Although, soil moisture at this depth was wettest of all three depths, the relationship showed decreased ψ_{pd} when predawn depth to groundwater was shallow and soil moisture at 60 cm dropped. Midday water potential was also related to deep soil moisture but in a positive relationship; decreased midday water potential occurred when soil moisture at 60 cm. was most moist. Since all parameters having significant relationships included 60 cm soil moisture, it might be inferred that both height and growth rate were also related to variability of ψ_{pd} and ψ_{md} and their relationships.

Later in July height was related to soil moisture at 60 cm and midday groundwater. This was the deepest groundwater for the growing season (Figure 46), and its relationship to height was negative meaning that taller plants were at locations with higher soil moisture at 60 cm and shallower groundwater. Variability in ψ_{pd} was explained by soil moisture at 30 cm and daily fluctuation in groundwater, and this also was a negative relationship where ψ_{pd} decreased when soil moisture was high and there was very little diurnal groundwater change. However, at this time 30 cm was the wettest soil layer, and while groundwater was deepest at this point, there was virtually no change between predawn and midday depths. Midday water potential variability was related to soil moisture at 15 cm and, similar to ψ_{pd} , by the diurnal change in groundwater. Again this was a negative relationship with increased ψ_{md} occurring when soil moisture was dry and there was very little change in groundwater.

In August ψ_{pd} was related to soil moisture at 30 cm, and showed more negative water potential (i.e., more plant water stress) when soil moisture was dry.

In September, sandbar willow exhibited significant relationships between growth rate and ψ_{md} . Plants exhibiting higher growth rates had more negative ψ_{md} . For Bebb, there were significant relationships for growth rate, height, and predawn water potential. Growth rate was related to midday groundwater in that plants at locations with deeper groundwater had higher growth rates for this time of year. Height showed a positive relationship with change in groundwater with taller plants occurring at sites with greater changes between predawn and midday groundwater readings. Predawn water potential was also positively related to predawn depth to groundwater with the more negative ψ_{pd} occurring with greater depths to groundwater.

Individual Willow Species, Crystal. In June, Bebb willow showed significant relationships between physical parameters and height, ψ_c , ψ_{pd} , and ψ_{md} . Taller plants were found at locations with greater depths to predawn groundwater. Daily fluctuation, ψ_c , and ψ_{pd} were both related to soil moisture at 60 cm. These were both negative relationships with increased ψ_c and decreased ψ_{pd} generally having drier soil moisture. Midday water potential relationships showed decreased water potentials when soil moisture at 15 and 30 cm. was dry. Booth had the same significant relationships as Bebb between ψ_c and the 60 cm soil moisture depth; the same type negative relationship existed for ψ_{md} and 60 cm soil moisture.

Relationships between plant functions and physical parameters for Bebb were found for height, ψ_c and ψ_{pd} in early July. Height was again positively related to predawn

depth to groundwater. Daily water potential fluctuation was greatest when daily groundwater fluctuation was greatest and soil moisture at 60 cm was wettest. Regression analysis showed ψ_{pd} was greatest when soil moisture at 15 cm was most dry. For Booth, height, growth rate, ψ_c and ψ_{pd} had linear relationships with various physical parameters. Height was positively related to predawn depth to groundwater the same as Bebb. Growth rate was greatest when diurnal change in water potential was small, while ψ_c was related to soil moisture at 60 cm and midday groundwater depth. Regression analysis showed that ψ_c increased when the midday depth to groundwater and soil moisture decreased.

For Bebb willow, in late July, taller plants were related to less diurnal fluctuation in groundwater depth (Table 12). This part of the month also showed midday groundwater being shallower than predawn groundwater (Figure 46). Booth plants showed growth rates being related to soil moisture at 15 cm and midday groundwater in that the regression showed increased growth present for plants with drier, shallow soil moisture and shallower depths to midday groundwater.

In August for Bebb, the relationship between height and predawn depth to groundwater again was significant with taller plants being related to greater depths to predawn groundwater.

Height and midday water potential for Bebb species were significantly related. Consistent with the previous months, taller plants were related to deeper predawn groundwater. Midday water potential was most negative when shallow soil

moisture was dry. Booth ψ_c was negatively related to soil moisture at 60 cm indicating that ψ_c was greatest when deep soils (60cm) had lower water contents (Figure 46).

Individual Willow Species, Sunlight. In June, at Sunlight, several physical parameters were significantly related to Booth growth rate, ψ_c , and ψ_{md} . Growth rate showed two equally significant multiple regressions (Table 12). Plants had higher growth rates when the change in depth to groundwater was small and when there was shallow predawn groundwater. Growth rates were also higher when diurnal groundwater fluctuation was small and when there was shallow midday groundwater. In this instance, predawn groundwater was deeper than midday groundwater. Change in water potential was greatest when the change between predawn and midday groundwater depths was small and shallow soils (15cm) had higher moisture contents. Consequently, growth rate was indirectly related to those factors influencing change in groundwater. Midday water potential was greatest when predawn groundwater was deep and soil moisture at 60 cm had a high moisture content.

Regressions showed that both Booth and Geyer had significant relationships in early July between plant functions or plant functions and physical parameters. Taller Booth plants had more negative ψ_{pd} values, and Geyer plants with higher growth rates had shallower predawn groundwater.

In late July, ψ_{pd} for Booth was more negative when midday groundwater was shallow and soil at 60 cm was wetter. Taller Geyer plants were associated with shallower predawn groundwater.

During August, Booth ψ_c was greatest when midday groundwater was deep. Geyer plants that are taller generally had smaller ψ_c .

In September, significant relationships between plant functions and physical parameters existed for height, growth rate, and ψ_{md} for Booth. Regressions show that when midday groundwater is shallow, plants are taller and growth rates are highest when both predawn and midday groundwater depths are shallow. Midday water potentials were more negative at this point when there was shallow predawn groundwater and shallow soils were moist (Table 12). Geyer growth rates were related to different sets of parameters based on two equally significant multiple regressions. Growth rates were greatest where there were greater changes between predawn and midday groundwater depth and shallow soils (15 cm) were dry. In addition, they were great when again there was a greater change in depths to groundwater and soil moisture at 30 cm was dry. At this time in the season when groundwater change became a significant factor, midday groundwater was shallower than predawn water elevations.

Table 11: Willow community relationships by site and major parameter for the 2004 growing season and each individual site visit. The tables show the major parameter being a function of the linear relationship between it and the simple or multiple regression factors in the below table. GW = groundwater, SM = soil moisture, ψ = water potential, p = predawn, m = midday, and c = change in, & = R2 and p-values were the same or each equally important, + = a multiple regression, and 15, 30, and 60 are the soil moisture reading depths. Dashed segments indicate nothing of significance was found. Bolded regression results signify a negative relationship, and italicized & underlined values indicate a relationship between water potential and growth regression results.

| HEIGHT ^{2,3} | | | | | | |
|--|----------------------|----------------------|------------|-----------------|---------------------------|--|
| Site | 2004 | June | Early July | Late July | August | September |
| Upper Eagle | --- | --- | --- | --- | --- | --- |
| Lower Eagle | GWc+SM30 | --- | --- | GWm | Ψm | GWm |
| Crystal | --- | --- | GWp | GWc | <u>GWp</u> | --- |
| Sunlight | --- | --- | Ψ m | --- | Ψc | GWm |
| GROWTH RATE (CM/DAY) ^{2,3} | | | | | | |
| Site | 2004 | June | Early July | Late July | August | September |
| Upper Eagle | --- | --- | --- | --- | --- | --- |
| Lower Eagle | --- | --- | --- | --- | --- | <u>Ψp+Ψm</u> |
| Crystal | --- | --- | GWp+SM15 | --- | --- | --- |
| Sunlight | --- | GWc | --- | --- | --- | GWc |
| CHANGE IN WATER POTENTIAL ^{2,3} | | | | | | |
| Site | 2004 | June | Early July | Late July | August | September |
| Upper Eagle | GWp+SM15 | --- | --- | --- | --- | --- |
| Lower Eagle | --- | --- | --- | --- | --- | SM60 |
| Crystal | --- | GWc | --- | --- | --- | --- |
| Sunlight | --- | GWp | --- | --- | GWm | --- |
| PREDAWN WATER POTENTIAL ^{2,3} | | | | | | |
| Site | 2004 | June | Early July | Late July | August | September |
| Upper Eagle | --- | --- | --- | --- | --- | --- |
| Lower Eagle | --- | --- | --- | SM15 | SM30 | <u>GWc</u> |
| Crystal | GWc+SM30+SM60 | SM15 | --- | --- | <u>GWp</u> | --- |
| Sunlight | --- | GWc | --- | SM60 | --- | --- |
| MIDDAY WATER POTENTIAL ^{2,3} | | | | | | |
| Site | 2004 | June | Early July | Late July | August | September |
| Upper Eagle | --- | --- | --- | --- | --- | --- |
| Lower Eagle | --- | --- | --- | GWc+SM15 | --- | --- |
| Crystal | SM15+SM60 | SM60 | --- | --- | --- | --- |
| Sunlight | --- | GWp+SM15+SM60 | --- | GWc+SM60 | GWm | --- |

Table 12: Regression result for each site by species and major parameter for the 2004 growing season and each individual site visit. The tables show the major parameter being a function of the linear relationship between it and the simple or multiple regression factors in the below table. GW = depth to groundwater, SM = soil moisture, ψ = water potential, p = predawn, m = midday, and c = change in, & = R2 and p-values were the same or each equally important, + = a multiple regression, and 15, 30, and 60 are the soil moisture reading depths. Dashed marks indicate nothing of significance was found. Similarly highlighted columns represent the same species at different sites. Non-highlighted segments are not species shared between sites. Bolded regression results signify a negative linear relationship, and italicized and underlined parameters indicate a relationship between water potential and growth (height or growth rate).

| HEIGHT ^{2,3} | | | | | | | |
|-------------------------------------|------------------|--------------------------|---|--|------------------------|---------------------------|------------------------|
| Site | Species | 2004 | June | Early July | Late July | August | September |
| Upper Eagle | <i>bebbiana</i> | --- | <u>GWc+<i>SM60</i></u> | GWm+SM30 | --- | --- | --- |
| Lower Eagle | <i>bebbiana</i> | GWm+SM30+ <u>SM60</u> | --- | SM30+SM60 | GWm+<u>SM30</u> | --- | GWc |
| | <i>exigua</i> | SM60 | --- | --- | --- | --- | --- |
| Crystal | <i>bebbiana</i> | GWp+SM15 | GWp | GWp | GWc | GWp | GWp |
| | <i>boothii</i> | SM15 | --- | GWp | --- | --- | --- |
| Sunlight | <i>geyeriana</i> | --- | --- | --- | GWp | Ψc | --- |
| | <i>boothii</i> | --- | --- | Ψp | --- | --- | GWm |
| GROWTH RATE (CM/DAY) ^{2,3} | | | | | | | |
| Site | Species | 2004 | June | Early July | Late July | August | September |
| Upper Eagle | <i>bebbiana</i> | --- | --- | <u>Ψp+Ψm</u> | --- | Ψm | SM30 |
| Lower Eagle | <i>bebbiana</i> | GWm+SM15 | SM15 | GWm+SM60 | --- | --- | GWm |
| | <i>exigua</i> | GWp+SM60 | --- | --- | --- | --- | Ψ m |
| Crystal | <i>bebbiana</i> | --- | --- | --- | GWp & GWm | --- | --- |
| | <i>boothii</i> | --- | --- | Ψc | GWm+SM15 | --- | --- |
| Sunlight | <i>geyeriana</i> | GWp+SM30 | --- | GWp | --- | --- | GWc+SM15 & GWc+SM30 |
| | <i>boothii</i> | --- | GWc+<u>GWp</u> & GWc+GWm | --- | --- | --- | <u>GWp</u>+GWm |

² For Upper Eagle, there were no groundwater readings for August and September of 2004; as the wells were dry.

