



Temperature, light, and soil effects on the establishment of Bebb's Willow. (*Salix bebbiana*)  
by Jennifer Laura Atchley

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in  
Range Science  
Montana State University  
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**Abstract:**

Bebb's willow (*Salix bebbiana*) is a common riparian shrub along Rocky Mountain foothill streams and springs. Decadent Bebb's willow along Cottonwood Creek, at the Red Bluff Research Ranch, near Norris, Montana, have not reproduced by seed in an eight year grazing enclosure.

Bebb's willow's establishment requirements are undocumented and its successional role uncertain. The effects of temperature, light, and soil type on Bebb's willow were examined in this study.

Percent germination was determined at five temperatures on a thermogradient plate. Seeds were collected on two dates. Differences among temperature treatments and collection dates were detected. Significantly more seeds germinated at 20° C.

Biomass, height, and percent survival after 60 days were used as indicators of Bebb's willow's ability to establish under four intensities of light. Seedlings grown under the highest light intensity, 20% of full sunlight, produced more biomass and taller shoots.

Seeds and stems were planted in field and commercial soils in the greenhouse. Biomass, height, and percent established in 60 days were the response variables measured. There were no significant differences among treatments, but more seed established in soils high in organic matter and silt. More biomass was produced in these soils also.

Responses within light and soil treatments were not consistent. Bebb's willow may possess a suite of reproductive strategies to establish under a variety of environmental conditions.

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MONTANA STATE UNIVERSITY  
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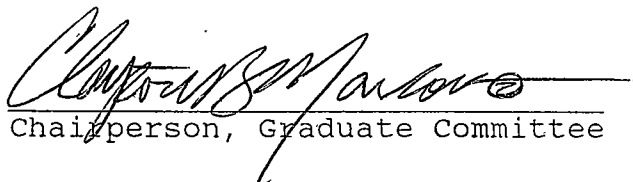
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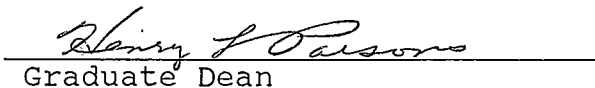


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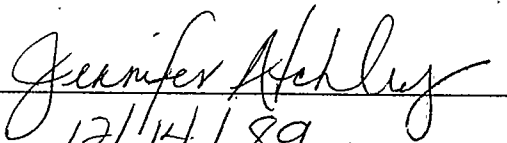
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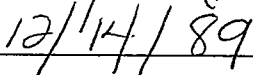
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## VITA

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## .ABSTRACT

Bebb's willow (Salix bebbiana) is a common riparian shrub along Rocky Mountain foothill streams and springs. Decadent Bebb's willow along Cottonwood Creek, at the Red Bluff Research Ranch, near Norris, Montana, have not reproduced by seed in an eight year grazing exclosure. Bebb's willow's establishment requirements are undocumented and its successional role uncertain. The effects of temperature, light, and soil type on Bebb's willow were examined in this study.

Percent germination was determined at five temperatures on a thermogradient plate. Seeds were collected on two dates. Differences among temperature treatments and collection dates were detected. Significantly more seeds germinated at 20° C.

Biomass, height, and percent survival after 60 days were used as indicators of Bebb's willow's ability to establish under four intensities of light. Seedlings grown under the highest light intensity, 20% of full sunlight, produced more biomass and taller shoots.

Seeds and stems were planted in field and commercial soils in the greenhouse. Biomass, height, and percent established in 60 days were the response variables measured. There were no significant differences among treatments, but more seed established in soils high in organic matter and silt. More biomass was produced in these soils also.

Responses within light and soil treatments were not consistent. Bebb's willow may possess a suite of reproductive strategies to establish under a variety of environmental conditions.

## Chapter 1

## INTRODUCTION

Successional Role of Willows

Maintaining biological diversity while exploiting natural resources challenges current expertise. Watersheds are exploited for timber, forage, water, and minerals, so preserving intact, productive watersheds requires knowledge of sensitive elements in the system. Documenting establishment requirements of flora in disrupted systems facilitates management. Although riparian zones are of special concern in arid western North America, their management has been constrained by inadequate knowledge of riparian structure, function, and succession (Carothers 1977, Knopf and Conner 1982, Platts 1986, Hansen et. al. 1988). Willows (Salix spp.) are common components of riparian communities, but the diversity of willow species and habitats defies generalization of the genus. Studies referring to Salix spp. are not always useful for management of a specific willow.

Recruitment of Bebb's willow (Salix bebbiana Sarg.) along Cottonwood Creek, a small stream in southwest Montana,

has been declining for at least eight years (Clayton Marlow, Montana State University, Personal Communication). Many individuals in the stand are decadent; dead branches outnumber live branches. Although many individual Bebb's willows produce new leaders, leaves, and catkins each year, the species is not regenerating.

At Cottonwood Creek, a grazing enclosure was erected in 1981 to observe changes in willow recruitment. We expected regeneration of this dominant shrub after release from grazing pressure. To date (1989), Bebb's willow has not regenerated from seed in the enclosure, although four saplings sprouted from buried stems 10 m from the streambank. This decline of Bebb's willow without replacement has not been reported in the literature, but its decadence has been noted in the Northern Rockies (Froiland 1962, Dorn 1970).

From this information it is not clear how activities such as livestock grazing have affected recruitment of Bebb's willow along Cottonwood Creek. Since reproductive strategies are integral to plant succession, we decided that the determination of Bebb's willow's successional role along streams, rivers, springs, and lakes might explain its decadence. Consequently, a series of experiments was designed to answer these questions:

1. What are the temperature requirements for germination of Bebb's willow seed?

2. How do seedlings respond to four different levels of light?
3. Do soil types affect establishment and biomass production of seeds or stems?

Answers to these questions could influence the management of Bebb's willow. Conclusions may also contribute to the growing body of knowledge needed for ecological studies and management of riparian systems (Hansen et. al. 1988).

#### Site Description

Cottonwood Creek is a small (0.03 to 0.01 m<sup>3</sup>/sec) stream fed by seeps and springs on the Montana Agricultural Experiment Station's Red Bluff Research Ranch, 66 km west of Bozeman, Montana. Cottonwood Creek is approximately four km long and flows northeast to join the Madison River in Beartrap Canyon (Pogacnik 1985). The creek is bordered by several vegetation zones: sagebrush/grassland, aspen/grass/forb, broadleaf shrub/coniferous tree, and aspen/willow bogs (Pogacnik 1985). The creek runs through pastures used for livestock grazing research and is grazed every year by cattle and sheep. The Red Bluff area has 75 to 100 frost free days. Up to 40% of the average annual precipitation (155 mm) falls during May and June, with minimum moisture from November to February (Clayton Marlow,

Montana State University, unpublished data). The geology, geomorphology, and hydrology of the Cottonwood Creek watershed have been documented by Aspie (1989).

## Chapter 2

## TEMPERATURE REQUIREMENTS FOR GERMINATION OF BEBB'S WILLOW

Introduction

Information on willows in the Northern Rocky Mountains is often descriptive (Froiland 1962, Brayshaw 1978). Experimental investigations of willows in Alaska have documented their role in successional stages along rivers and receding glaciers (Bliss and Cantlon 1957, Viereck 1966, Walker et. al. 1986).

Feltleaf willow (Salix alaxensis [Anderss.] Cov.) is often the first shrub to appear after perennial herbaceous vegetation colonizes sandbars and riverbanks of glacially fed streams. Seed establishes on bare mineral soil, and drifting branches lodge and sucker. By anchoring floodwater silt deposits, feltleaf willow has a physical as well as a biotic role in Alaskan floodplain development. The deposits create higher, less frequently flooded bars and banks which become suitable for grass and forb establishment. Increased herbaceous cover insulates soils, thereby maintaining the permafrost layer closer to the soil surface and later into the growing season. Drainage decreases and species composition tends toward a wet meadow-moss community.

Willow species composition also changes with increasing distance from a river's edge in response to soil type and drainage (Bliss and Cantlon 1957).

Along glacial outwash, feltleaf willow is present but its role is less prominent. Low clumps of Salix brachycarpa Nutt., Salix barclayi Anders. and Salix glauca L. provide 20% cover in meadow stages, the seral stage developed from the pioneering herbaceous community. These willow clumps create microenvironments suitable for establishment of mosses, which eventually dominate the climax tundra community (Viereck 1966).

