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NAME

Salix bebbiana Sarg.

COMMON-NAME

Bebb's willow

DESCRIPTION

The tree willow, Salix bebbiana occurs in Eurasia and in North America. In North America, it occurs from Alaska to California and Pennsylvania (Froiland 1962, Dorn 1977) (Figure 1). It's populations in the San Francisco Peaks and the White Mountains in Arizona represent the southernmost extent of its distribution in North America. Salix bebbiana or Bebb's willow occurs in high elevation riparian habitats (Brown 1982, Densmore and Zasada 1978).

Bebb's willow was named Salix bebbiana in 1895 by Sargent, after twice being misnamed after existing species (Sudworth 1934). It is thought that S. bebbiana was first encountered near Hudson Bay, in Canada, by surgeon-naturalist J. Richardson during the Franklin expedition of 1819-1822 (Richardson 1823).

Salix bebbiana populations are known to occur in a 'decadent' form in many areas, causing concern about the species' current ability to replace itself (Atchley 1989, Dorn 1970, Froiland 1962). One population in southeastern Montana has been protected from grazing pressure for eight years and shows no evidence of recruitment (Atchley 1989).

HABITAT

Salix bebbiana habitat ranges in elevation from 10,000 feet down to sea level at higher latitudes (Sudworth 1934). Over this range it has colonized a variety of habitats including borders of mountain streams, swamps, lakes, hillsides, open meadows, forest margins and even irrigation ditches (Goodrich 1983, Froiland 1962). In southeastern Wisconsin it is found in shrub-carr communities, which occur in ice-block depressions formed during the Pleistocene Epoch (White 1965).

These 'wet-ground' tall shrub communities are colonized initially by herbs such as Carex sp., Calamagrostis sp., and Muhlenbergia sp., and later by Salix spp., Alnus sp., and Betula sp.

Salix bebbiana has been characterized as abundant and/or dominant in many parts of its range. Sudworth (1934) suggested that it is most abundant in the Hudson Bay region, while Richardson (1823) described it as one of the two most common willows in Rupert's Land in Canada. In the United States, S. bebbiana is regarded as the most abundant willow in the Black Hills of North Dakota (Froiland 1962), and less abundant and more scattered in the Rocky Mountain region (Sudworth 1934).

Salix bebbiana colonizes a variety of soils, including cobble, gravel, sand, loam, and clay and combinations of these (Atchley 1989, Sudworth 1934, Waring, personal observation). In Utah, soils colonized by Salix bebbiana are comprised of dark, loamy alluvium with accumulated organic material (Padgett et al. 1989). In general, colonized soils are probably relatively nutritious, as willows tend to have high nutrient requirements (Pregent et al. 1986, Stevens 1989).

In southeastern Montana, Salix bebbiana often dominates stream and seep zones (Atchley 1989). In the Rocky Mountains Bebb's willow is most abundant along 1st and 2nd order streams between 1,100 and 2,700 m (Brunsfeld and Johnson 1985). At lower elevations in the Rockies, species of Salix often co-occur with Populus angustifolia and P. sargentii, and at higher elevations they occur in monogeneric stands or with aspen, birch or alder (Cannon and Knopf 1984). In Utah S. bebbiana occurs with other willow species such as S. boothii and S. lutea, and Pinus ponderosa, Populus tremuloides, Quercus gambelii and Picea spp. (Padgett et al. 1989). In parts of Canada, S. bebbiana is commonly associated with S. discolor and S. eriocephala on seasonally inundated upland meadows and well-drained slopes (Mosseler and Papadopol 1988). Similarly, in Alaska Bebb's willow is regarded as an upland species, that is, it typically occurs upslope from nearby drainages (J. Bryant, U. Alaska, pers. comm.). In New Mexico and Arizona Salix bebbiana occurs with alder (Alnus tenuifolia) and conifers, although it comprises up to 90% of the total tree density at some sites including Fern Mt., AZ, and Fenton Lake, NM (Szaro 1989). Willows are often replaced by alder and spruce at higher elevations and successionally in undisturbed habitats (White 1965, Walker et al. 1986, Walker and Chapin 1986).