³ For Lower Eagle, there were no groundwater readings for August; as the wells were dry.

| CHANGE IN WATER POTENTIAL ^{2,3} | | | | | | | |
|--|------------------|---------------------------------|------------------------|------------------------|------------------------|-------------|-----------------|
| Site | Species | 2004 | June | Early July | Late July | August | September |
| Upper Eagle | <i>bebbiana</i> | --- | <u>SM60</u> | --- | --- | --- | --- |
| Lower Eagle | <i>bebbiana</i> | --- | --- | --- | --- | --- | --- |
| | <i>exigua</i> | --- | --- | --- | --- | --- | --- |
| Crystal | <i>bebbiana</i> | --- | SM60 | GWc+SM60 | --- | --- | --- |
| | <i>boothii</i> | GWc | SM60 | <u>GWm+SM60</u> | --- | --- | SM60 |
| Sunlight | <i>geyeriana</i> | --- | --- | --- | --- | --- | --- |
| | <i>boothii</i> | --- | <u>GWc+SM15</u> | --- | --- | GWm | --- |
| PREDAWN WATER POTENTIAL ^{2,3} | | | | | | | |
| Site | Species | 2004 | June | Early July | Late July | August | September |
| Upper Eagle | <i>bebbiana</i> | --- | --- | SM15 | --- | --- | --- |
| Lower Eagle | <i>bebbiana</i> | --- | --- | <u>GWp+SM60</u> | <u>GWc+SM30</u> | SM30 | GWp |
| | <i>exigua</i> | --- | --- | --- | --- | --- | --- |
| Crystal | <i>bebbiana</i> | GWc+SM15+ SM60 | SM60 | SM15 | --- | --- | --- |
| | <i>boothii</i> | SM30+GWc | --- | --- | --- | --- | --- |
| Sunlight | <i>geyeriana</i> | --- | --- | --- | --- | --- | --- |
| | <i>boothii</i> | --- | --- | --- | GWm+SM60 | --- | --- |
| MIDDAY WATER POTENTIAL ^{2,3} | | | | | | | |
| Site | Species | 2004 | June | Early July | Late July | August | September |
| Upper Eagle | <i>bebbiana</i> | --- | --- | --- | SM15+SM60 | --- | --- |
| Lower Eagle | <i>bebbiana</i> | --- | --- | SM60 | GWc+SM15 | --- | --- |
| | <i>exigua</i> | --- | --- | --- | --- | --- | --- |
| Crystal | <i>bebbiana</i> | SM15+SM60 | SM15+SM30 | --- | --- | --- | SM15 |
| | <i>boothii</i> | SM15+SM60 | SM60 | --- | --- | --- | --- |
| Sunlight | <i>geyeriana</i> | GWm | --- | --- | --- | --- | --- |
| | <i>boothii</i> | --- | GWp+SM60 | --- | --- | --- | SM15+GWp |

| UPPER EAGLE | | | | | | |
|--------------------|-------------------|----|----|------------------|------|--------|
| Month/Spp. | Soil Moisture (%) | | | Groundwater (cm) | | |
| | 15 | 30 | 60 | Pre | Mid | Change |
| June Bebb | 65 | 77 | 87 | 14.5 | 16.8 | 2.2 |
| Early July Bebb | 65 | 77 | 87 | 22.8 | 25.4 | 2.6 |
| Late July Bebb | 93 | 98 | 94 | 45.3 | 46.0 | 0.7 |
| August Bebb | 93 | 98 | 94 | --- | --- | --- |
| September Bebb | 90 | 91 | 95 | --- | --- | --- |

| LOWER EAGLE | | | | | | |
|--------------------|-------------------|----|----|------------------|------|--------|
| Month/Spp. | Soil Moisture (%) | | | Groundwater (cm) | | |
| | 15 | 30 | 60 | Pre | Mid | Change |
| June Bebb | 63 | 81 | 89 | 21.6 | 28.0 | 6.3 |
| Exigua | 43 | 75 | 89 | 18.3 | 16.1 | -2.1 |
| Early July Bebb | 61 | 82 | 87 | 53.3 | 58.0 | 4.7 |
| Exigua | 44 | 75 | 88 | --- | --- | --- |
| Late July Bebb | 90 | 92 | 89 | 60.8 | 62.0 | 1.2 |
| Exigua | 93 | 95 | 90 | --- | --- | --- |
| August Bebb | 87 | 90 | 87 | 49.5 | 47.5 | -2.0 |
| Exigua | 92 | 93 | 88 | --- | --- | --- |
| September Bebb | 73 | 80 | 88 | 61.0 | 56.9 | 1.8 |
| Exigua | 71 | 77 | 86 | --- | --- | --- |

| CRYSTAL | | | | | | |
|--------------------|-------------------|----|-----|------------------|-------|--------|
| Month/Spp. | Soil Moisture (%) | | | Groundwater (cm) | | |
| | 15 | 30 | 60 | Pre | Mid | Change |
| June Bebb | 95 | 99 | 107 | 45.8 | 46.2 | 0.3 |
| Booth | 95 | 97 | 99 | 44.1 | 43.9 | -0.2 |
| Early July Bebb | 95 | 98 | 99 | 49.9 | 53.9 | 0.7 |
| Booth | 93 | 94 | 98 | 43.3 | 53.1 | 1.4 |
| Late July Bebb | 93 | 97 | 99 | 69.8 | 68.5 | -1.3 |
| Booth | 90 | 94 | 96 | 70.7 | 69.2 | -1.5 |
| August Bebb | 80 | 89 | 97 | 67.6 | 65.0 | 2.0 |
| Booth | 74 | 83 | 92 | 70.0 | --- | --- |
| September Bebb | 71 | 80 | 94 | 89.9 | 88.6 | -0.2 |
| Booth | 66 | 75 | 88 | 106 | 100.3 | 0.0 |

| SUNLIGHT | | | | | | |
|---------------------|-------------------|----|----|------------------|------|--------|
| Month/Spp. | Soil Moisture (%) | | | Groundwater (cm) | | |
| | 15 | 30 | 60 | Pre | Mid | Change |
| June Booth | 76 | 79 | 90 | 46.4 | 44.7 | -1.7 |
| Geyer | 74 | 53 | 80 | 50.7 | 51.7 | 1.0 |
| Early July Booth | 82 | 80 | 90 | 64.2 | 66.3 | 2.1 |
| Geyer | 72 | 51 | 82 | 72.7 | 73.6 | 0.87 |
| Late July Booth | 80 | 78 | 73 | 71.0 | 72.3 | 1.3 |
| Geyer | 62 | 41 | 31 | 77.5 | 79.0 | 1.5 |
| August Booth | 69 | 72 | 67 | 79.4 | 79.8 | 0.3 |
| Geyer | 48 | 39 | 47 | 87.0 | 86.7 | -0.2 |
| September Booth | 75 | 75 | 77 | 80.3 | 83.1 | 2.7 |
| Geyer | 59 | 41 | 44 | 86.5 | 81.5 | -5.0 |

Height
 Growth Rate
 Ψ_p
 Ψ_m
 Ψ_c

Figure 46: A supplemental figure to (Table 12). Significant linear relationships by site and species between soil moisture at three depths and groundwater (predawn, midday, and change in) to height, growth rate, and predawn, midday, and change in water potential based on water availability. Soil moisture values are percent soil moisture and groundwater readings are depth to groundwater or the change between the predawn and midday readings.

Isotope Analysis

The use of $\delta^{18}\text{O}$ revealed plant water source by individual species and plant location in August and September at Crystal Creek; the two dates allowed for assessment of water source changes between months. General trends for soil moisture results show enrichment throughout the season indicating potential fractionation due to increased evaporative demand and decreased precipitation. In August, the water source grouping was much tighter about soil moisture with only one plant departing from these sources. In addition, end member values (isotope signatures) between the two soil moisture depths were less unique than earlier in the season. Plant B1 is most likely taking advantage of a rainfall event that has had time to infiltrate into shallow soil layers. In contrast, Geyer and B3 were using deeper soil moisture such as vadose water at this time. In September, the plants became more spread out, and there were small shifts between plants. B1 shifts to potentially deeper soil moisture, Geyer to shallower, and B2 most likely taking advantage of a rainfall event. B3, on the other hand, remains using deeper soil moisture or a combination of soil and stream/groundwater. (Table 12, Figure 47).

When comparing the results based on distance from the stream, those plants closest to the stream on the west bank remained using deep soil moisture or vadose water while those on the east bank also remained fairly consistent between August and September. Those plants closest to the east bank tended to use shallow soil moisture and may have been taking advantage of some precipitation events. Those plants farther from the stream showed more variability in water source between times during the late growing season. In August, those plants farthest from the stream on both banks were

using soil moisture. However, in September, those plants on the west bank remained using water from deeper soils while those on the east bank changed water source drastically to the use of precipitation derived water (Figure 48).