Studies in the mid-western United States described primary and secondary succession along hardwood river bottoms (Weaver 1960, Wilson 1970). The appearance of Salix interior Rowlee on recently deposited silt and sand bars prepare a stable surface for the invasion of Populus deltoides. Wilson suggested S. interior was intolerant to shade and was eliminated in about 15 years by the taller growing P. deltoides. P. deltoides persists for 20 more years, after which it ceases root-sprouting. The stands deteriorate and are invaded by Fraxinus pennsylvanica Marsh, Ulmus americana L., and Acer negundo L., which then dominate the floodplain bottomlands. Boggs and Weaver (In manuscript) described similar scenarios for colonizing Salix fluviatilis (S. interior Rowlee) along the Yellowstone River in Eastern Montana. They suggested silt deposition was

responsible for eliminating S. fluviatilis. Silt increased the height of the bar or bank. Adventitious roots of sandbar willow sprouted in the new deposits since deeper roots were deprived of oxygen. Because new roots were above the capillary fringe, sandbar willows were replaced by deeper rooted P. deltoides. Weaver (1960) described streamside succession in the central Missouri Valley. After many years of observation he determined that succession depended on stream size, aspect, water salinity, wind, and proximity to woodlands (Weaver 1960).

Successional processes along lakes, ponds, marshes, seeps, and smaller first and second order streams in the Northern Rockies are less well documented. Consequently, identifying the successional stage and maintaining the integrity of riparian communities in arid and semiarid regions is a challenge to land managers. Autecological knowledge of species within these less studied ecosystems will facilitate the classifying, monitoring, and managing of riparian communities (Stauffer et. al. 1980, Knopf 1982, Platts et. al. 1987, Quimby 1989).

#### Objectives

In southwest Montana, Bebb's willow, Salix bebbiana Sarg., commonly dominates stream and seep riparian zones; however, its primary mode of reproduction and its role in succession are not known. Bebb's willow has been reported

as a pioneering species by Hansen et al. (1988). Atchley and Marlow (1989) have documented a lack of seedling establishment in decadent Bebb's willow communities. Seedling recruitment, soil requirements, and response to disturbance, water, and light, are unknown aspects of the biology of Bebb's willow.

Some studies on members of the Salicaceae family have documented germination characteristics. Aspen (Populus tremuloides Michx.) seed collected in Logan Canyon, Utah, has high germinability at 5° C (McDonough 1979). These aspen seeds also germinate rapidly, most within the first five days. Like Bebb's willow, aspen is small-seeded, clonal, and often a riparian species (Schier 1974).

Salix spp. have short-lived seeds that lost viability 10-90 days after dispersal, except for seeds of a few fall dispersing species which remain viable until the following spring (Densmore and Zasada 1983). Moss (1938) found that the viability of Bebb's willow seed drops from 100% at day 10 after natural dispersal to 50% by day 42.

One objective of this study was to determine germination rates and success of Bebb's willow seeds at a range of temperatures. Selected temperatures were those that seeds were likely to encounter during dispersal. A second objective was to determine if seed collected on different dates would have different germination success, at the given temperatures.

A study examining temperature effects on Bebb's willow seed germination in Alaska reported 90 to 100% germination at all treatment levels (Densmore and Zasada 1983). Using this information, the hypothesis tested in the present study was that different temperatures will not affect germination success. The hypothesis tested for collection dates was that percent of germination will depend on date of harvest.

#### Materials and Methods

Catkins of Bebb's willow were collected twice during natural dispersal. Collection Date I was 30 May 1987, and Date II was 11 June 1987. Individual Bebb's willows were randomly selected but all grew on the banks of Cottonwood Creek. Catkins were collected from the same willows on both dates. They were collected in paper bags, brought to the laboratory, and oven-dried at 25° C for three days, as recommended by Zasada and Viereck (1975). Catkins were stored at -5° C prior to germination trials (Zasada and Densmore 1977). Extracting seed from the dense comose by gently carding individual catkins by hand was more effective than by air-blowing as described by Harder (1970).

Catkins produced a variety of seed sizes, colors, and shapes. Large (>0.5mm), plump green seeds had the highest viability (100%) in tetrazolium tests. Consequently, these plump, green seeds were selected over dark, brown, small, or wrinkled seeds for the germination trials.

To determine optimum germination temperatures, a one-way thermogradient plate was first covered with germination blotter paper. The edge of the blotter paper extended into a reservoir of distilled water, and saturation was maintained by capillary action (Webb et al. 1987). Thermocouples and a channel data logger monitored temperatures set at 5° C, 10° C, 15° C, 20° C, and 25° C. Actual temperatures fluctuated  $\pm 2^{\circ}$  C.

Two replicates from each collection date were placed on each isotherm. Each replicate had 50 seeds. Seeds were in a light-dark regime of 16 h light and 8 h dark. Light was supplied by four fluorescent tubes. A 4 mm thick plexiglass sheet covering the plate prevented rapid evaporation from the blotter paper.

Each treatment replicate was inspected daily for 30 days; germinated seeds were counted then removed. Seeds were considered germinated if the hypocotyl had emerged and extended, and the cotyledons had developed and split. Germinants were removed from the plate.

Replicates were arranged in a completely randomized design. Univariate ANOVA was used to analyze differences between collection dates and among temperatures. ANOVA was used to detect temperature by date interactions. Tukey's Studentized Range test was used to separate means of germination success at the five treatment levels, and germination success between collection dates. Differences

were considered significant at the  $P < 0.10$  level.

### Results and Discussion

#### Collection Dates

Almost four times more Date II seeds germinated than Date I seeds at  $10^{\circ}$  C (Fig. 1) This resulted in a significant date by temperature interaction (Table 1). Forty-seven percent of the seeds at  $10^{\circ}$  C germinated by day 30 (Fig. 2). However, only 20% of Date I seed had germinated by day 30, whereas 74% of the Date II seed had germinated. Even though the Date II seed consistently germinated at a faster rate than Date I seed at  $10^{\circ}$  C,  $15^{\circ}$  C,  $20^{\circ}$  C, and  $25^{\circ}$  C, cumulative germination percentages were significantly greater only at  $10^{\circ}$  C ( $p=0.0000$ ; Fig. 1).

Table 1. Analysis of variance for temperature and date effects on percent germination of seeds.

SOURCE	DF	S.S.	M.S.	F-VALUE	P-VALUE	C.V.
TEMP	4	5.814	1.453	84.11	.0000	7.3
DATE	1	.375	.375	21.73	.0000	
TEMP*DATE	4	.213	.053	3.08	.0677	
RESIDUAL	10	.172	.017			

Difference in germinability between Date I and Date II seed at  $10^{\circ}$  C may be due to a degree of maturity not yet attained by Date I seeds. Date I seeds at  $10^{\circ}$  C and both dates at germinated poorly at  $5^{\circ}$  C. The date by temperature

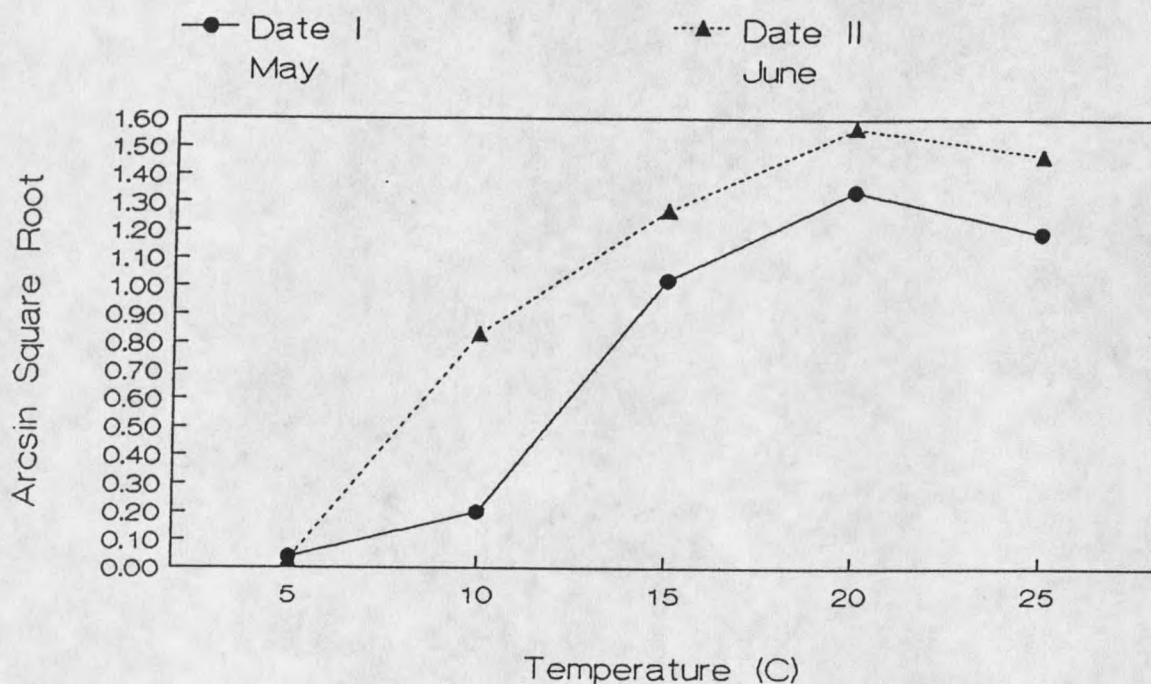


Fig. 1. Percent germination of seeds with increasing temperature. Percent germination transformed to the arc sine of the square root. Significant date by temperature interaction at 10° C ( $P=.067$ ).