BIOLOGY-ECOLOGY

Taxonomy -- Salix bebbiana occurs in the subgenus Vetrix in the section Vetrix, along with S. discolor and S. petiolaris (Mosseler 1990). Froiland (1962) has proposed a second variety of Salix bebbiana to be Salix bebbiana var. perrostrata (Rybd.) Schneid, also called smooth Bebb's willow. It is characterized primarily by glabrous and weakly reticulated leaves and apparently grows more vigorously in the Black Hills of ~~North~~ South Dakota (Froiland 1962). It has a wide distribution in the United States (Froiland 1962; Fig. 2). Argus (1957) found the two forms difficult to distinguish in areas of overlap. This designation is somewhat controversial, however, as Goodrich (1983) states that 'this separation probably merits no recognition.'

AGE: -- The lifespan of Salix bebbiana is not known and will be difficult to determine. It is known that they do live to at least 60 years of age (Atchley 1989).

REPRODUCTION: SEXUAL-- Salix bebbiana is among a group of willow species that reproduces early in the growing season, flowering as early as April in Canada (Mosseler and Papadopol 1988). The length of its flowering period in Canada ranges from 9 to 12 days (Mosseler and Papadopol 1988). This species is dioecious and the flowers, like other willows, are thought to be largely insect-pollinated (Sacchi 1987, Argus 1974). Seed dispersal occurs in late May and early June in southeastern Montana (Atchley 1989) and in late June and early July at Fern Mt. in northern Arizona (Waring, pers. observ.).

A great deal is known about germination of Salix bebbiana seeds (Atchley 1989, Densmore and Zasada 1983, Moss 1938). Salix bebbiana seeds are small and short-lived, and need ideal conditions for survival (Atchley 1989, Densmore and Zasada 1983, Moss 1938). Brinkman determined that Bebb's willow seeds weigh about 0.20 mg (Brinkman 1974). Moss (1938) found that seed viability dropped from nearly 100% initially to 50% within 42 days in seeds collected near Edmonton, Ontario. Atchley (1989) found that seeds from southern Montana were inviable after 30 days. She also determined that seeds collected towards the end of the seed dispersal period were significantly more viable than those collected earlier.

Latitude and elevation have exerted an evolutionary influence on the timing of seed germination in Bebb's willows. Seeds on plants from Paxson, Alaska (elev. 850m), germinated at a lower temperature than those from Fairbanks (elev. 120m) (Densmore and Zasada 1983). While more than 90% of Bebb's willow seeds from Alaska

germinated at 5° C, less than 5% of Bebb's willow seeds from southeastern Montana germinated at 5° C, with most germinating at 20° C (Atchley 1989). Reproduction in willows is strongly tied to cumulative growing degree-days and atypical weather patterns can lead to overlap in the timing of reproduction of species that normally do not overlap (Mosseler and Papadopol 1988).

According to Argus (1986) the primary ecological determinants for the establishment and growth of most willows are a moist substrate for seed germination and ample sunlight for subsequent growth. Seed germination and survival in some willow species has been shown to be positively affected by increased sunlight (Stevens 1989, Sacchi 1987), Hosner and Minckler 1960). Atchley (1989) determined that Bebb's willow is tolerant of moderate shade, although increased levels of light resulted in increased survivorship and growth. She tested seedling survivorship and growth at four light levels: 1% full sun (f.s.), 3% f.s., 10% f.s. and 20% f.s. Regrettably, she did not use higher 'f.s'. levels in her experiments. Seedling survivorship and growth were strongly tied to available light, with no seedlings surviving at 1% full sun (fs). Plants grown at 3% fs were susceptible to diseases, while plants grown at 10% fs were tall, but spindly. Plants exposed to 20% full sunlight had the highest levels of survivorship and grew the most, producing tall and thick stems. Larcher (1975) characterizes shade plants as tolerant of 20% full sun or less. While Bebb's willow does appear tolerant of 20% full sun, it would be useful to compare its performance at this level with that in higher 'full sun' levels. Bebb's willow may be a full-sun oplant that is able to tolerate low levels of shade. This should broaden its ability to invade or persist in communities in different successional stages.

Bebb's willow seeds undergo epigeal germination, which is characteristic of small seeds and shade intolerant plants (Atchley 1989). During germination, epigeal seeds extend the cotyledons (firsts sets of leaves) above the ground surface, so that they can capture light and photosynthesize (Ng 1978). After ten days in complete darkness, imbibed Bebb's willow seeds extended cotyledons up to 20 cm (Brinkman 1974).