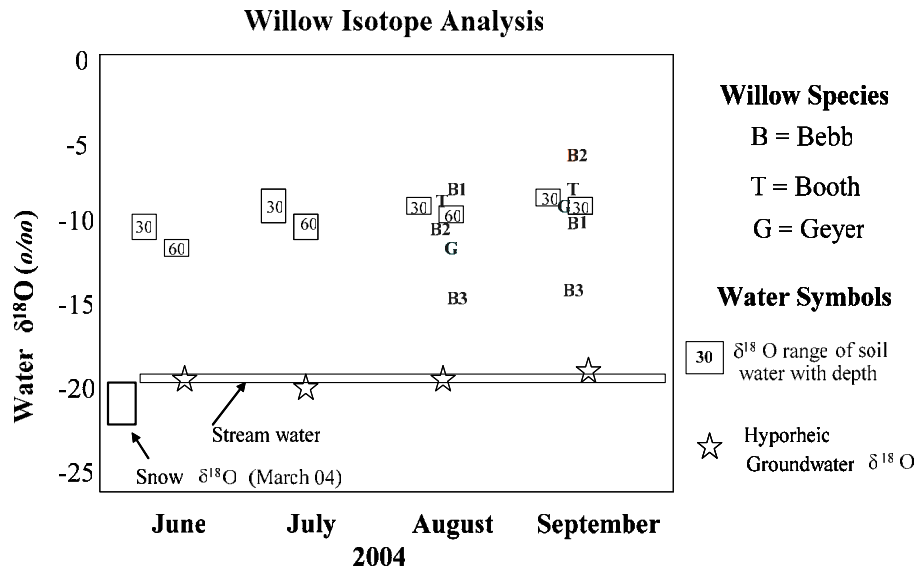


Figure 47: Results of δ¹⁸O analysis by individual species for Crystal Creek. Following the species designation, numbers were assigned to designate the same individual between months.

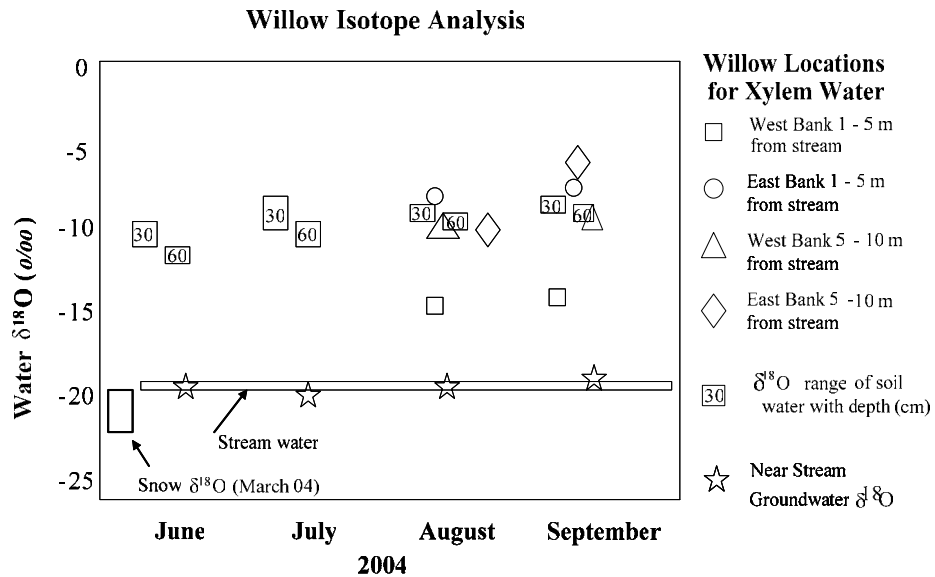


Figure 48: Results of δ¹⁸O analysis grouping species by distances from the surface water source at Crystal Creek.

DISCUSSION

The fate of willows in the northern range of Yellowstone has been a major point of contention among scientists, resource agencies and Yellowstone National Park (NRC 2002a). Excess browsing and changing climate are often suggested as the cause of the willow decline, but other factors may come into play as willows respond to browsing with summer regrowth (Baker 1990, Singer et al. 1994, Chadde and Kay 1996, Romme et al. 1997, Singer et al. 1998, Ripple and Larsen 2000, Beschta 2003). This study was designed to determine willow response to browse and different environments. Sites were selected to produce heterogeneity among environments and species, consequently, there was little expectation of a finding of uniformity among sites and species; although some common themes were expected.

These results do suggest few discernable relationships for willow communities as a whole but with definite differences between species at individual sites, for example, the timing of plant responses between the four hydrologic settings. On the other hand, some consistencies were found for individual species that transcend the physical and biologic differences among sites and persist regardless of location.

Vegetative Composition

Each of the sites in this study represented unique flow regimes, and it is recognized that variation in flows or water regime are dominant factors in the development or riparian plant community character and composition (Baker 1990, Busch et al. 1992, Scott et al. 1997, Michener and Haeuber 1998, Shafroth et al. 2002, Beschta

2003). In addition, the community diversity resulting from fluvial dynamics is also increased based on the degree of hydrologic connectivity (Amoros and Bornette 2002). Flow variation (as represented by seasonal water table fluctuations and stage measurements) between the four sites exists between sites as well as through their individual seasonal fluctuations. Of the four sites, the beaver dam has the highest likelihood for providing flood conditions of which frequency and duration impact community establishment (Casanova and Brock 2000). Our results showed Sunlight and Lower Eagle having the highest species diversity in general. They are vegetatively and hydrologically least similar but most diverse, particularly for graminoids and forbs. These type plants appear to be most diverse where there is either frequent flooding and water is not a limited resource early in the season or on sites that are generally moisture limited. The beaver dam site, while exhibiting flood conditions early in the season, actually becomes an anoxic environment serving as a medium for growth and not a resource for water (Thorburn et al. 1993). At Sunlight, the sandier soil textures provided little water holding capacity, and this larger mountain stream was also the most groundwater limited system of the four sites. Crystal, where the depth to groundwater was approximately an average of the previous two, had the most willow diversity. Willow are recognized as shallow groundwater indicators, and changes in groundwater are known to initiate changes in riparian communities (Busch et al. 1992); however, their distribution is also a function of water table depth, rooting characteristics, and textures and hydraulic conductivity of soil substrates (Amlin and Rood 2002). The results suggest that while they are indicators of shallow groundwater, their diversity and abundance are

also a function of the degree of shallow groundwater where water conditions are not characteristic of the extremes (saturation and soils with limited water availability).

Willow Structure & Establishment

Willow species in this study had different wetland status designations, which might result in species individuality and little similarity in functional attributes. Bebb and Geyer willow are both facultative wetland species, while Booth and sandbar willow are obligate wetland species, and each is dependent on different water sources. Bebb and Geyer are expected to establish where there is available soil water and depend primarily on wetted soil in the unsaturated zone while the obligate plants rely mostly on surface and groundwater (Hansen 1992, Patten 1998).

However, while willow species are thought to establish where there are multiple water sources (Shafroth et al. 2000), in this study, they appear to persist on sites that are soil moisture limited early in the season. Soil moisture at both Upper and Lower Eagle are quite dry for the upper two depths early in the season, and yet the dominant species, Bebb, a facultative wetland species, is adapted to relying predominantly on these water sources (NRCS 2005). While much of the literature describes willow as being specialists relying predominantly on specific water sources (Hansen 1992, Smith et al. 1998, Shafroth et al. 2000), this research suggest that they are foremost generalist, opportunistic plants with perhaps preferred water sources but capable of shifting to utilize water where it's most available (See *Regression Results* section).

Willow Browse & Compensatory Growth

Repeated or chronic browsing of woody plants is said to reduce belowground carbon reserves required for rapid vertical growth recovery, and plant growth-form and size act as determinants of photosynthetic gain or potential, nutrient uptake, and reproduction. Directly related to photosynthetic potential are height and crown growth (Brookshire et al. 2002). Other research shows that willow respond to disturbances (including herbivory) with rapid growth, but that repeated browse causes long-term growth suppression or limited compensatory growth responses (Brookshire et al. 2002). Plant stature or initial height of willow at the beginning of the growing season was considered a potential factor influencing seasonal growth in this study. However, early season plant stature per se does not appear to be a major control on plant growth, but the amount of winter browse a plant is subject to does impact its subsequent summer growth. Plants browsed less than 20 cm (height loss) generally exhibit the most summer growth followed by those plants browsed between 20 and 40 cm. In addition, specifically for Bebb willow, plants browsed less than 40 cm, there are obvious regrowth gradients between sites suggesting other environmental controls on growth. Browse levels > 40 cm showed very little regrowth and often few distinctions between browse classes. One possible reason for the reduced growth responses for plants browsed more than 40 cm, in addition to the above research, is that the degree of winter browsing is also critical to subsequent vertical growth.

There was also preferential browsing; though comparisons could only be made between species at individual sites, since all species weren't present at each site. When

the following willow species were present in combination, Booth was preferred over Bebb, Bebb over sandbar willow, and Geyer over Booth and Bebb. In several instances, plants less available at each site were sought out over those more prevalent. No ready explanation can be given for this plant selection, but preference based on protein or energy value is unlikely since each of these species have equal energy and protein values (Hansen 1992). Other possible explanations for preferential browsing are the concentrations of secondary chemicals in plant tissues, as plants with lower concentrations are preferentially selected by herbivores (Singer et al. 1994, Singer and Renkin 1995, Wagner et al. 1995, Brookshire et al. 2002, NRC 2002b).

Recovery growth in response to browse loss was greatest at Crystal, followed by Sunlight, Lower Eagle, and then Upper Eagle. This order of sites also represents the order of magnitude of winter browse. This growth may result from both Booth and Geyer having higher biomass potentials (i.e., standing crop) than Bebb and sandbar willow on an annual basis (Hansen 1992). This is however just potential biomass, and while Booth is present at Crystal, Bebb is the dominant species which suggests that other environmental factors were governing plant growth. Growth rates of any one species common to more than one site are consistent and seem to override differences in other environmental constraints.

Willow Relationships with the Physical and Biologic Parameters

Multiple linear relationships were determined between the physical and biologic parameters and willow growth, and in finding these relationships, the existence and importance of other physiological characteristics for willow at all sites were revealed.

Physiological Characteristics

One of the overall trends for willow at the three free-flowing (i.e., no beaver dam) sites was decreasing ψ_{md} and increasing ψ_{pd} as the growing season progressed, indicating an inability of the plants to maintain maximum hydration throughout the day. Because of decreasing water availability, the midday decrease was expected; however, the ψ_{pd} increases throughout the season was not expected. This might be explained by a plant physiologic response to long-term drought stress in that, in plants under water stress respond with osmotic adjustments as well as a thickening of the leaf cuticle which allows for increased water retention (Orcutt 1987). Decreased water potentials have also been reported for browsed plants versus unbrowsed plants (Alstad et al. 1999). These findings, relative to ψ_{pd} , support the potential for both willow earlier in the season showing physiologic signs of browse pressure, and as water sources generally become less available, willow respond by developing thicker cuticular tissue.

Interrelationships Among Biologic and Physical Factors

The relationships among biotic and physical factors suggest possible shifts in water sources used by willows. While Bebb is a facultative wetland species, it appears to

be most opportunistic utilizing groundwater much of the time, or at least using soil moisture in combination with groundwater. On the other hand, Booth willow appears to be more of a specialist, showing predominantly plant functional relationships, such as growth and water potential responses, to groundwater sources.