interaction at 10° C may indicate a critical time for seeds from southwest Montana when more mature seeds have an advantage. Higher temperatures may compensate for the less mature seed and promote germination.

### Temperature

Germination of seed in the 5° C treatment reached 3.5% by day 30. By day eight, many seeds were brown, and by day 30, over half were moldy or rotten. Densmore and Zasada (1983) reported successful germination (90%) of seed at 5° C. Alaskan Bebb's willows are subject to wider temperature fluctuations and shorter growing seasons, so their seeds may be physiologically adapted to germinate at lower temperatures.

A separation of percent germination means, Dates I and II combined, indicated that germination at 20° C was significantly greater than germination at 5° C, 10° C, or 15° C, and that seeds at 15° C and 25° C responded similarly (Fig. 2 and Table 2).

Table 2. Mean separation (arcsin square root of percent germination). Different letters indicate a significant difference.

TRT	MEAN
5° C	.035 A
10° C	.318 B
15° C	1.146 C
20° C	1.458 D
25° C	1.330 CD

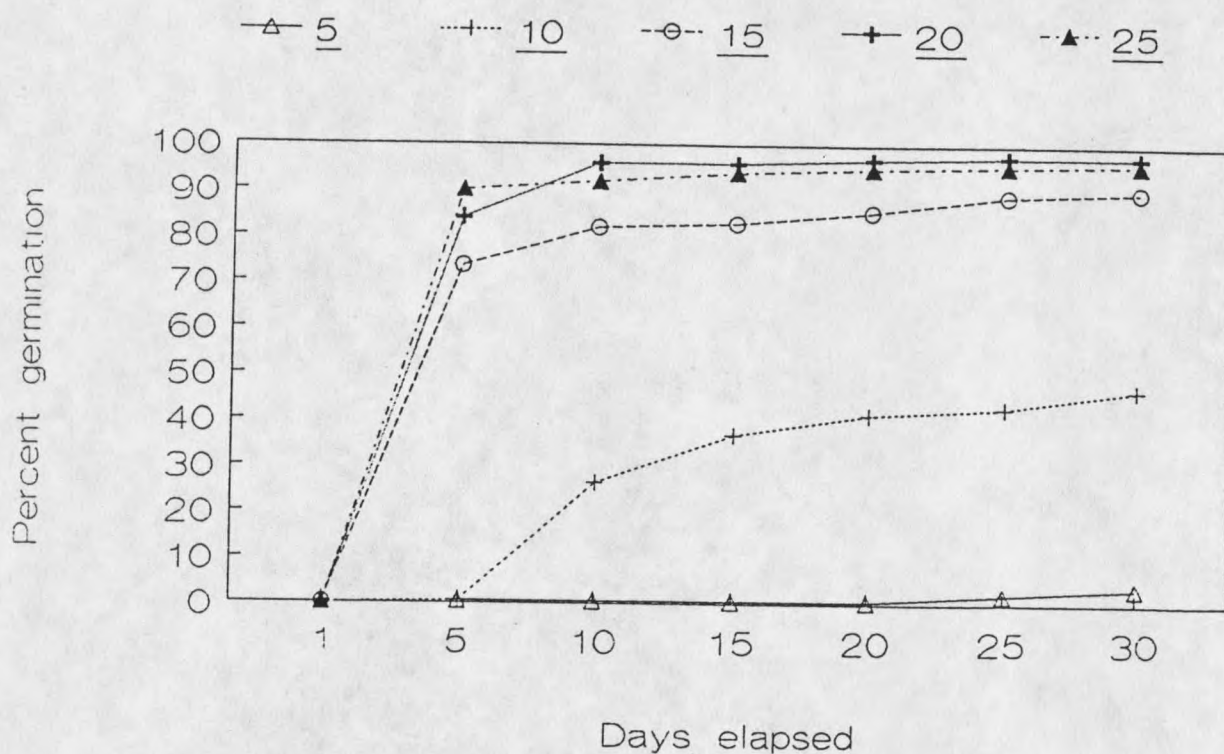


Fig 2. Germination of seeds over time. Dates I and II are averaged.

In the first five days of the study, 50% of all but the 5° C seed germinated. Total percent germination of all but the 5° C treatment was 90% or greater, and 80% or more germinated within the first 10 days (Fig 2). Seed continued to germinate at all temperatures during the 30 day study until 66.8% of all seed germinated (Fig 2). In the study by Zasada and Densmore (1983), the same range of temperatures

as used in the present study resulted in 97 to 100% germination in the first 10 days, except at 5° C where 90% germinated. Moss (1938) also reported nearly 100% germination of Bebb's willow seed within 10 days at room temperature (usually 21° C). His seeds were collected near Edmonton Alberta.

Rapid germination at 15° C, 20° C, and 25° C may indicate a response to the generally cool growing season in Montana, similar to other regions where this seed has been tested. Germination on saturated sandbars and riverbanks might be inhibited by cool water.

#### Conclusions

Germination is rapid and high from 15° C to 25° C. The hypothesis that temperatures from 5° to 25° C would not affect germination success was not supported. Seeds did not germinate well at 5° C and had varied responses at 10° C.

Date of seed collection only affected germination at 10° C, which supported the hypothesis that germination success differs between seeds collected on different dates. Germination rate and success for Date I were slightly depressed across all temperatures.

## Chapter 3

## BEBB'S WILLOW SEEDLING ESTABLISHMENT UNDER FOUR LIGHT INTENSITIES

Introduction

Establishment requirements for Bebb's willow are part of a web of interacting factors. Bebb's willow may be affected by several factors while establishing: herbivory (sheep, cattle, moose, elk, beaver, small mammals, insects), fungal infection, drought, temperature extremes, snowdrift, flood, and wind.

Light is another establishment factor, interacting with moisture and nutrients to produce carbohydrates through photosynthesis. Studies of light as a factor in riparian communities are few (Menges and Waller 1983) thus, light effects on crop, woodland, and grassland communities must suffice for preliminary literature investigations.

Larcher (1980) presented data from several researchers that estimates proportion of full sunlight reaching the ground surface in several communities (Table 3). A ground surface beneath a grass-clover sward typically receives five percent of full sunlight (Stern and Donald 1962). A deciduous forest canopy during the growing season intercepts

80-90% of the sunlight. After abscission, bare trees intercept only 30-50% (Larcher 1980).

Table 3. Percentages of full sunlight (direct and diffuse radiation) reaching ground surface (Larcher 1980).

COMMUNITY	% Full Sunlight
Boreal birch-spruce mixed forest	2
Pine forest with herbaceous understory	2
Sunflower field	19
Wheat field	7
Deciduous forest	10-20

Adaptations to different light intensities are apparent in seed size, physiology, and morphology. Large seeds store more carbohydrates than small seeds and are therefore better adapted to establish in shadier environments (Grime and Jefferey 1965). Since woodland and forest species must often establish in low light they may be considered shade tolerant. They have low photosynthetic compensation points and low respiration rates. Hypocotyls, cotyledons, internodes, and petioles extend in these shade plants but do not etiolate. Extension is complete and slow. Etiolation would exhaust resources in the seedling, disabling it against fungal pathogens (Grime 1981).