Both the texture and nutrient content of soil influence seedling establishment and growth in Bebb's willow. Atchley (1989) reported that plants in soil with higher silt and clay content tended to grow more than plants in soils with higher sand content. This may relate to the greater water-holding capacity of clays compared to sand. Atchley (1989) tested responses of Bebb's willow

to soils with varying nutrient levels, including four field soils (including sandy loam from a bank cut and from silt bars) and commercial soils (inert sand, unfertilized mix of silt loam, sand and peat moss, and fertilized mix of peat moss, vermiculite and perlite). The only soils that produced a significant increase in growth were fertilized soils (Atchley 1989), suggesting that natural soils are often nutrient-poor. Pregent et al. (1987) found that Bebb's willow seedlings grew only 34 cm in 6 years following introduction into nitrogen-poor borrow pits in eastern Canada. They performed more poorly than seedlings of jack pine or nitrogen-fixing alders.

In an experiment evaluating the effect of different intensities of fire on plant colonization, Bebb's willow along with other willow species had highest levels of germination and survivorship on plots that had been severely burned (Zasada et al. 1983). This result may be due to reduced plant competition and to improved nutrient status of such soils following fire. Levels of inorganic or available nitrogen in soil are typically higher following fire (Covington and Sackett 1990, Covington and de Bano 1990).

While pre- and post-zygotic forms of reproductive isolation exist amongst many willow species, Salix bebbiana produces vigorous F_1 hybrids when crossed with S. petiolaris (Mosseler 1990, Mosseler and Zsuffa 1989). Some of these hybrid progeny were more vigorous than parentals. Crosses with S. eriocephala (Subgenus Vetrix, Section Cordatae) and S. exigua (Subgenus Salix, Section Vetrix) were variable, producing large proportions of inviable and 'distinctly' inferior progeny (Mosseler 1990).

Salix bebbiana has a chromosome number of 38 (2n count), while some members of the section Vetrix are tetraploid or hexaploid (Mosseler 1990).

REPRODUCTION: ASEXUAL -- Cuttings of most riparian willow species produce roots from primordial buds or adventitious roots from other plant parts (e.g. Chmelar 1974), and this vegetative form of reproduction is more important than sexual reproduction for some species (Stevens 1989, Krasny 1988). The ability of stem tissue to propagate itself through rooting is highly adaptive for riparian species that experience major episodes of flooding likely to remove plant parts and for colonization of sites unavailable to seedlings, such as dry or nutrient-poor sites (Stevens 1989, Krasny 1988, Densmore and Zasada 1983).

Salix bebbiana may rely more on sexual reproduction than asexual reproduction. In one experiment cuttings of S. bebbiana did not produce roots or become vegetatively propagated (Densmore and Zasada 1978). Densmore and Zasada concluded that S. bebbiana is not a truly riparian species compared with other willow species that rapidly produced roots and stem growth in the same experiment. Mosseler (1990) also found S. bebbiana to have 'a poor rooting ability' and suggested that this species may lack primordial buds that are capable of producing roots. Forty percent of S. bebbiana cuttings produced roots and shoots in several studies (Atchley 1989, Holloway and Zasada 1979). Atchley found that stems younger than three years did not produce roots. She also found that stems grown in soils higher in organic matter and water holding capacity produced more root and shoot biomass than stems grown in soils devoid of organic matter and with poor water retention. (Atchley 1989). Overall, it appears that vegetative propagation does not play a major role in S. bebbiana reproduction. The occurrence of Bebb's willow along and near smaller 1st and 2nd order streams suggests that it does not experience major flooding events.

ROLE IN RIPARIAN COMMUNITIES:

The role that Salix bebbiana plays in riparian communities is difficult to assess due to a paucity of studies focused on this subject. With available information, I have tried to piece together a sense of its position in such communities and the factors determining this. Aside from a recently conducted survey of Bebb's willow populations in the West, most information on this subject comes from studies and observations made of Bebb's willow populations in Alaska. The information on Alaskan populations provides many insights into the natural history of Bebb's willow, although some of it may not apply to Bebb's willow as it occurs at lower latitudes in the western U.S.