Plant Height. The only significant relationships between the biotic variable plant height and physical factors for Bebb willow through the growing season are quite different for both Upper and Lower Eagle compared to Crystal. At the Eagle sites, taller plants generally occurred where 30 and 60 cm soils retained the most moisture. There is however, a time delay to when these parameters become significant. Upper Eagle has a significant height/soil water relationship with moisture at 60 cm in June and at 30 cm soil in early July, while this relationship doesn't become significant until early and late July at Lower Eagle. This latter phenomenon is probably a result of the increased water holding capacity of the beaver dammed system. Soil moisture regime is either a product of precipitation, overland flow events, or groundwater regimes, and that soil moisture can be used to explain the temporal dynamics of specific ecosystems (Castelli et al. 2000) and to some degree, the timing of the shifts between available soil moisture. These results cannot however explain shifts from deeper to shallower soil moisture later in the season. No identifiable trends for height/ groundwater relationships were found for the Eagle sites. However, the Crystal site appears to be much more influenced by groundwater fluctuations relative to height of Bebb. Taller plants were generally located where there was the greatest depth to predawn groundwater perhaps a function of tall plants having deeper root systems which can readily utilize deep groundwater, but this resource

significance is counter-intuitive to this species' wetland status. No consistent relationships could be determined for the Sunlight site. In general, height may be an indicator of areas having resources conducive for establishment; as multiple resource options are highly influential for plant establishment (Shafroth et al. 1998, Shafroth et al. 2000, Karrenberg et al. 2002), and these regression relationships may be more indicative of conditions where they are able to persist but do not fully explain plant growth.

Growth Rates. Willow growth rates appear to be a function of the same biophysical relationships for all sites and species, but with distinct temporal differences. While these differences are indicative of the parameters most influential to both obligate and facultative species (Hansen 1992, Patten 1998, Shafroth et al. 2000, Beschta 2003), these results provide support for willow being capable of becoming generalist phreatophytes, typical to moisture limited environments, taking water whenever and wherever it's available (Schwinning and Ehleringer 2001). In this study, growth rates were generally found to be higher where soil moisture was drier (typically at 30 and 60 cm), and where midday groundwater is most shallow. The soil moisture parameters typically precede groundwater significance. Occurrence of significance for growth/soil moisture relationships changes seasonally by site: Lower Eagle in June and early July, Crystal in August, and Upper Eagle and Sunlight in September. External factors that drive soil moisture, especially rainfall patterns, may influence this phenomenon.

Relationships between growth rate and groundwater becomes significant when midday groundwater is shallow or when there is little diurnal fluctuation in groundwater (relative to each specific sampling date); however this is usually less significant or co-

significant with the soil moisture relations. Upper Eagle, a site with a small intermittent stream, has no significant growth rate/groundwater relationships. Similar to soil water relationships, occurrence of significant growth/groundwater relationships change over time for each site: Lower Eagle in late July, Crystal in August, and Sunlight in September.

In other riparian systems, the same shifts from soil moisture or surface runoff to groundwater also were documented as groundwater, surface flows, and soil water diminished (Busch et al. 1992). However, in this study, because of the comparisons between different hydrologic sites, there is evidence to suggest hydrologic controls and thresholds influence growth. Timing and type of significance may indicate the existence of specific thresholds for plant growth relative to limited water sources or decreased midday plant water stress. As one water source (i.e., soil moisture) becomes depleted, plants respond with increased growth perhaps triggering the shift to other sources (i.e., groundwater). However, while higher growth rates exist under these conditions, they are not comparable to initial early season growth rates, as the degree of growth under increased stress was magnitudes smaller.

In some instances, growth rates were related to water potential, which helps explain the full water-stress/growth relationships, that is, water stress is often a function of available water. At Upper Eagle ψ_{pd} became more negative when soil moisture at 15 cm was most moist, and the negative water potentials were related to higher growth rates. At Crystal in early July there were higher growth rates where there was little ψ_c , and the ψ_c was smallest when there was deeper midday groundwater and more soil water at 60

cm (though to a lesser degree than earlier in the season). These relationships do show an extended picture but do not provide full explanations; for example, why plants are not utilizing the available water at Upper Eagle. Relationships at Crystal are somewhat clearer and indicate that plants may be using water from deeper soil moisture layers both predawn and midday where it is most available resulting in smaller differences in the diurnal plant water stress fluctuations and consequent growth. Suggested conclusions are that increased water stress or small changes in diurnal water stress promote growth. Other implications of this data are that hydrological connectivity within these sites is not strong throughout the entire growing season, and thus plant functions shift between hydrologic and plant water relations both seasonally and temporally.

Water Status. Plant water potential is a function of water availability and transpirational loss of water (Porporato et al. 2001). It is a measure of plant stress as water uptake cannot keep up with water loss. The willows had few connections between those factors that impact plant water stress and how that stress in turn affects plant growth (Figure 12). Water potential is the link between water availability and growth, but these results show limited occurrence of these relationships. However, in some instances, parameters related to water potentials were also related to either growth rate or height. So, while water potential does not appear significant, it could potentially be inferred as important based on common parameters influencing both the growth and water potential during the same time period. For instance, at Upper Eagle in June, ψ_c and height are related to 60 cm soil moisture, and in late July at Lower Eagle, 30 cm soil moisture influences both ψ_{pd} and height. At Lower Eagle decreased soil moisture

resulted in decreased ψ_{pd} and taller plants also occurred where soils were most dry. This may imply that plants are able to maintain themselves in areas with increased water stress (given that significant relationships related to height were concluded to represent plant persistence but not resilience (i.e., ability to recover from a disturbance) in this study).

Few linear relationships existed between ψ_c , and other biophysical factors. The apparent connections that can be made are for Crystal, Lower, and Upper Eagle where soil moisture was most commonly related ψ_c , but there is no consistency with either positive or negative relationships.

There were no distinct differences in factors influencing ψ_{pd} and ψ_{md} between sites. As a generalization, when ψ_{pd} was more negative, there was less soil water (most often at 60 cm). For ψ_{md} , most relationships explaining variability were with soil moisture, but no consistent significant relationships existed.

In general, this study cannot provide detailed information on the relationships between plant water stress and plant growth.

Willow Water Source

The discussion above indicates a great deal of variability in willow water relations and factors which may influence them. Knowing when and where willow plants obtain water may help explain some of the apparent conundrums. Water from multiple sources can be identified, as the unsaturated and saturated zones can typically be distinguished based on degree of enrichment (Busch et al. 1992). Water extracted from plant xylem tissue prior to evaporative and transporational demands are isotopically equivalent to

water absorbed by the roots (Busch et al. 1992, Brunel et al. 1995, Dodd et al. 1998, Smith et al. 1998) and may also provide insight into root structure and function (Busch et al. 1992, Brunel et al. 1995, Dodd et al. 1998, Smith et al. 1998, Snyder and Williams 2000). Within each of the plant tissues, soil water was most prominent with some exceptions of very deep and very shallow soil moisture or rain water. This information supports regression results relating soil water to water potential, and suggests that not only are there significant relationships but that these relationships support an argument for causation. The water source data may also validate other process related relationships such as growth rate.

Water sources, analyzed by plant distance from the stream, show groups are using more enriched water sources later in the season. These sources are most closely related to stream isotopic ratios. Plant location also appears to be related to water sources utilized, and water gradients within sites are apparent showing these willow diversifying their use of summer moisture sources (Schwinning et al. 2003). At Crystal, the only site where water isotopes were measured, plants close to the stream on the west bank were using either deep soil moisture, hyporheic or stream water while those farther from the stream on both the east and west banks utilized shallower soil water or rain water later in the season. Plants closer to surface water sources are shown to use shallow groundwater; although there do appear to be other environmental constraints since this is not the case for both banks. Plants farther from the stream generally use soil water sources.

Riparian Zone & Hydrologic Regime

Groundwater in general is shallower and thus most available at Lower Eagle followed by Upper Eagle, Crystal, and then Sunlight. Although, no specific patterns could be discerned, precipitation events appear to be the most likely reason for some of the variability in groundwater and soil moisture fluctuation. Rain events cause pulses of soil moisture in shallow soils, but these single small events generally don't recharge below 20 or 30 cm. However, large or multiple events do infiltrate into deeper soil layers (Schwinning and Ehleringer 2001). In addition to these rain recharge characteristics, the beaver ponds at Lower Eagle most likely increased the water holding capacity of the site sustaining hyporheic flows between ponds. When precipitation was slight, as at Crystal, late in the season (September) as well as in August water table depths fell below the maximum monitoring depth and soil moisture decreased. When soil texture is coarse, as at Sunlight, soil water holding capacity is low and therefore soil moisture showed less response to precipitation events. At Sunlight, it's plausible that soil moisture fluctuations are more affected by diurnal streamwater fluctuations from snow melt than precipitation events. The other sites, however, may show a more of a prolonged response to rain events due to their higher water holding capacity (soil textures). It's evident that rain did contribute to moisture regimes but this study did not find distinct relationships linking the two.

Streams varied between gaining and losing reaches, but maintained their general flowpath shape throughout the season indicating geomorphic and topographic controls over hydrologic exchanges at the local reach scale (Boulton et al. 1998). All but Sunlight

showed increased depth to groundwater as distance from the stream, and all but Lower Eagle had fairly level water tables. The conical shape of Lower Eagle water table was a result of an elevated pond near the site with groundwater declining with distance from the stream/beaver pond.

Nutrients

Nitrogen (N), phosphorus (P), and potassium (K) are essential mineral elements (Sumner 2000), and are unevenly distributed throughout the sites. Differences in their presence in soils at the sites may explain some of the higher growth rates, as P and N are critical to plant growth while K helps to regulate plant cell osmotic potential (Taiz and Zeiger 1991).

Crystal has the highest soil organic matter (SOM) content of the sites providing increased carbon (C) reserves, one of their necessary nutrients for soil organisms which in turn can convert macronutrients, such as (N) and (P), from their organic form to inorganic and thereby available to plants. Increased SOM also aids in increasing soil water retention; although this only affects the plants if that retained water is within a capacity still available to plants (Sumner 2000).

Of all the sites, Crystal had the highest levels of available and total N, but low P and K. It is possible that the ready source of soluble nitrogen and high SOM content at Crystal may have aided in making these latter two vital nutrients available, as willows at this site had the greatest growth response following browse. While Crystal had high soil nitrogen levels, it may have been more available, as it generally remains in solution

moving freely with water flows readily being taken up by plants in well aerated soils (Sumner 2000). This suggests ponding and consequent anaerobic environments (e.g., Lower Eagle) being potentially nutrient limited regardless of their plant available state.

Conclusions

If willows are to persist in the northern range, environmental factors must be appropriate for plants to be resilient to browse pressures. In this study, establishment and persistence of willow varies between sites based on both physical and biologic conditions or parameters, but water regime appears to be the major controlling factor. As the growth of riparian vegetation is attributed to multiple environmental factors, but particularly those affecting moisture availability (Ripple and Beschta 2003). Each site represented a “typical” willow community was unique vegetatively, hydrologically, and in the condition and degree of resilience of willow by species.