Shade tolerant plants have slower rates of production in full sunlight than shade intolerant plants (Grime 1966). Because shade intolerant species are accustomed to an open canopy they are less plastic, extending only the hypocotyl

when shaded. Etiolation may occur in the established seedling after a canopy expands or closes.

Two germination strategies described by Ng (1978), epigeal and hypogeal, characterize cotyledon function in light adapted plants. In species with hypogeal germination cotyledons do not extend above the soil into the light for photosynthesis. Cotyledons are the food source. In epigeal germination, the hypocotyl is extended so the cotyledons may capture light and photosynthesize. Epigeal seeds tend to be small than hypogeal seeds. Bebb's willow seeds are extremely small, weighing about 0.20 mg (Brinkman 1974). Studies preliminary to this experiment indicate an epigeal germination strategy. After ten days in complete darkness, imbibed Bebb's willow seeds extended hypocotyls up to 20 cm.

Grime (1966) has distinguished five type of light habitats for temperate plants: 1. dry unproductive, 2. recently cleared, moist, productive, 3. grassland, 4. open woodland, and 5. dense woodland or forest. Although riparian zones may be found in any of these habitats, the zone itself fits into Grime's recently cleared, moist productive type. Riparian zones are characterized by flooding, grazing, or harvest (beaver). High in organic matter and rich in silts, riparian zones support highly productive communities requiring high water tables (Hansen et. al. 1988). Grime (1966) proposed that this habitat type

is colonized by species with prolific seed production and efficient dispersal. Feltleaf willow may disperse 380 viable anemophilous seed/m<sup>2</sup> in Alaska (Zasada 1986).

Because these recently cleared, moist, productive areas produce dense vegetation, competition for available light can be high. Consequently, taller, faster growing plants tend to be successful. To be successful, rapid elongation of petioles and internodes is advantageous to the growing seedling under low light conditions.

Shade adaptations in individual species may affect community structure over time. Hosner and Minckler (1960) found that as overstory decreased, seedling success of S. interior and Salix nigra Marsh increased. A decrease in willow seedlings under dense canopies is attributed to "shade intolerance." Wet-ground shallow basins in southeastern Wisconsin, known as shrub-carrs, are described by White (1965). These shrub-carrs support a tall-shrub community where Bebb's willow serves as a tree layer, intercepting light. Salix candida Fluegge and Salix pumila colonize peat soils. Bebb's willow is seral, occurring after initial colonization of the peat. Bebb's willow is replaced by forests of Fraxinus nigra and Ulmus americana. Unfortunately, factors that may have changed species composition were not discussed. Bebb's willow occurs most frequently in shrub-carrs with little disturbance in the past 20 years. In low disturbance areas, trees invade the

shrub-carrs.

### Objectives

Settling of the United States led to manipulation of watersheds and this has obscured their original condition (Reisner 1986). Distribution of Bebb's willow in North America is an example of an ecosystem component affected by development. Before damming of the Missouri River in South Dakota, Bebb's willow grew above the Missouri's immediate riverbank, on higher terraces, and up into tributary canyons (Sven Froiland, Augustanna College, personal communication). Habitats appropriate for Bebb's willow were drowned.

Bebb's willow is presently abundant along first and second order streams in the Northern Rockies, between 1100 and 2700 meters in elevation (Brunsfeld and Johnson 1985). When dominant, Bebb's willow often excludes other willows on these streams. When part of a willow thicket along seeps or streams, Bebb's willow has been found on the periphery of willows lining the water column and is not dominant. The spatial and temporal placement of Bebb's willow in these riparian environments may depend on light availability or shade tolerance.

The objective of this study was to determine if different light intensities affected seedling size, morphology, and percent establishment in the lab. This study tested the hypothesis that given equal growth

conditions, biomass and height of seedlings will vary with the intensity of light. The hypothesis that higher percentages of establishment depend on greater light intensities was also tested.

### Materials and Methods

Seeds collected from Cottonwood Creek on Red Bluff Research Ranch, were harvested, stored, and separated from catkins as described in Chapter 2.

Fungi, primarily Aspergillus spp., grew on seeds in preliminary experiments using growth chambers and germinators. We attempted control by applying anti-fungal powder and bleach. Anti-fungal powder, tetrachloroparabenzquinone, killed the seed. A 1% bleach bath killed the seeds, and a .01% bleach bath did not deter fungal growth. Instead, a 24 hour water bath eliminated much of the fungal growth. Seed in a muslin bag placed inside a 50 mL Erlenmeyer flask were bathed in running tap water for 24 hours. This waterbath also imbibed the seed.

Initial experience also revealed the delicate nature of these small seeds. Seeds were less than 1 mm long and less than .05 mm wide. After imbibing water, seeds were very soft and easily smashed if squeezed with forceps. The seed coat was thin and hyaline, sloughing off after seeds imbibed. Only 0.2% of the seeds emerged from soil in some plantings. Mortality in greenhouse soils could rarely be

described because the small seeds could not be identified nor found once planted.

To minimize mortality during germination, seeds were germinated and grown for 10 days on germination blotter soaked with full strength Hoagland's nutrient solution. Plastic trays with covers were used to hold the germination blotter. The trays were placed in a germinator. The germinator illuminated the seeds with 16 fluorescent tubes and 12 100 watt bulbs for 16 hours, at a temperature of 25° C. During the dark cycle, the temperature was 10° C. The temperature and light cycles are similar to the cycles in June in southwest Montana (Clayton Marlow, Montana State University, Unpublished data).

On day 10, hypocotyls had extended, root hairs at the hypocotyl-cotyledon junction had developed, and cotyledons had expanded. Some first leaves were beginning to emerge. Seedlings were transplanted to pots containing a mixture of 1/3 Bozeman silt loam, 1/3 sand, and 1/3 peat moss.

Each light intensity had two replications with 18 pots per replication. Treatment pots were placed in metal trays to facilitate movement and subirrigation. Four seedlings were transplanted to each pot to ensure that at least one plant per pot survived. An initial experiment indicated low success even under controlled, ideal conditions. Moist soil was maintained by subirrigation.

Levels of light intensity in the germinator were

created by lowering the bank of lights to simulate 20% full sunlight (f.s) on all pots. One treatment was uncovered and so received 20% f.s. Lower light intensities were simulated with plastic garden shade cloth, cotton surgical gauze, and doweling. Six 12 cm dowels were fastened erect to sides of a tray. Ten layers of gauze were draped over the dowels so that 10% f.s. radiated to the pot soil level. To achieve lower levels of light, dark grey plastic garden shade cloth and gauze were draped over dowels on the two remaining treatments. A single layer of cloth and 3 layers of gauze simulated 3% f.s., and a double layer of cloth simulated 1% f.s. Light intensity was measured with a Parkinson light meter.

Every three days trays were randomly moved within the germinator. Pots were subirrigated weekly with full strength Hoagland's solution. Rapid evaporation from the soil surface by the 20% f.s. treatment necessitated scattering Perlite on the surface to limit drying of soil and roots.

Plants grew for 60 days. Roots and shoots were harvested from established plants on day 60. Establishment was defined as a plant past the second leaf stage. Roots and shoots were separated and shoot heights were measured to the nearest 0.5 cm. Roots and shoots were oven dried at 80° C for 24 h and weighed to the nearest 0.0001 g. Weights and heights of seedlings from pots with more than one survivor

were averaged.

The study was a completely randomized design. Seedling weights, heights, and percent success were analyzed using ANOVA to detect differences in the measured variables among treatments. Differences between replicates and a treatment by replicate interaction were also tested. Differences were considered significant at  $P < 0.10$ .

### Results and Discussion

All seedlings under the 1% f.s. canopy died by day 60. Three leaves were seldom produced; no seedling produced four leaves. Most seedlings withered within the first 30 days.

Seedlings in the 3% f.s. treatment developed slowly; roots were shallow and shoots averaged less than 3 cm tall (Table 4). The compensation point for Bebb's willow may lie between 1% f.s. and 3% f.s. (Fig 3.). At less than 3% f.s., respiration probably exceeds carbon synthesis. Three percent f.s. seeds had lower percent establishment than 10 and 20% f.s. (Table 4.). Plants at 3% f.s. appeared to be less vigorous seedlings and would be less capable of withstanding fungal infection and disease. Smaller seedlings would also have fewer resources to recover after herbivore damage. Thus chances for survival under a dense canopy could be low.