WATER REQUIREMENTS: Bebb's willow has been described as a nonriparian willow species (Densmore and Zasada 1978), and it adult plants may have lower water requirements than other riparian willow species, although this has not been tested. In Alaska, Bebb's willow commonly occurs in drier upland terraces associated with older floodplains, according to three scientists who have studied this species (J. Bryant and L. Viereck, U of Alaska, Fairbanks Alaska; J. Zasada, N.S.F.S. Institute of Northern Forestry, Fairbanks, Alaska; and PNW Exp. Stat., Corvallis, Ore.). Another

upland species, Salix scouleriana, is commonly found with it in these habitats. Bebb's willow rarely occurs in close proximity to stream channels where other willow species are found (Viereck, pers. comm.).

In the western U.S., Bebb's willow occurs along stream channels, on the edges of drainages, along seeps, and in perched sites that appear to be receiving little water (Atchley 1989, Waring pers. observ.). These patterns suggest that it's occurrence along stream margins may be a facultative rather than obligate phenomenon. These patterns also suggest that the absence of other willow species at some sites may be due to lower water availability, as well as to chance.

While adult Bebb's willow can persist in seemingly dry sites, such as Fern Mountain, AZ, there is no doubt that establishment of Bebb's willow seedlings is strongly dependent on ample water. This is borne out by recent experiments by Atchley (1989), Maschinski (unpublished), and Waring (unpublished), and observations of seedling distributions in western populations (Waring, pers. observ., Geography report). In a recent study, Waring determined that seeds placed in plots near established plants would not germinate without supplemented water (Waring, pers. observ.).

LIGHT REQUIREMENTS: Although most information suggests that Bebb's willow thrives in high light conditions, there is some indication that this species is tolerant of considerable shade. Experiments and field observations verify its positive responses to sunny conditions (Atchley 1989, Maschinski report, Waring pers. observ.; Bryant, Viereck, and Zasada, personal communications from these), while Atchley (1989) determined that it can germinate and grow in 10-20% full sun. Conflicting information does suggest a tolerance of low and high light conditions. Although high densities of seedlings and juvenile plants were found only in sunny microsites during a recent survey of western populations (Waring, pers. observ.), it has been reported that this species often colonizes communities with well-established vegetation that might limit available sunlight (White 1965, Bryant, Viereck, and Zasada, pers. comm.). In the shrub-carrs of Wisconsin, Bebb's willow colonizes peat soils only after they have been previously colonized by other shrub species including Salix candida and Betula pumila (White 1965), perhaps because colonizing plants may improve the nutrient status of such soils. Light conditions in colonization microsites were not given in this study. In the northern Rockies, it is abundant along first and second order streams where it is often dominant and may have colonized following disturbance

events which opened up habitat. It has been suggested that adults are able to survive considerable and long-term shading by species such as spruce, although willow growth in such conditions appears to be nearly negligible and no one knows how long it can tolerate such conditions (Bryant, pers. comm.). It seems clear that Bebb's willow does well in full sun. However, its behavior in partial shade is not clear.

SUCCESSIONAL STATUS: Bebb's willow seedlings colonize habitats that are newly disturbed, and habitats that have been previously colonized by species such as grasses, Carex and shrubs (White 1965, and Waring, Bryant, Zasada and Viereck, pers. comm.). These patterns suggest that it may play an intermediate successional role in some plant communities. This successional scheme has been proposed for other willow species (Fig. 3)(Walker et al. 1986, Walker and Chapin 1986). The poor performance of Bebb's willow seedlings in levels of sunlight below 10% (Atchley 1989) would suggest that this species would not be able to replace itself as larger tree species begin to colonize a community, although this relationship is not resolved (See above). Although the details of Bebb's willow colonization in Alaskan sites are not well-studied, Viereck (pers. comm.) suggests that this species may colonize wooded upland sites following largescale or smallscale fires that open up otherwise heavily shaded habitat.

Other willow species such as Salix nigra and S. interior are considered to be early colonizers because the success of their seedlings increases as overstory decreases (Hosner and Minckler 1960). More information is needed on the light requirements of Bebb's willow seedlings to determine conditions under which it enters riparian communities. As with other willows (e.g. Salix nigra, McLeod and McPherson 1973), it can not be inferred that the conditions that adult Bebb's willow occur in are suitable for seedling establishment (See Waring 1991 Fern Mountain report). Adult plants appear to be tolerant of less disturbance and less water than seedlings.