The most intense browsing pressure occurred in YNP, followed by each of the closest sites to the Park boundary on the north and east sides. An array of ungulates that browsed willow was established at each site through observation. These included bison, elk, deer, moose, and antelope. Regrowth of browsed plants varied, with the most heavily browsed putting on the most growth the following season while the site being browsed least also had the least regrowth. When considering plant stature at the beginning of the growing season, there is no evidence to suggest that stature influences growth, however, the degree of winter browse does.

Relationships among plant height, growth, and water stress, assuming isotope analysis validates possible causation, showed shifts in significant water sources over time and space. Plants at both Eagle sites (spring and beaver dam) relied on soil moisture more than groundwater for growth, and those at Crystal (narrow mountain stream) and Sunlight (wide mountain stream) relied more on groundwater. This latter relationship was tied to plant height distribution and wetland plant designations for establishment locations.

Willow growth, on the other hand, was more opportunistic with water sources varying by hydrologic system instead of plant species. In most cases, however, growth was limited by soil water before groundwater sources. However, with decreasing resources, growth responses continued but were quite low relative to early season rates suggesting water availability controls on plant growth.

Although water is considered the primary factor influencing regrowth of willows after browsing, nutrients may also play a role. At Crystal, the site along a mountain stream with the most growth, also had the most potential for available nutrients to influence growth. The distribution of those nutrients were aided by increased hyporheic connectivity as the most developed hyporheic zones occur in intermediate reaches, such as the Crystal site, are less developed in lowland rivers (e.g., Sunlight and Lower Eagle), and least developed in headwater streams like Upper Eagle (Amoros and Bornette 2002). All these latter sites had less growth recovery following browse than Crystal.

Summary. Ecosystem functions that influence willow presence in the northern range include establishment, browse pressure, and maintenance and resilience. Establishment of willow is a result of availability of their preferred water source while

winter decline is a function of location and herbivore preferential selection. Maintenance and resilience are dominated by soil water in the early season, groundwater later in the season but with distinct variations between hydrologic systems. Water source shifts occurred first at the beaver dam site (Lower Eagle), followed by the narrow mountain stream (Crystal), and the spring fed site (Upper Eagle) and wide mountain stream (Sunlight). Nutrient availability and hyporheic connectivity essential to dispersing those nutrients among the plant communities also may influence growth and resilience of willow plants. Excess or even “acceptable” levels of only one of these factors is not enough alone to control plant growth; however, water alone does appear to impact their maintenance and persistence.

In answer to the primary objectives of this research, for individual willow communities and particular willow species within that community:

Is plant growth a function of plant stature at the beginning of the growing season? For both entire willow communities and specific species within each, plant growth is not a function of plant stature at the beginning of the season with any difference between initial height class and resultant growth. It is a function of the amount of winter browse.

Is plant growth a function of plant water stress, and if so, is that water stress related to water availability? For willow communities with all species considered together, there were not enough significant relationships to suggest plant growth is a function of water stress. For individual species, there were however similar parameters influencing both growth and water stress at the same time during the growing season. In several instances

water stress was related to water availability with increased stress occurring concurrently with decreasing water availability.

Is growth influenced by a particular water source or sources throughout the growing season, and if so, is that source related to water availability? For both willow communities as a whole and individual species, growth was influenced by two sources in general: soil water and groundwater. For individual species, the utilization of these sources do seem to be influenced by water availability with a shift to groundwater from soil water later in the season when soil moisture is in declines.

How does water availability vary between hydrologic systems? Groundwater is most available at the Lower Eagle (beaver dam) followed by Upper Eagle (spring-fed stream), Crystal (small mountain stream), and Sunlight (mountain river). Soil water is more variable between depths and sampling dates, but in general, Crystal had the highest amount of soil water for the season followed by Upper Eagle, Lower Eagle, and Sunlight.

Additional Recommended Research

The dominant species included in this study were non-clonal species with the exception of sandbar willow. The documentation on willow decline includes all species, but the functionality and resilience of clonal willow species may deviate from those factors that are most influential to non-clonal species. Further research oriented toward those factors controlling the growth of both growth forms may aid in determining the causes of the decline or resilience as well as the limiting factors for both types of willow.

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APPENDICES

APPENDIX A

SIMPLE LINEAR REGRESSION

This appendix is a series of tables for simple linear regression results. Tables represent willow communities (i.e., 2004) for the entire growing season and individual willow within a community for a date (i.e., 6-23-03, Bebb). Tables are separated by dependent variables and site (header row), and community or individual willow regressions (first column). The information provided in each cell, in the following order represents the R², coefficient, and constant for each equation, and significance is denoted by the number of asterisks. Groundwater and stem water potential have been abbreviated with GW and SWP. Where there was no data available for a specific parameter, the symbol X was used in a series.

| Dependant Variable: | Height | Site: Upper Eagle Willow | | | | | | | |
|---------------------|-------------------------|--------------------------|-------------------------|----------------------------|----------------------------|----------------------------|----------------------|----------------------|----------------------|
| Date | Change in GW depth (cm) | Predawn depth to GW (cm) | Midday depth to GW (cm) | % Soil saturation at 15 cm | % Soil saturation at 30 cm | % Soil saturation at 60 cm | Change in SWP (MPa) | Predawn SWP (MPa) | Midday SWP (MPa) |
| 2004 | | 4.9* | 4.8* | | | 6.2* | | | |
| | | 0.327 | 0.333 | | | 168.72 | | | |
| | | 80.93 | 80.14 | | | -56.68 | | | |
| | * $\rho \leq 0.1$ | * $\rho \leq 0.1$ | * $\rho \leq 0.1$ | * $\rho \leq 0.1$ | * $\rho \leq 0.1$ | * $\rho \leq 0.1$ | * $\rho \leq 0.1$ | * $\rho \leq 0.1$ | * $\rho \leq 0.1$ |
| | ** $\rho \leq 0.05$ | ** $\rho \leq 0.05$ | ** $\rho \leq 0.05$ | ** $\rho \leq 0.05$ | ** $\rho \leq 0.05$ | ** $\rho \leq 0.05$ | ** $\rho \leq 0.05$ | ** $\rho \leq 0.05$ | ** $\rho \leq 0.05$ |
| | *** $\rho \leq 0.01$ | *** $\rho \leq 0.01$ | *** $\rho \leq 0.01$ | *** $\rho \leq 0.01$ | *** $\rho \leq 0.01$ | *** $\rho \leq 0.01$ | *** $\rho \leq 0.01$ | *** $\rho \leq 0.01$ | *** $\rho \leq 0.01$ |

| Dependant Variable: | Height | Site: Upper Eagle Willow | | | | | | | |
|---------------------|-------------------------|--------------------------|-------------------------|----------------------------|----------------------------|----------------------------|---------------------|-------------------|------------------|
| Date Species | Change in GW depth (cm) | Predawn depth to GW (cm) | Midday depth to GW (cm) | % Soil saturation at 15 cm | % Soil saturation at 30 cm | % Soil saturation at 60 cm | Change in SWP (MPa) | Predawn SWP (MPa) | Midday SWP (MPa) |
| 6-23-03 | | | | | | | | | |
| Bebb | XXXX | XXXX | XXXX | | | | XXXX | XXXX | XXXX |
| 7-9-03 | | | | | | | | | |
| Bebb | | | | | 14.4* | | | | |
| | | | | | 160 | | | | |
| | | | | | 51.5 | | | | |
| 7-28-03 | | | | | | | | | |
| Bebb | | | 47.5*** | 25.6** | | | | | |
| | | | -107.31 | -337.6 | | | | | |
| | | | 268.44 | 387.1 | | | | | |

| Dependant Variable: | Height | Site: Sunlight Willow | | | | | | | |
|---------------------|-------------------------|--------------------------|-------------------------|----------------------------|----------------------------|----------------------------|----------------------|----------------------|----------------------|
| Date | Change in GW depth (cm) | Predawn depth to GW (cm) | Midday depth to GW (cm) | % Soil saturation at 15 cm | % Soil saturation at 30 cm | % Soil saturation at 60 cm | Change in SWP (MPa) | Predawn SWP (MPa) | Midday SWP (MPa) |
| 6-27-03 | XXXX | XXXX | | 17.4* | 16.3* | | XXXX | XXXX | XXXX |
| | | | | 207.7 | 230.9 | | | | |
| | | | | -81.60 | -115.5 | | | | |
| 2004 | | | | | | 6.0* | | | |
| | | | | | | -23.53 | | | |
| | | | | | | 128.93 | | | |
| 7-6-04 | | | | | | | | | 25.2** |
| | | | | | | | | | 57.45 |
| | | | | | | | | | 36.41 |
| 8-19-04 | | | | | | | 25.0** | | 23.0* |
| | | | | | | | -72.51 | | -71.38 |
| | | | | | | | 222.63 | | 226.07 |
| 9-11-04 | | | 28.2** | | | | | | |
| | | | -1.714 | | | | | | |
| | | | 260.9 | | | | | | |
| | * $\rho \leq 0.1$ | * $\rho \leq 0.1$ | * $\rho \leq 0.1$ | * $\rho \leq 0.1$ | * $\rho \leq 0.1$ | * $\rho \leq 0.1$ | * $\rho \leq 0.1$ | * $\rho \leq 0.1$ | * $\rho \leq 0.1$ |
| | ** $\rho \leq 0.05$ | ** $\rho \leq 0.05$ | ** $\rho \leq 0.05$ | ** $\rho \leq 0.05$ | ** $\rho \leq 0.05$ | ** $\rho \leq 0.05$ | ** $\rho \leq 0.05$ | ** $\rho \leq 0.05$ | ** $\rho \leq 0.05$ |
| | *** $\rho \leq 0.01$ | *** $\rho \leq 0.01$ | *** $\rho \leq 0.01$ | *** $\rho \leq 0.01$ | *** $\rho \leq 0.01$ | *** $\rho \leq 0.01$ | *** $\rho \leq 0.01$ | *** $\rho \leq 0.01$ | *** $\rho \leq 0.01$ |

| Dependant Variable: | Height | Site: Sunlight Willow | | | | | | | | |
|---------------------|---------|-------------------------|--------------------------|-------------------------|----------------------------|----------------------------|----------------------------|---------------------|-------------------|------------------|
| Date | Species | Change in GW depth (cm) | Predawn depth to GW (cm) | Midday depth to GW (cm) | % Soil saturation at 15 cm | % Soil saturation at 30 cm | % Soil saturation at 60 cm | Change in SWP (MPa) | Predawn SWP (MPa) | Midday SWP (MPa) |
| 6-27-03 | | | | | | | | | | |
| | Geyer | XXXX | XXXX | | | | | XXXX | XXXX | XXXX |
| | Booth | XXXX | XXXX | | 26.0* | | | XXXX | XXXX | XXXX |
| | | | | | 269.7 | | | | | |
| | | | | | -136.5 | | | | | |