Bebb's willow seedlings under the 10% f.s. treatment were tall and robust compared to plants grown under the

lower light intensities. Roots were fibrous and deep, and shoot height averaged 6.3 cm. Shoots and roots were lighter in weight than the 20% f.s. shoots (Table 4 and Fig. 3). As petioles and internodes elongated the stems bent over.

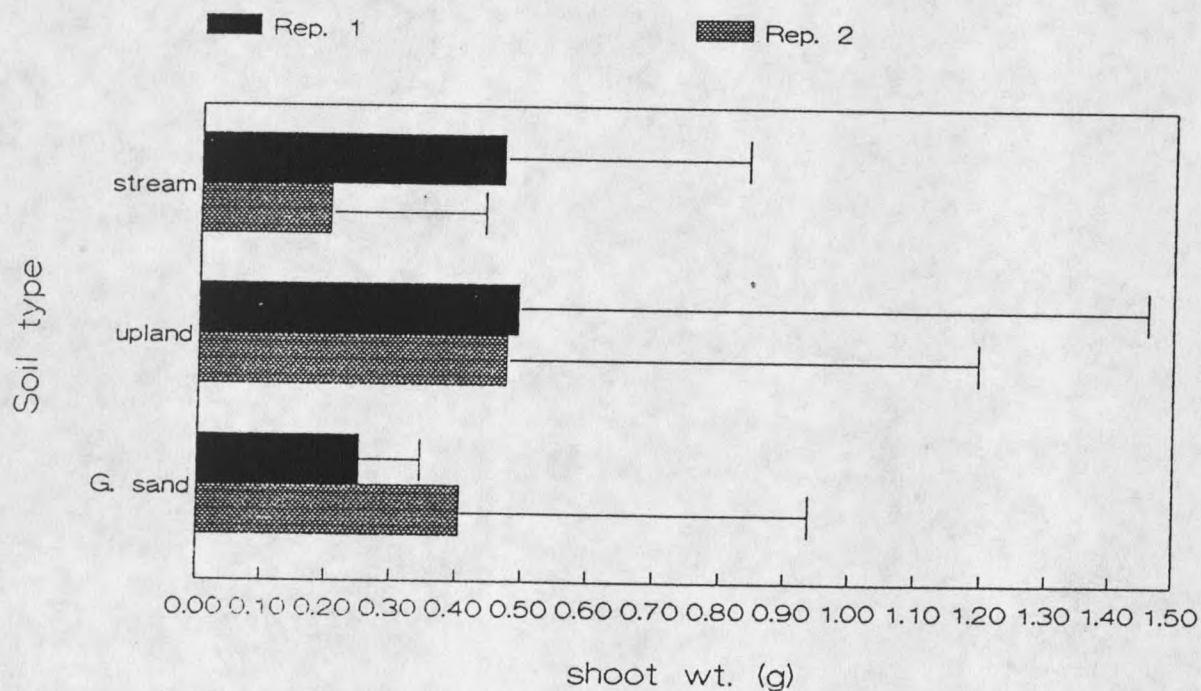


Fig. 3. Averages of shoot wt. at increasing levels of light for two replications. Bars represent the high range.

Apparently they were not completely self-supporting. Weight of shoot growth for each cm of growth in the 10% f.s. seedlings was lower than in the .20% f.s. plants (Table 4).

Table 4. Summary effects of light intensity of average root and shoot weight (g), percent established at day 60, average shoot height (cm) and gram of shoot weight per centimeter of shoot height.

% f.s	root wt. (gm)	shoot wt. (gm)	% est. d 60	shoot ht. (cm)	g shoot/ cm
20	.085	.273	69	8.0	.028
10	.029	.115	77	6.3	.014
3	.003	.001	47	3.0	.003

The 20% f.s. seedlings also grew fibrous roots. Although not measured, the stems, petioles, and leaves appeared thicker than those of the 10% f.s. shoots. Seedling height averaged 8.0 cm (Table 4). The heavier weights/height at 20% f.s. are probably a result of photosynthesis exceeding respiration due to increased radiation. Leaves and stems thicken to conduct more water and develop layers of cells with more chloroplasts (Larcher 1975). Leaf thickening under higher light intensity has also been documented by Kozlowski (1977).

All differences were non-significant at the chosen levels because number of replicates was low (n=2) and their variance was high. Trends can be suggested, however, and we have depicted the summary statistic of shoot weight average

against light intensity (Fig. 3).

A treatment of 50% f.s. would have helped confirm whether Bebb's willow seedlings were more shade adapted. At 50% f.s., weights should not be significantly greater than those at 20% f.s. for a shade adapted plant (Loach 1970). Bebb's willow seedlings are probably not shade-adapted, however. The morphogenic responses at 10% f.s. were similar to responses of colonizing species subjected to shade (Fenner 1978).

Colonizing species are often shade intolerant (Fenner 1978). Other willow species, e.g. S. interior, are colonizers and are shade intolerant (Wilson 1970). The term "colonizer" as used by Fenner (1978) and Grime (1977) refers to quick-growing and short-lived species which are shade intolerant. Bebb's willow may colonize but this has not been documented. Larcher (1975) categorizes shade plants as tolerant of 20% f.s. or less. In 60 days, Bebb's willow established and grew vigorously at 20% f.s. Bebb's willow exhibited characteristics of colonizer (shade intolerant) and shade adapted (shade tolerant) plants.

Using values presented by Larcher (1975), twenty percent f.s. should be common at the ground layer beneath a diffuse deciduous canopy in southwest Montana in early June. The same canopy in full flush in early July should intercept 90% of the radiation. If our establishment and biomass data

are accurate, Bebb's willow seed, dispersed in early June, could establish in 20% f.s. and continue to grow in 10% f.s. in July.

Diffuse and direct light reaching the ground will change seasonally and daily. Light effects on riverine riparian species must consider not only seasonal changes of light, but also the forces of erosion and deposition along streams and rivers. Stochastic events like flooding alter the physical structure of the riparian community, increasing light in some areas (e.g. a stream bank shorn of its vegetation) while removing all light in others (e.g. matting of reeds). Light availability may also depend on channel width.

Percentages of full sunlight are general guides helping to discern if Bebb's willow is a shade adapted plant. If full sunlight could be created in the germinator we could more accurately define Bebb's willow's establishment requirements. In the laboratory we cannot account for unpredictable environmental variables like sunflecks, gaps, and clouds. Classification could also be more precise if the ecological vocabulary i.e. "colonizer" and "shade tolerant" did not conflict.

Our results suggest Bebb's willow could not establish from seed in shade similar to the understory of a dense coniferous forest, which is less than 3% f.s. Slow growth in dark shade, plastic responses in moderate shade, and

vigorous growth in light shade are modicative responses, characteristics adapted by individual plants during development of photosynthetic organs (Larcher 1975). Modicative responses among treatments and the high variation within treatments may indicate an array of reproductive strategies. Bebb's willow may colonize soil or sand with a constant water supply and adequate light, but they may also establish in sparse meadows, deciduous forests, and shrubby streambank communities.

A tolerance for lower light intensities (10% f.s.) would explain Bebb's willow's presence in bogs and Carex spp. communities. Moderate shade may prevent establishment of known colonizers like S. exigua but may be adequate for establishment of Bebb's willow. S. exigua is an aggressive colonizer of bare sandbars and streambanks (Hansen et. al. 1988). If Bebb's willow can tolerate moderate shade, it may establish on the fringe of S. exigua colonies, closer to herbaceous shading on shores or banks that deter S. exigua colonization. This type of peripheral establishment was noted throughout southwest Montana during this study.

Repetition of this study with many replications might detect and confirm the trends our research merely suggests. There was high variance in the data (Fig. 3). Differences in establishment among treatments (Table 4) may be due to handling of seedlings. Fewer seedlings under 3% f.s. may have established because of uneven drying of the soil

surface. The shallow roots under 3% f.s. may have desiccated under water stress since the roots from day 10 to day 30 were very fine and delicate. The soil mixture was chosen for its water holding properties, not uniformity of texture. Microsite variation within the soil could have led to inequitable growing conditions. Variable results attest to the difficulty in handling this seed, and reinforce ideas on the erratic nature of Bebb's willow establishment.

### Conclusions

Different light intensities affect establishment and biomass of Bebb's willow seedlings. Seedlings were intolerant of 1% f.s. As light intensity increased heights and weights of seedlings increased. Percent establishment depend on light intensity, but was low for seedlings grown under 3% f.s.. Bebb's willow established in moderate and low light conditions given adequate moisture and nutrients. It grew slowly under low light conditions, like those found beneath dense coniferous or herbaceous overstories.