Bebb's willow is often replaced by alder and spruce in undisturbed habitats (White 1965, Padgett et al. 1989). Bebb's willow is one of the last willow species to die out as sites develop into forest communities in interior Alaska because it can grow taller than most other willows, which helps it to escape moose damage (Miquelle and Van Ballenberghe 1989). However, it is being outshaded by taller forest trees such as spruce (Miquelle and Van Ballenberghe 1989).

DISTURBANCE FACTORS AFFECTING BEBB'S WILLOW ESTABLISHMENT AND PERSISTENCE: Disturbance factors such as flooding, fire and herbivory are regarded as major organizing factors in plant communities. They can exert a strong influence on both successful recruitment and persistence in plant populations by affecting plants directly and indirectly by influencing processes such as succession.

A recent survey of western Bebb's willow populations revealed that most populations are comprised largely or entirely of large, old individuals, indicating that recruitment is a relatively rare event in most populations. The same appears to be true for Bebb's willow in Alaska, that is, young plants are rarely encountered (L. Viereck, pers. comm.). However, in Alaska, Bebb's willow is most commonly represented by older plants that occur in a shrubby juvenilized form due to severe and chronic fire and herbivory (Bryant, Viereck and Zasada, pers. comm.).

In the western U.S. Bebb's willow recruitment was found to be occurring in several types of habitats: at seeps where the ground was wet, sunny, open and colonized by Carex; at open areas along streams; in wide floodplain sites and in wet disturbed sites, such as along roadways. These patterns suggest that disturbed sites, such as road margins, are readily colonized, and less disturbed sites, such as Carex stands, are also colonized. This latter may be possible as long as water and sunlight are adequate. Juvenile plants, as well as seedlings, were most commonly found at the seep sites. Current year seedlings only were found growing in cobble and sand bars along streams, suggesting that these sites are unstable due to increased seasonal water flows, or low level flooding. Saplings were found at a stream site in the White Mt.'s, AZ, at the stream edge and up to 30 m away, on the edge of the floodplain.

In Alaska, recruitment occurs in upland terraces associated with old floodplains, and in highly disturbed sites including the sides of roadways and gardens (Bryant, Viereck and Zasada, pers. comm.) The upland sites are sediment terraces that have accumulated over considerable time, are removed from flowing stream channels and are being colonized by plants (Viereck, pers. comm.). At these sites, Bebb's willow appears to colonize sites that are in an intermediate stage of succession, such as sites that have been colonized by shrubs and spruce trees (Viereck, pers. comm.).

In a recent experiment conducted at the Fern Mountain site, it was determined that seedling germination and survivorship were greatest in plots that had been cleared of additional vegetation (Waring, unpubl.). Intermediate levels of germination occurred in plots with intermediate levels of vegetation. From this it appears that disturbance is likely to enhance recruitment in Bebb's willow.

One woody plant association that may be beneficial for Bebb's willow involves alder, Alnus spp., a genus of nitrogen-fixing species. Bebb's willow often occurs with alders and it may benefit directly from this because alder increases ambient nitrogen levels in soil. In experiments, Walker and Chapin (1986) and Walker et al. (1986) showed that willows grew more when grown in 'alder' soil than in soil not previously occupied by alder. This may be a beneficial association if soil nutrient levels are low.

There is typically a layer of low shrubs and herbaceous plants associated with Salix bebbiana communities including Ribes spp., Rosa spp., Symphoricarpos oreophilus, Actaea spp., Carex spp., Iris missouriensis, Juncus spp., and Geranium spp. (Padgett et al. 1989, Szaro 1989). Many of these species are consistently found under Bebb's willow canopies, implying that this species provides valuable habitat. This suggests that the presence of Bebb's willow in riparian communities strongly enhances plant diversity.