| Dependant Variable: | | Site: Lower Eagle Willow | | | | | |
|---------------------|------------------------------|--------------------------|--------------------------|-------------------------|----------------------------|----------------------------|----------------------------|
| Date | Midday water potential (MPa) | Change in GW depth (cm) | Predawn depth to GW (cm) | Midday depth to GW (cm) | % Soil saturation at 15 cm | % Soil saturation at 30 cm | % Soil saturation at 60 cm |
| 7-8-03 | | | | | | 25.0* | |
| | | | | | | -2.091 | |
| | | | | | | 2.959 | |
| 7-30-03 | 36.8** | | | | | | 42.4* |
| | -0.0041 | | | | | | -5.946 |
| | 1.728 | | | | | | 7.006 |
| 2004 | | | 12.3* | | | 6.8* | |
| | | | -0.005 | | | 1.294 | |
| | | | 1.143 | | | -0.300 | |
| 8-16-04 | XXXX | XXXX | XXXX | XXXX | | | |
| | * $\rho \leq 0.1$ | * $\rho \leq 0.1$ | * $\rho \leq 0.1$ | * $\rho \leq 0.1$ | * $\rho \leq 0.1$ | * $\rho \leq 0.1$ | * $\rho \leq 0.1$ |
| | ** $\rho \leq 0.05$ | ** $\rho \leq 0.05$ | ** $\rho \leq 0.05$ | ** $\rho \leq 0.05$ | ** $\rho \leq 0.05$ | ** $\rho \leq 0.05$ | ** $\rho \leq 0.05$ |
| | *** $\rho \leq 0.01$ | *** $\rho \leq 0.01$ | *** $\rho \leq 0.01$ | *** $\rho \leq 0.01$ | *** $\rho \leq 0.01$ | *** $\rho \leq 0.01$ | *** $\rho \leq 0.01$ |

APPENDIX B

MULTIPLE LINEAR REGRESSION

This appendix is a series of tables for multiple linear regression results. Tables represent willow communities (i.e., 2004) for the entire growing season and individual willow within a community for a date (i.e., 6-23-03, Bebb). Tables are separated by dependent variables and site (header row), and community or individual willow regressions (first column). The equation coefficients per parameter are listed in the table, and the R^2 and constant are listed in the last column. Significance is denoted by the number of asterisks. Groundwater and stem water potential have been abbreviated with GW and SWP. Where there was no data available for a specific parameter, the symbol X was used in a series.

| Dependant Variable: | | Site: Upper Eagle Willow | | | | | | | MULTIPLE REGRESSION | | |
|---------------------|--------|--------------------------|--------------------------|-------------------------|----------------------------|----------------------------|----------------------------|---------------------|---------------------|------------------|-------------------|
| Date | Height | Change in GW depth (cm) | Predawn depth to GW (cm) | Midday depth to GW (cm) | % Soil saturation at 15 cm | % Soil saturation at 30 cm | % Soil saturation at 60 cm | Change in SWP (MPa) | Predawn SWP (MPa) | Midday SWP (MPa) | R^2 constant |
| 7-9-03 | | | | | | | | | | | |
| | Bebb | | | 1.28 | | 178.56 | | | | | 36.9*** 136 |
| 6-5-04 | | | | | | | | | | | |
| | Bebb | 27.06 | | | | | 872.1 | | | | 64.1*** -730.0 |
| | Bebb | | | 1.073 | | | 780.2 | | | | 53.4** -611.9 |
| | Bebb | | 1.090 | | | | 772.0 | | | | 52.6** -602.7 |
| | Bebb | | 1.188 | | | 206.34 | | | | | 46.1*** -90.5 |
| 7-2-04 | | | | | | | | | | | |
| | Bebb | | | 0.844 | | 175.57 | | | | | 35.0** -67.81 |

* $\rho \leq 0.1$
** $\rho \leq 0.05$
*** $\rho \leq 0.01$

| Dependant Variable: | | Growth Rate (cm/day) | | | | | | | Site: Upper Eagle Willow | | MULTIPLE REGRESSION | |
|---------------------|---------|-------------------------|--------------------------|-------------------------|----------------------------|----------------------------|----------------------------|---------------------|--------------------------|------------------|-------------------------|--|
| Date | Species | Change in GW depth (cm) | Predawn depth to GW (cm) | Midday depth to GW (cm) | % Soil saturation at 15 cm | % Soil saturation at 30 cm | % Soil saturation at 60 cm | Change in SWP (MPa) | Predawn SWP (MPa) | Midday SWP (MPa) | R ² constant | |
| 7-28-03 | | | | | | | | | | | | |
| | Bebb | | | | -14.5 | -6.1 | | | | | 39.1*** 18.3 | |
| | Bebb | | | | -17.5 | -7.96 | | | | 0.0464 | 52.5*** 18.9 | |
| | Bebb | | | | | | -60.75 | | | 0.0459 | 57.1** 55.2 | |
| 7-2-04 | | | | | | | | | | | | |
| | Bebb | | | | | | | | -0.637 | -0.954 | 60.1** 1.371 | |

* $p \leq 0.1$
 ** $p \leq 0.05$
 *** $p \leq 0.01$

| Dependant Variable: | Change in SWP (MPa) | | Site: Upper Eagle Willow | | | MULTIPLE | REGRESSION |
|---------------------|-------------------------|--------------------------|--------------------------|----------------------------|----------------------------|----------------------------|-------------------------|
| Date | Change in GW depth (cm) | Predawn depth to GW (cm) | Midday depth to GW (cm) | % Soil saturation at 15 cm | % Soil saturation at 30 cm | % Soil saturation at 60 cm | R ² constant |
| 2004 | -0.158 | | | 1.271 | | | 49.7*** |
| | | 0.0115 | | 1.529 | | | 0.151 |
| | | 0.00922 | | | 2.214 | | 55.5*** |
| | | | 0.0114 | 1.581 | | | -0.664 |
| | | | 0.00903 | | 2.303 | | 51.1*** |
| | | | | | | | -1.346 |
| | | | | | | | 54.8*** |
| | | | | | | | -0.722 |
| | | | | | | | 50.7*** |
| | | | | | | | -1.433 |

* $p \leq 0.1$
 ** $p \leq 0.05$
 *** $p \leq 0.01$

| Dependant Variable: | Midday water potential (MPa) | | Site: Upper Eagle Willow | | | MULTIPLE | REGRESSION |
|---------------------|------------------------------|--------------------------|--------------------------|----------------------------|----------------------------|----------------------------|-------------------------|
| Date | Change in GW depth (cm) | Predawn depth to GW (cm) | Midday depth to GW (cm) | % Soil saturation at 15 cm | % Soil saturation at 30 cm | % Soil saturation at 60 cm | R ² constant |
| 7-25-04 | | | | | | | |
| Bebb | | | | 2.57 | | 6.63 | 83.1** |
| | | | | | | | -6.74 |

* $p \leq 0.1$
 ** $p \leq 0.05$
 *** $p \leq 0.01$

| Dependant Variable: | Growth Rate (cm/day) | | Site: Sunlight Willow | | | | MULTIPLE REGRESSION | | | |
|--|-------------------------|--------------------------|-------------------------|----------------------------|----------------------------|----------------------------|---------------------|-------------------|------------------|-------------------------|
| Date | Change in GW depth (cm) | Predawn depth to GW (cm) | Midday depth to GW (cm) | % Soil saturation at 15 cm | % Soil saturation at 30 cm | % Soil saturation at 60 cm | Change in SWP (MPa) | Predawn SWP (MPa) | Midday SWP (MPa) | R ² constant |
| 9-11-04 | | -0.0274 | -0.0404 | | | | | | | 32.3** 1.31 |
| * $\rho \leq 0.1$ ** $\rho \leq 0.05$ *** $\rho \leq 0.01$ | | | | | | | | | | |

| Dependant Variable: | Growth Rate (cm/day) | | Site: Sunlight Willow | | | | MULTIPLE REGRESSION | | | |
|--|-------------------------|--------------------------|-------------------------|----------------------------|----------------------------|----------------------------|---------------------|-------------------|------------------|------------------|
| Date Species | Change in GW depth (cm) | Predawn depth to GW (cm) | Midday depth to GW (cm) | % Soil saturation at 15 cm | % Soil saturation at 30 cm | % Soil saturation at 60 cm | Change in SWP (MPa) | Predawn SWP (MPa) | Midday SWP (MPa) | P-value |
| 2004 | | | | | | | | | | |
| Geyer | | -0.0137 | | | | -0.393 | | | | 36.8** 1.422 |
| 6-8-04 | | | | | | | | | | |
| Booth | 0.208 | | -0.05341 | | | | | | | 69.7* 2.699 |
| Booth | 0.155 | -0.053 | | | | | | | | 69.7* 2.699 |
| 9-11-04 | | | | | | | | | | |
| Booth | | 0.0391 | -0.0496 | | | | | | | 44.1** 1.220 |
| Geyer | 0.00589 | | | 0.869 | | | | | | 99.8** -0.427 |
| | 0.00589 | | | | 0.505 | | | | | 99.8** -0.123 |
| * $\rho \leq 0.1$ ** $\rho \leq 0.05$ *** $\rho \leq 0.01$ | | | | | | | | | | |

| Dependant Variable: | | Change in SWP (MPa) | | Site: Sunlight Willow | | | MULTIPLE | REGRESSION |
|---------------------|---------|-------------------------------|--------------------------|-------------------------|----------------------------|----------------------------|----------------------------|--|
| Date | Species | Change in GW depth (cm) | Predawn depth to GW (cm) | Midday depth to GW (cm) | % Soil saturation at 15 cm | % Soil saturation at 30 cm | % Soil saturation at 60 cm | R ² constant |
| 6-8-04 | Booth | 0.0271 | | | -1.760 | | | 88.9*** 1.764 |
| | | | | | | | | * $\rho \leq 0.1$ ** $\rho \leq 0.05$ *** $\rho \leq 0.01$ |
| Dependant Variable: | | Predawn water potential (MPa) | | Site: Sunlight Willow | | | MULTIPLE | REGRESSION |
| Date | Species | Change in GW depth (cm) | Predawn depth to GW (cm) | Midday depth to GW (cm) | % Soil saturation at 15 cm | % Soil saturation at 30 cm | % Soil saturation at 60 cm | R ² constant |
| 7-31-04 | Booth | -0.0529 | | | | | 0.398 | 87.4** 0.233 |
| | | | -0.0143 | | | | 0.403 | 86.7** 1.2 |
| | | | | -0.0123 | | | 0.412 | 89.1** 1.068 |
| | | | | | | | | * $\rho \leq 0.1$ ** $\rho \leq 0.05$ *** $\rho \leq 0.01$ |

| Dependant Variable: | | Midday water potential (MPa) | | Site: Sunlight Willow | | | MULTIPLE | REGRESSION |
|---------------------|-------------------------|------------------------------|-------------------------|----------------------------|----------------------------|----------------------------|-------------------------|------------|
| Date | Change in GW depth (cm) | Predawn depth to GW (cm) | Midday depth to GW (cm) | % Soil saturation at 15 cm | % Soil saturation at 30 cm | % Soil saturation at 60 cm | R ² constant | |
| 6-8-04 | | -0.0182 | | 1.608 | | -1.133 | 98.6*** 1.702 | |
| | | -0.00723 | | | | 0.287 | 84.7** 1.142 | |
| 7-31-04 | 0.172 | | | | | -0.449 | 81.7** 1.722 | |