## Chapter 4

ESTABLISHMENT OF BEBB'S WILLOW BY SEED AND STEM  
IN SEVERAL SOILSIntroduction

Studies investigating floodplain and riparian species establishment have addressed tolerance or response to flooding and burning (Zasada et. al. 1983, Knighton 1981, Krasny et. al. 1988), and drought and nutrient stress (McLeod and Mcpherson 1973, Walker and Chapin 1986), and have described life history traits (Walker et. al. 1986) and community composition (Bliss and Cantlon 1957, Wilson 1970, Viereck 1966, Wilson 1970, Youngblood et.al. 1985, Kovalchek 1987 Hanson et. al. 1988). Establishment of individuals of the Salicaceae family has been specifically researched by Moss (1938), McLeod and McPherson (1973), Schier (1974), Zasada and Viereck (1975), McDonough (1979), Densmore and Zasada (1983), Krasny (1988), and Krasny et. al. (1988).

Krasny (1988) studied the establishment of some Salicaceae (Populus balsamifera L., P. tremuloides, S. alaxensis, and S. interior) in Alaska river floodplains by propagating seeds in several soil types under field and greenhouse conditions. In a complementary experiment, she

determined the relationship between root suckering and soil type. She found that sexual reproduction was of secondary importance in establishing P. balsamifera, S. alexensis, and S. interior along an Alaskan river. Low in water holding capacity, sandy riverbar sites were not conducive to seed germination. Seeds germinated under mesic conditions but this did not explain patterns of distribution among early successional river bar species. Soil moisture content and electrical conductivity accounted for 50% of the variation in germination among seven soil types. Root suckers expanding from mesic to xeric sites (i.e. sandy river bars), stem sprouting, and lodging of root and shoot fragments colonized and recolonized sites along the river.

#### Objectives

In southwest Montana, the lack of regeneration of Bebb's willow stands prompted studies on sexual and asexual establishment requirements (Atchley and Marlow 1989). Germination requirements for Bebb's willow have been documented (Densmore and Zasada 1983, Zasada and Viereck 1975), but requirements for establishment are uncertain. Because the growing season at Red Bluff Research Ranch ranges from 75 to 100 days, establishment was defined for this chapter to be survival of a willow seedling after 60 days of an imposed treatment. Germination studies by Zasada and Viereck (1975), Densmore and Zasada (1983) and Zasada

et. al. (1983) were short, up to 30 days, and they were not conducted in soil.

The objective of the study was to determine soil type effects on asexual and sexual establishment. One hypothesis tested was: Soils of varying texture and nutrient availability will produce seedlings with varying amounts of biomass. A second hypothesis was: Soil type affects percent establishment. This knowledge might help explain current lack of regeneration on Cottonwood Creek. It might also explain Bebb's willow's presence and influence on successional changes along streams and seeps.

### Materials and Methods

#### Stem Trial

Stems were collected in May 1988 from 10 individual ortets (the original plant of a clone) along Cottonwood Creek. All stems were four years old as determined by annual ring counts, and were trimmed to 16 cm.

Four field soils and three prepared greenhouse soils were used. Each soil and its characteristics are listed in Table 5. Stream, upland, and Gallatin sand were replicated twice. All other soils were used in preliminary experiments and were not replicated but data are reported here. Stems were placed horizontally on three cm of soil in metal trays and then covered with six cm of soil. Stems were subirrigated until shoots emerged, which varied for each

soil type. Stem trays were then irrigated from above. After 60 days, all stems with shoots and roots were harvested and washed. Roots and shoots were separated from the stem and dried at 85°C for five days. Weights were recorded to the nearest 0.0001 g.

### Seed Trial

Seeds were collected and stored as described in Chapter 2. Seeds were stored for 22 months before this study began. Zasada and Densmore (1980) projected a 1.2% to 6.5% loss in germination of Bebb's willow seeds after 24 months of storage at -5° C.

In the seed trial, four seeds were planted in each of 18 pots for five soil types. Pots were placed in metal trays with three replications. Pots were 6 cm x 6 cm x 6 cm, and were filled to a depth of 4 cm. Five soils were used: bank, stream, upland, Gallatin sand, and Sunshine mix. Seeds were placed in 2 mm deep holes then topped with soil so that holes were covered level with the soil surface. Pots were subirrigated by pouring water into the metal trays. Trays were refilled two to three times per week. The various soil types dried at unequal rates so each treatment was irrigated individually to maintain moist soil. Trays were placed on a greenhouse bench in April 1989 and were moved randomly once a week. The greenhouse was maintained at 20° C +- 4° C for 16 daylight hours and at

Table 5. Soil descriptions; four field soils and three commercial soils. Soil tests of field soils provided by Montana State University Soils Testing Lab. N=N03-N ug/g, P and K = ug/g, EC = mmhos/cm.

FIELD SOILS

- Bank-----Sandy loam from a bank cut, exposed by livestock hoof action along Cottonwood Creek.<sup>1</sup>
- Stream-----Sandy loam from silt bar beneath mature Bebb's willow on Cottonwood Creek.<sup>2</sup>
- Upland-----Sand slumped onto creek bank from upland range site occupied by Artemisia spp., Festuca spp., and Agropyron spp..<sup>3</sup>
- Gallatin Sand----Loamy sand from a periodically submerged sand bar in the Gallatin River, beneath Axtell Bridge.<sup>4</sup>

Soil	Sand	Silt	Clay	pH	EC	N	P	K	O.M.
<sup>1</sup> Bank	63	19	18	6.5	1.5	2.9	12.4	70	4.3
<sup>2</sup> Stream	70	20	10	6.2	1.6	2.3	16.4	82	4.0
<sup>3</sup> Upland	85	7	8	6.5	0.3	4.3	12.9	62	0.3
<sup>4</sup> G.sand	81	15	4	7.5	0.6	2.0	10.3	100	0.3

COMMERCIAL SOILS

- Inert Sand-----Inert commercial sand used in sand blasting.
- Greenhouse Mix---Montana State University Plant Growth Center mix. Sterilized mix of 1/3 Bozeman silt loam, 1/3 sand, 1/3 peat moss.
- Sunshine Mix-----Commercial peat moss, vermiculite and perlite, with a fertilizer which leaches out after 3 waterings.

10° C +- 4° C for the 8 dark hours.

During the growing period, pots were monitored for cotyledon emergence and mortality. On day 60, seedlings were harvested. Roots were separated from shoots and washed. Shoot height was measured. Roots and shoots were dried at 85° C for three days and weighed. If a pot had two or more established seedlings, the seedling data were averaged.

Two replications were not sufficient for statistical analysis of stem growth results. Results from the seedling growth trial were analyzed using ANOVA with a significance value of ( $P < 0.10$ ). Results were analyzed for treatment and replicate effects. Weight and height means were separated using Student's T test.

## Results and Discussion

### Stem Suckering Trial

Biomass production from Bebb's willow stems was inconsistent within treatments (Table 6 and Fig. 4). Variability in biomass from stem to stem within a soil type indicated that some factor influencing growth was unaccounted for by soil differences (Fig. 4). All stems were four years of age and 16 cm in length. Differences may be due to traits such as carbohydrate concentration or hormone activity.

Table 6. Average weights (gm) of biomass produced from stems in three field soils. Percent suckering success was the percent of stems which suckered per tray.