* $p \leq 0.1$
 ** $p \leq 0.05$
 *** $p \leq 0.01$

| Dependant Variable: | | Midday water potential (MPa) | | Site: Sunlight Willow | | | MULTIPLE | REGRESSION |
|---------------------|---------|------------------------------|--------------------------|-------------------------|----------------------------|----------------------------|----------------------------|-------------------------|
| Date | Species | Change in GW depth (cm) | Predawn depth to GW (cm) | Midday depth to GW (cm) | % Soil saturation at 15 cm | % Soil saturation at 30 cm | % Soil saturation at 60 cm | R ² constant |
| 6-8-04 | Booth | | -0.0182 | | | | 27.82 | 98.6** -23.81 |
| 9-11-04 | Booth | | -0.0103 | | 0.931 | | | 49.4 1.244 |

* $p \leq 0.1$
 ** $p \leq 0.05$
 *** $p \leq 0.01$

| Dependant Variable: | Height | Site: Lower Eagle Willow | | | | | | | MULTIPLE | REGRESSION |
|---------------------|-------------------------|--------------------------|-------------------------|----------------------------|----------------------------|----------------------------|---------------------|-------------------|------------------|-------------------------|
| Date | Change in GW depth (cm) | Predawn depth to GW (cm) | Midday depth to GW (cm) | % Soil saturation at 15 cm | % Soil saturation at 30 cm | % Soil saturation at 60 cm | Change in SWP (MPa) | Predawn SWP (MPa) | Midday SWP (MPa) | R ² constant |
| 6-23-03 | XXXX | XXXX | 0.836 | | | 850.9 | XXXX | XXXX | XXXX | 41.6* -650.6 |
| 7-8-03 | | | | -239.24 | 212.6 | | | | | 33.7* 158.79 |
| 2004 | -0.892 | | | -140.51 | | | | | | 32.3*** 245.61 |
| | | 0.375 | | -156.21 | | | | | | 28.5*** 237.20 |
| | -1.509 | | | | | | -335.02 | | | 37.7*** 432.89 |

* $p \leq 0.1$
 ** $p \leq 0.05$
 *** $p \leq 0.01$

| Dependant Variable: | | Site: Lower Eagle Willow | | | | | | | MULTIPLE REGRESSION | | |
|---------------------|--------|--------------------------|--------------------------|-------------------------|----------------------------|----------------------------|----------------------------|---------------------|---------------------|------------------|-------------------------|
| Date | Height | Change in GW depth (cm) | Predawn depth to GW (cm) | Midday depth to GW (cm) | % Soil saturation at 15 cm | % Soil saturation at 30 cm | % Soil saturation at 60 cm | Change in SWP (MPa) | Predawn SWP (MPa) | Midday SWP (MPa) | R ² constant |
| 2004 | | | | | | | | | | | |
| | Bebb | -0.840 | | | -125.84 | | | | | | 25.5*** |
| | | | 0.581 | | -143.82 | | | | | | 235.27 |
| | | -1.556 | | | | | | -332.88 | | | 28.4*** |
| | | | | | | | | | | | 219.25 |
| | | | 0.464 | | | | | | | | 37.9*** |
| | | | | | | | | | | | 433.28 |
| | | | | | | | | | | | 47.5*** |
| | | | | | | | | | | | 88.6 |
| | | | | 0.146 | -116.43 | | | | | | 18.3** |
| | | | | | | | | | | | 218.04 |
| | | | | | | | | | | | 47.2*** |
| | | | | | | | | | | | 54.9 |
| 6-30-04 | | | | | | | | | | | |
| | Bebb | -0.365 | | | | | | -1073.8 | | 169.5 | 94.2*** |
| | | | | | | | | | | | 915.9 |
| | | -3.104 | | | -684.20 | | | | | 705.10 | 81.6** |
| | | | | | | | | | | | -11.5 |
| 7-25-04 | | | | | | | | | | | |
| | Bebb | | 1.753 | | | | | | | | 71.4** |
| | | | | | | | | | | | 711.7 |
| | | | | 1.999 | | | | | | | 74.5** |
| | | | | | | | | | | | 713.1 |

* $\rho \leq 0.1$
 ** $\rho \leq 0.05$
 *** $\rho \leq 0.01$

| Dependant Variable: | Growth Rate (cm/day) | | Site: Lower Eagle Willow | | | | | MULTIPLE REGRESSION | | |
|---------------------|-------------------------|--------------------------|--------------------------|----------------------------|----------------------------|----------------------------|---------------------|---------------------|------------------|-------------------------|
| Date | Change in GW depth (cm) | Predawn depth to GW (cm) | Midday depth to GW (cm) | % Soil saturation at 15 cm | % Soil saturation at 30 cm | % Soil saturation at 60 cm | Change in SWP (MPa) | Predawn SWP (MPa) | Midday SWP (MPa) | R ² constant |
| 2004 | | | | | -9.783 | 13.748 | | | | 8.4** -3.023 |
| | | -0.0565 | | | -9.039 | | | | | 18.2** 11.863 |
| | | | -0.0496 | | -13.879 | | | | | 19.8** 15.833 |
| 9-13-04 | | | | | | | | 3.985 | 2.947 | 62.7** -1.644 |

* $\rho \leq 0.1$
 ** $\rho \leq 0.05$
 *** $\rho \leq 0.01$

| Dependant Variable: | | Growth Rate (cm/day) | | | | | | | Site: Lower Eagle Willow | | MULTIPLE REGRESSION | |
|---------------------|---------|-------------------------|--------------------------|-------------------------|----------------------------|----------------------------|----------------------------|---------------------|--------------------------|------------------|-------------------------|--|
| Date | Species | Change in GW depth (cm) | Predawn depth to GW (cm) | Midday depth to GW (cm) | % Soil saturation at 15 cm | % Soil saturation at 30 cm | % Soil saturation at 60 cm | Change in SWP (MPa) | Predawn SWP (MPa) | Midday SWP (MPa) | R ² constant | |
| 2004 | | | | | | | | | | | | |
| | sandbar | | -0.348 | | | | 168.98 | | | | 97.2** -125.21 | |
| | Bebb | | | | -4.88 | | 7.529 | | | | 18.5*** -2.457 | |
| | | | -0.0351 | | | | | -7.094 | | | 22.0** 8.599 | |
| | | | | -0.0197 | -6.972 | | | | | | 32.7*** 6.970 | |
| | | | | | -0.0338 | | | -10.951 | | | 26.9** 12.028 | |
| | | | -0.0302 | | | | | -9.766 | 37.91 | | 32.0** -23.23 | |
| | | | | | -0.0267 | | | -10.823 | 40.75 | | 33.4** -24.91 | |
| 6-5-04 | | | | | | | | | | | | |
| | Bebb | | | | -6.3056 | | | 20.306 | | | 99.9* -13.810 | |
| | Bebb | | -0.014020 | | -6.7891 | | | | | | 96.5* 5.1324 | |
| | Bebb | | | -0.005781 | -7.0280 | | | | | | 98.2** 5.1558 | |
| 6-30-04 | | | | | | | | | | | | |
| | Bebb | | | | | | -5.716 | -13.939 | | | 44.4* 17.11 | |
| | | | | 0.0328 | | | | | | | 81.1** 23.52 | |
| | | | 0.0279 | | | | | | -31.25 | | 76.1** 26.096 | |
| | | | | | | | | | | | * $\rho \leq 0.1$ | |
| | | | | | | | | | | | ** $\rho \leq 0.05$ | |
| | | | | | | | | | | | *** $\rho \leq 0.01$ | |

| Dependant Variable: | Predawn water potential (MPa) | | Site: Lower Eagle Willow | | | MULTIPLE | REGRESSION |
|---------------------|-------------------------------|--------------------------|--------------------------|----------------------------|----------------------------|----------------------------|--|
| Date | Change in GW depth (cm) | Predawn depth to GW (cm) | Midday depth to GW (cm) | % Soil saturation at 15 cm | % Soil saturation at 30 cm | % Soil saturation at 60 cm | R ² constant |
| 8-16-04 | XXXX | XXXX | XXXX | | -2.878 | 3.399 | 60.9* 0.332 |
| | | | | | | | * $\rho \leq 0.1$ ** $\rho \leq 0.05$ *** $\rho \leq 0.01$ |

| Dependant Variable: | Predawn water potential (MPa) | | Site: Lower Eagle Willow | | | MULTIPLE | REGRESSION | |
|---------------------|-------------------------------|-------------------------|--------------------------|-------------------------|----------------------------|----------------------------|----------------------------|--|
| Date | Species | Change in GW depth (cm) | Predawn depth to GW (cm) | Midday depth to GW (cm) | % Soil saturation at 15 cm | % Soil saturation at 30 cm | % Soil saturation at 60 cm | R ² constant |
| 7-8-03 | Bebb | | 0.000733 | | | | -1.750 | 89.3*** 1.894 |
| 7-30-03 | Bebb | -0.00162 | | | | -0.478 | | 70.4** 0.784 |
| | | | | | | | | * $\rho \leq 0.1$ ** $\rho \leq 0.05$ *** $\rho \leq 0.01$ |

| Dependant Variable: | Midday water potential (MPa) | | Site: Lower Eagle Willow | | | MULTIPLE | REGRESSION |
|---------------------|------------------------------|--------------------------|--------------------------|----------------------------|----------------------------|----------------------------|---|
| Date | Change in GW depth (cm) | Predawn depth to GW (cm) | Midday depth to GW (cm) | % Soil saturation at 15 cm | % Soil saturation at 30 cm | % Soil saturation at 60 cm | R ² constant |
| 7-30-03 | -0.00582 | | | -1.478 | | | 61.4** 2.909 |
| | -0.0683 | | | | | -4.129 | 70.6** 5.728 |
| 7-25-04 | -0.0119 | | | -0.848 | | | 98.7** 2.182 |
| | | | | | | | * $p \leq 0.1$ ** $p \leq 0.05$ *** $p \leq 0.01$ |

| Dependant Variable: | Midday water potential (MPa) | | Site: Lower Eagle Willow | | | MULTIPLE | REGRESSION | |
|---------------------|------------------------------|-------------------------|--------------------------|-------------------------|----------------------------|----------------------------|----------------------------|---|
| Date | Species | Change in GW depth (cm) | Predawn depth to GW (cm) | Midday depth to GW (cm) | % Soil saturation at 15 cm | % Soil saturation at 30 cm | % Soil saturation at 60 cm | R ² constant |
| 7-25-04 | Bebb | -0.0119 | | | -0.848 | | | 98.7** 2.182 |
| | | | | | | | | * $p \leq 0.1$ ** $p \leq 0.05$ *** $p \leq 0.01$ |

| Dependant Variable: | Height | Site: Crystal Willow | | | | | | MULTIPLE | REGRESSION | |
|---------------------|-------------------------|--------------------------|-------------------------|----------------------------|----------------------------|----------------------------|---------------------|-------------------|------------------|--|
| Date | Change in GW depth (cm) | Predawn depth to GW (cm) | Midday depth to GW (cm) | % Soil saturation at 15 cm | % Soil saturation at 30 cm | % Soil saturation at 60 cm | Change in SWP (MPa) | Predawn SWP (MPa) | Midday SWP (MPa) | R ² constant |
| 2004 | | 0.685 | | | 157.93 | | | | | 22.4*** -88.05 |
| | | 0.569 | | 89.26 | | | | | | 23.5*** -8.38 |
| 7-29-04 | -9.247 | | | | 283.3 | | | | | 43.6*** -167.1 |
| 8-14-04 | | | | 324.46 | -183.18 | | | | | 44.7*** 31.62 |
| | | | | 284.3 | | -251.9 | | | | 36.0** 142.0 |
| | | | | | | | | | | * $\rho \leq 0.1$ ** $\rho \leq 0.05$ *** $\rho \leq 0.01$ |

| Dependant Variable: | | Site: Crystal Willow | | | | | | | MULTIPLE REGRESSION | | |
|---------------------|--------|-------------------------|--------------------------|-------------------------|----------------------------|----------------------------|----------------------------|---------------------|---------------------|------------------|-------------------------|
| Date | Height | Change in GW depth (cm) | Predawn depth to GW (cm) | Midday depth to GW (cm) | % Soil saturation at 15 cm | % Soil saturation at 30 cm | % Soil saturation at 60 cm | Change in SWP (MPa) | Predawn SWP (MPa) | Midday SWP (MPa) | R ² Constant |
| 2004 | | | | | | | | | | | |
| | Bebb | -3.515 | | | | | | -60.24 | | | 18.0*** 168.77 |
| | | | 0.897 | | 156.75 | | | | | | 52.4*** -86.09 |
| | | | | 0.887 | 145.71 | | | | | | 47.8*** -75.27 |
| 6-4-04 | | | | | | | | | | | |
| | Bebb | | | 0.6899 | | | | -50.7 | | | 34.9* 114.9 |
| 8-14-04 | | | | | | | | | | | |
| | Bebb | | | | 378.8 | | | -342.23 | | | 69.5*** 134.14 |
| | | | | | 363.63 | | | -512.5 | | | 68.3*** 336.1 |
| 9-10-04 | | | | | | | | | | | |
| | Bebb | | | | | | | -275.9 | | -95.17 | 54.0* 529.6 |

* $\rho \leq 0.1$
 ** $\rho \leq 0.05$
 *** $\rho \leq 0.01$

| Dependant Variable: | | Growth Rate (cm/day) | | | | | | | Site: Crystal Willow | | MULTIPLE REGRESSION |
|---------------------|-------------------------|--------------------------|-------------------------|----------------------------|----------------------------|----------------------------|---------------------|-------------------|----------------------|-------------------------|---------------------|
| Date | Change in GW depth (cm) | Predawn depth to GW (cm) | Midday depth to GW (cm) | % Soil saturation at 15 cm | % Soil saturation at 30 cm | % Soil saturation at 60 cm | Change in SWP (MPa) | Predawn SWP (MPa) | Midday SWP (MPa) | R ² constant | |
| 6-4-04 | | | 0.009 | | 6.549 | | | | | 25.4* -6.873 | |
| 7-5-04 | | 0.005 | | 1.874 | | | | | | 28.5** -1.362 | |
| | | | 0.005 | 1.784 | | | | | | 23.2* -1.275 | |

* $\rho \leq 0.1$
 ** $\rho \leq 0.05$
 *** $\rho \leq 0.01$

| Dependant Variable: | | Growth Rate (cm/day) | | | | | | | Site: Crystal Willow | | MULTIPLE REGRESSION |
|---------------------|---------|-------------------------|--------------------------|-------------------------|----------------------------|----------------------------|----------------------------|---------------------|----------------------|------------------|-------------------------|
| Date | Species | Change in GW depth (cm) | Predawn depth to GW (cm) | Midday depth to GW (cm) | % Soil saturation at 15 cm | % Soil saturation at 30 cm | % Soil saturation at 60 cm | Change in SWP (MPa) | Predawn SWP (MPa) | Midday SWP (MPa) | R ² constant |
| 7-5-04 | Booth | | | 0.010 | | | 9.947 | | | | 92.1*** -9.542 |
| 7-29-04 | Booth | 0.184 | | | -10.850 | | | | | | 81.9** 10.666 |
| | | | -0.0186 | | -7.343 | | | | | | 92.1*** 8.523 |
| | | | | -0.020 | -6.934 | | | | | | 92.2*** 8.243 |

* $\rho \leq 0.1$
 ** $\rho \leq 0.05$
 *** $\rho \leq 0.01$

| Dependant Variable: | Change in SWP (MPa) | | Site: Crystal Willow | | | MULTIPLE | REGRESSION |
|---------------------|-------------------------|--------------------------|-------------------------|----------------------------|----------------------------|----------------------------|--|
| Date | Change in GW depth (cm) | Predawn depth to GW (cm) | Midday depth to GW (cm) | % Soil saturation at 15 cm | % Soil saturation at 30 cm | % Soil saturation at 60 cm | R ² constant |
| 6-4-04 | | | | | -3.588 | -0.499 | 52.7** 4.689 |
| | | | | | | | * $\rho \leq 0.1$ ** $\rho \leq 0.05$ *** $\rho \leq 0.01$ |

| Dependant Variable: | Change in SWP (MPa) | | Site: Crystal Willow | | | MULTIPLE | REGRESSION | |
|---------------------|---------------------|-------------------------|--------------------------|-------------------------|----------------------------|----------------------------|----------------------------|--|
| Date | Species | Change in GW depth (cm) | Predawn depth to GW (cm) | Midday depth to GW (cm) | % Soil saturation at 15 cm | % Soil saturation at 30 cm | % Soil saturation at 60 cm | R ² constant |
| 7-5-04 | Bebb | -0.101 | | | | | 6.564 | 68.7** -5.916 |
| | Booth | | | -0.00615 | | | -6.185 | 93.3* 7.128 |
| | | | | | | | | * $\rho \leq 0.1$ ** $\rho \leq 0.05$ *** $\rho \leq 0.01$ |

| Dependant Variable: | Predawn water potential (MPa) | Site: Crystal Willow | | | | MULTIPLE | REGRESSION |
|---------------------|-------------------------------|--------------------------|-------------------------|----------------------------|----------------------------|----------------------------|-------------------------|
| Date | Change in GW depth (cm) | Predawn depth to GW (cm) | Midday depth to GW (cm) | % Soil saturation at 15 cm | % Soil saturation at 30 cm | % Soil saturation at 60 cm | R ² constant |
| 2004 | 0.019 | | | -0.901 | | -1.019 | 32.3*** 2.254 |
| | 0.024 | | | | -1.402 | -0.829 | 34.3*** 2.595 |
| | | | | | -1.537 | -0.191 | 28.4*** 2.045 |
| | | | | -1.093 | | -0.608 | 23.4*** 1.986 |
| 8-14-04 | | | | 0.518 | -0.349 | | 35.6* 0.131 |

* $p \leq 0.1$
 ** $p \leq 0.05$
 *** $p \leq 0.01$

| Dependant Variable: | | Predawn water potential (MPa) | | Site: Crystal Willow | | | MULTIPLE | REGRESSION |
|---------------------|---------|-------------------------------|--------------------------|-------------------------|----------------------------|----------------------------|----------------------------|-------------------------|
| Date | Species | Change in GW depth (cm) | Predawn depth to GW (cm) | Midday depth to GW (cm) | % Soil saturation at 15 cm | % Soil saturation at 30 cm | % Soil saturation at 60 cm | R ² constant |
| 2004 | Bebb | 0.024 | | | -1.033 | | -1.001 | 37.6*** 2.356 |
| | | 0.023 | | | | -0.947 | -0.787 | 26.3** 2.112 |
| | | | | | | -1.490 | -0.141 | 23.3*** 1.952 |
| | | | | | -1.123 | | -0.439 | 21.6*** 1.842 |
| | Booth | 0.055 | | | | -2.565 | | 59.1*** 2.955 |

* $\rho \leq 0.1$
 ** $\rho \leq 0.05$
 *** $\rho \leq 0.01$

| Dependant Variable: | Midday water potential (MPa) | | Site: Crystal Willow | | | MULTIPLE | REGRESSION |
|---------------------|------------------------------|--------------------------|-------------------------|----------------------------|----------------------------|----------------------------|-------------------------|
| Date | Change in GW depth (cm) | Predawn depth to GW (cm) | Midday depth to GW (cm) | % Soil saturation at 15 cm | % Soil saturation at 30 cm | % Soil saturation at 60 cm | R ² constant |
| 2004 | | | | -1.679 | | 0.281 | 46.2*** 4.331 |
| | | | | | -1.551 | -1.087 | 37.8*** 3.961 |
| | | 0.0034 | | | | -1.122 | 33.6*** 2.261 |
| | | 0.0024 | | -1.151 | | -1.241 | 42.3*** 3.469 |
| | | | 0.0032 | | | -1.270 | 32.7*** 2.417 |

* $p \leq 0.1$
 ** $p \leq 0.05$
 *** $p \leq 0.01$

| Dependant Variable: | Midday water potential (MPa) | | Site: Crystal Willow | | | MULTIPLE | REGRESSION | |
|---------------------|------------------------------|-------------------------|--------------------------|-------------------------|----------------------------|----------------------------|----------------------------|-------------------------|
| Date | Species | Change in GW depth (cm) | Predawn depth to GW (cm) | Midday depth to GW (cm) | % Soil saturation at 15 cm | % Soil saturation at 30 cm | % Soil saturation at 60 cm | R ² Constant |
| 2004 | Bebb | | | | -1.750 | | -1.437 | 48.7*** 4.447 |
| | Booth | | | | -1.081 | | -3.605 | 57.7*** 5.758 |
| 6-5-04 | Bebb | | | | 5.929 | -3.700 | | 86.7*** -0.800 |

* $p \leq 0.1$
 ** $p \leq 0.05$
 *** $p \leq 0.01$