Soil	Rep	Root wt.	Shoot wt.	% Success
Stream	1	.062	.465	38.9
	2	.032	.201	40.0
Upland	1	.219	.491	41.2
	2	.107	.473	47.4
G. sand	1	.047	.251	16.7
	2	.128	.405	50.0

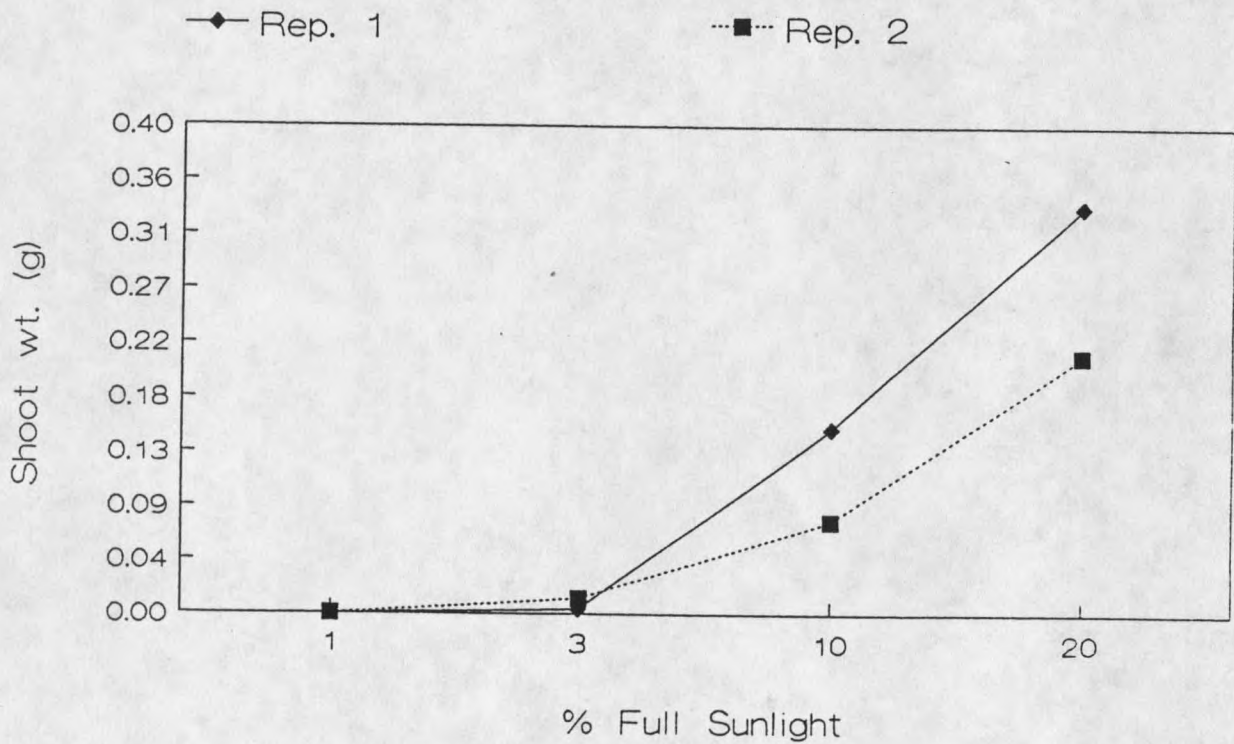


Fig. 4. Averages of shoot weight (g) of suckering stems for three soil types.

Shoot production, or suckering, in Salicaceae root and shoot cuttings has been well documented (Carlson 1950, Chmelar 1974, Schier 1974, Schier and Zasada 1973, Densmore and Zasada 1978, Everett et. al. 1978, Krasny et. al. 1988). Preformed root primordia within the periderm are suppressed by auxins from apically dominant meristems of aspen (Schier and Zasada 1973). Once apical dominance is removed, inhibitor levels decline and primordia develop into adventitious roots. Under the same hormonal regulation, dormant buds on stems produce new shoots (Carlson 1950).

Schier and Zasada (1973) analyzed total nonstructural carbohydrate (TNC) concentrations in suckering aspen roots. TNC concentrations affected the dry weight of shoots from buried roots, which produced shoots in darkness. Dry weight depended on the number of developing apices. With more shoots developing on a root segment, the limited supply of TNC was distributed among more shoots, and therefore individual shoots were lighter. There was a significant but weak correlation ( $r=0.35$ ,  $p<.0026$ ) in my study between shoot weight and shoot number on a stem, however, the same principal should apply. TNC concentrations may have been low in the stems cut in spring (Kozlowski 1977). In the present study, low concentrations of TNC could produce a range of growth rates which would mask effects of different soils. Later in the growing season, when TNC concentrations

are highest, soil type may have a more direct effect on shoot production.

Auxin concentrations could also be extremely variable in each season, or in each ortet and ramet (Kozlowski 1971). If auxins that prevent root primordia development were present in varying levels in a stem, this would explain why we did not find a strong correlation between shoot number and shoot biomass. Furthermore, once stems and leaves developed, they would have contributed photosynthate to the plant, increasing root and shoot development.

Forty percent of all stems produced roots and shoots. The percent success of rooting and suckering stems in this study (Table 6) was similar to a 42% average success of suckering Bebb's willow stem cuttings in Alaska (Holloway and Zasada 1979). The Alaska figures were from softwood of the current year. In contrast, in our preliminary experiment stems younger than three years did not root or sucker.

Data from two prepared greenhouse soils and a commercial, inert sand indicated potential differences in biomass production at two extremes (Appendix A, Fig. 5). Stems grown in two soils high in organic matter and water holding capacity produced more suckers than those grown in soil devoid of organic matter and with poor water retention. Stems lodged in organic soils would probably have an advantage establishing over stems lodged in sandbars,

although moist sandbars could be adequate for establishment. Without an influx of nutrients, growth in sandbars should be limited.

Adequate moisture in sand, loamy sand, and sandy loam may be the only external requirement to establish Bebb's willow stem cuttings. Root and shoot biomass might differ among soil types in a riverine environment, which receives periodic influxes of nutrients via flooding, drainage, decay, and fire. The ability of a soil to retain or provide nutrients should affect vegetatively established willow once it has used its stem TNC supply.

Krasny (1988) grew root cuttings in several soil types and did not report a relationship between soil type and ability to sucker. Vegetative reproduction expanded S. interior willow into areas that were inhospitable to seeds.

#### Seedling Growth Trial

Sunshine mix was the only soil to produce significantly more biomass than other treatments in the seedling growth experiment (Table 7 and 8). Differences were expected among the sandy loams, loamy sands, and sands in biomass production because each soil offered different water holding capacities and nutrient availability.

ANOVA (Table 7) indicated significant differences between treatments, but a mean separation indicated only Sunshine mix to be significantly different. There were apparent differences, however.

Table 7. Analysis of Variance for shoot weights in five soil types.

SOURCE	DF	M.S.	F-VALUE	P-VALUE
Soil	4	.9197E-03	9.95	.0028
Rep	2	.5352E-04	.57	.5727
Error	8	.9247E-04		

The bank treatment produced shoots two times heavier than the upland and Gallatin sand treatments. Field soils were analyzed without the Sunshine mix data but there was neither replicate effect nor treatment effect.

Table 8. Shoot and root weight (g) are averages of seedlings grown from seed. Height is average (cm).

Soil	Shoot wt.	Root wt.	Height	Shoot/root	%Emerg.
Bank	.0120a	.0035a	1.5a	3.4ab	28.2a
Stream	.0126a	.0029a	1.9a	4.4b	21.7a
Upland	.0070a	.0025a	1.2a	2.8a	21.2a
G. sand	.0092a	.0037a	1.3a	2.4a	5.2b
Sunshine	.4908b	.0129b	4.8b	3.7ab	24.0a

Most seedlings in the upland and Gallatin sand treatments were shallowly rooted. Roots were fine and delicate and easily broken compared to roots in the bank and stream treatments, which were more resistant to breaking and more abundant. However, the Gallatin sand and upland treatments produced some seedlings which had the same

characteristics as those grown in bank and stream treatments. Similarly, bank and stream treatments occasionally produced small, delicate seedlings more characteristic of the upland and Gallatin sand treatments.

Seedling response was varied within treatments in this experiment and in the light experiment (Chapter 3). The seeds may possess inherent genetic variability undetected in seed morphology. A range of responses within treatments could be a reproductive strategy ensuring some establishment given any set of possible conditions in the field.

There were significant differences among field soils in the shoot to root ratios (Table 8). Stream ratios were higher than Sunshine and bank, which were higher than Gallatin sand and upland. However, the shoot to root ratios were high in all soil types, indicating adequate nutrients and water for developing foliage and increasing photosynthesis (Russell 1977).

Phosphorous levels in all field soils were low, but not limiting based on the shoot to root ratios (Russell 1977). Potassium levels were moderate (McLeod and McPherson 1973). Sunshine mix may have produced more biomass over all because of its initial nutrient supplement (Table 5).

Percent emergence was the percent of all seeds planted per treatment which germinated and emerged from the soil with expanded cotyledons and extended hypocotyl. Only 5% of the seed emerged from Gallatin sand. Emergence in other

soil types ranged from 21%-28% (Table 8). Ninety-five percent of seed on germination blotter germinated in the temperature experiment (Chapter 2), suggesting that the low emergence level was not due to seed viability. On a heavily burned site of organic soil sown with Bebb's willow seed, about 23% of seed sown survived from seed dispersal date, around June 20, to September 10, about 80 days later (Zasada et. al. 1983). The low emergence rate, 5.2%, in the Gallatin sand (a loamy sand) could reflect greater interstitial space where a small Bebb's willow seed may not contact free water, which is necessary for germination (Krasny 1988). The crown of hairs at the base of the hypocotyl is an absorption organ in the first week after germination (McLeod and McPherson 1973).

In Alaska, one out of 438 seeds (.23%) that were sown lived to the end of a three year study (Zasada et. al. 1983). In our controlled greenhouse study, 100 seeds out of 1070 planted (9.3%) met our establishment criterion, which was survival to day 60. The Alaskan seeds were sown on a floodplain and subjected to temperature and water fluctuations, and herbivory. If our soils had been influenced by environmental fluctuations, or had been in drought to flooded soils, seedling biomass and percent established may have differed considerably among the different soils.

Seedlings emerged between day 2 and day 30. After 30

days, no seedlings emerged. Most Bebb's willow seeds germinate quickly (Chapter 2, and Zasada and Densmore 1983). The 30 day emergence interval has also been documented by Zasada et. al. (1983). Most willow with summer dispersing seeds have short-lived seed; 90% may germinate in the first four days (Zasada et. al. 1983, Densmore and Zasada 1983). When a seed is imbibed, it must remain moist until germination. I found that after a second desiccation, seeds were no longer viable.

Aging may be responsible for aspen and willow deterioration (Froiland 1963, Schier 1974). Older ortets and ramets are susceptible to disease and are less competitive. Along Cottonwood Creek many Bebb's willows are mature (some are up to 60 years of age), as determined by annual ring counts of stem cores. In overmature aspen, deteriorating and diseased roots are incapable of suckering even when apical dominance is removed (Schier 1974). Frequent flooding, fire, or beaver activity may rejuvenate mature, but not decadent, Bebb's willow.

The influences of flooding and fire have been described by Zasada et. al. (1983), Walker et. al. (1985) and Walker and Chapin (1986). The timing of seed dispersal and flood events determine seed establishment of some Alaskan willows. Cottonwood Creek, and many seeps where Bebb's willows are found, are not frequently flooded. Scouring and small sandbar formation are typical in Cottonwood Creek. This

spring fed creek is in a region with a history of frequent fire (Arno and Gruell 1983). Zasada et. al. (1983) reported high germination of Bebb's willow on heavily burned sites in Alaska. No germination on lightly burned and unburned plots was recorded. The heavily burned site had an ash layer, but the organic layer was consumed by fire. Moisture was not limiting in this study (Zasada et. al. 1983). Fire may be an important disturbance factor influencing Bebb's willow seedling establishment.

#### Conclusions

Sunshine mix produced more seedling biomass than all other soils. There were no significant differences in seedling establishment and biomass of seedlings grown in field soils. Stem establishment did not vary due to soil type.

Requirements to establish, under our definition, may not be different from requirements to germinate. However, preliminary stem data, and data from seed sown in a fertilized peat soil, indicated a response to nutrition and water availability. Soil type did not appear to affect establishment unless interstitial spaces limited adequate water availability for seeds. Increasing and decreasing growth rates of roots and shoots in Bebb's willow in these experiments are not conclusively due to soil type.

## Chapter 5

## SYNTHESIS

Researchers have speculated on the reproductive strategies of Bebb's willow. Experimental data was lacking. Consequently, environmental variables affecting sexual and asexual establishment were tested under controlled conditions. Biomass produced, percent established, and percent germinated were tested using five temperatures, four light intensities, and seven soil types.

Temperature below 10° C may inhibit rapid germination of Bebb's willow seed in the field. Seeds germinating on a thermogradient plate at 5° C were susceptible to fungi and bacteria infection and had low germinability. Germinability was significantly depressed at 10° C in less mature seed. A higher percentage of mature seed germinated at warmer temperatures than less ripe seed.

Bebb's willow seedlings produced more biomass with increasing percentages of full sunlight. Seedlings succumbed to fungal infection and wilt at 1% f.s. At 3% f.s., they established but grew slowly. And at 10 and 20% f.s., plants grew rapidly and vigorously. Plants grown under 20% f.s. produced more biomass than those under 10%

f.s.

Field soil type did not affect seedling biomass significantly. However, seedlings grown in a sandy loam high in organic matter were taller and heavier than seedlings grown in sand and loamy sand. Seedlings exhibited morphological variation within soil treatments. Individual seed physiology may influence biomass production and percent establishment.

Soil type did not significantly affect stem production of roots and shoots. Treatment response may be affected by hormone and carbohydrate concentrations, which change seasonally. Water availability may be the only requirement for biomass production in the first 60 days of suckering.

Future studies on Bebb's willow should focus on water effects on seed and stem establishment. Physiological studies on seed would also be useful in understanding variation within the seed.

Field studies on Bebb's willow distribution would be valuable. An age class distribution study in several drainages might demonstrate common historical occurrences promoting establishment by seed. Studies of establishment near and below beaver ponds could describe asexual reproduction of Bebb's willow. The affects of disturbance would also illuminate more of its successional role. A survey of seedling establishment could reveal actual sexual establishment, which this limited study did not encounter.

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## APPENDIX

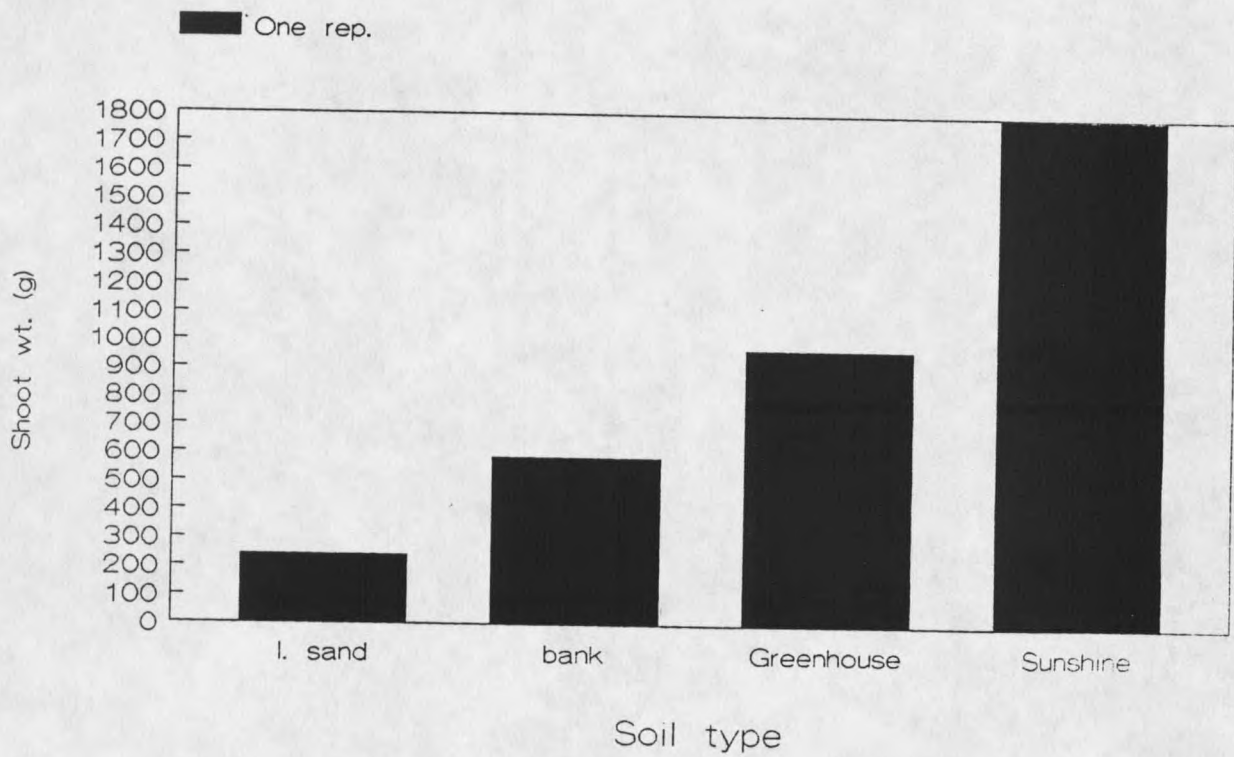


Fig. 5. Shoot weights (g) of preliminary soil treatments.

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