FLOODING: The consensus among the three aforementioned scientists and the literature is that major flooding has probably not been an important selective factor in Salix bebbiana's evolutionary history. The evidence for this includes the following patterns: 1) the occurrence of this species along small 1st and 2nd order streams that are unlikely to experience severe flooding (V. Baker, U of Ariz., pers. comm.), 2) the occurrence of this species farther away from stream edges than other willow species (Waring, pers. obs.), 3) the poor rooting ability of its stem tissue (See Asexual Reproduction section), 4) its low leaf water-vapor conductance levels and 5) apparently low photosynthesis rates. The presence of Bebb's willow, including saplings and adults, on terraces and slopes above stream channels as well as along stream margins suggests that it may be capable of occurring across a greater moisture gradient than many willow species. This appears to be true of willow species such as Salix lasiolepis and may relate to the fact that many willow species are thought to have deep root systems (P. Price, pers. comm.).

Lafleur (1988) found that Salix bebbiana had the lowest level of leaf stomatal conductance of four Alaskan wetland species including Carex paleacea, Alnus rugosa and Salix discolor. Carex paleacea had the highest conductance, while Salix discolor had the highest conductance of the woody species. Maximum leaf conductance is an important ecological and physiological plant characteristic since it determines the upper limit for transpiration losses and CO_2 uptake (LaFleur 1988). This physiological 'conservatism' may contribute to Bebb's willow's ability to occur farther away from streamsides, because lower conductance involves reduced evapotranspirational loss of water. Xerophytic plants have lower conductance levels than mesic plants (Noble 1983). Similarly, John Bryant and students (pers. comm.) have found that Bebb's willow has a lower photosynthetic rate than many other Alaskan willow species.

These patterns suggest that Bebb's willow typically does not occur in areas that are likely to be subjected to major flooding events, and consequently, major flooding probably does not influence establishment or persistence in this species.

While major flooding events seem unimportant to Bebb's willow population dynamics, seasonal runoff or low level flooding in the small streams that seedlings sometimes colonize may be responsible for the absence of more than current year seedlings in these habitats. During a recent survey, colonizable sites-sunny sites-along streams were found to be rare. This latter is also thought to be an important source of mortality for Salix lasiolepis seedlings (P. Price, pers. comm.).

FIRE: In Alaska, fire is regarded as a major selective factor for Bebb's willow, and the consensus is that this species is highly tolerant of it (Zasada and Viereck, pers. comm). Zasada et al. (1983) have shown that seedling success is enhanced in severely burned soils (See Sexual Reproduction section), and Viereck (pers. comm.) has speculated that seedling germination in upland sites in Alaskan drainages may be tied to local burns that clear away vegetation including spruce. This aspect of Bebb's willow biology is not well-documented, however. Bryant suggests (pers. comm.) that fire may be a more prominent factor for Bebb's willow in Alaska than in the lower 48 states. Alaska has a 'let-burn' policy about forest fires, and fires of the recent Yellowstone Park magnitude are relatively common. The average frequency of major fires in interior Alaska is thought to be about every 50 years.

Apparently mature Bebb's willow are highly tolerant of fire in Alaska. Individual plants are commonly reduced to stumps, which then resprout in a juvenilized form (Bryant, Zasada, Viereck, pers. comm.). It has been suggested that this species can tolerate hotter fires than can associated plants such as black or white spruce (Picea spp.) (Viereck, pers. comm.). According to Zasada (pers. comm.), although the fate of individual plants following fire has not been studied, it is thought that fires must be hot enough to 'burn to mineral soil' in order to kill Bebb's willow. Therefore, fire appears to be a highly beneficial factor by enabling Bebb's willow to persist in regions where it might otherwise be replaced by later successional species.

In the western U.S., Bebb's willow may occur in habitats that are less likely to experience intense, hot fires. Bebb's willow typically occurs at a higher elevation than ponderosa pine (Pinus ponderosa), which is a major fuel producing species. Another willow, Salix lasiolepis, occurs at lower elevations along streams that transect P. ponderosa forests and used to be exposed more often to frequent and hot fires that could open up habitat (P. Price, pers. comm.). While fire clearly enhances seedling establishment and stands to remove later successional species such as spruce, it may not be as important a factor in Bebb's willow natural history in the western U.S. as it appears to be in Alaska. It has been suggested that the greater fire frequency in Alaska has resulted in the creation of more habitat that is suitable for higher mammal densities (Bryant, pers. comm).

HERBIVORY: There is considerable evidence that herbivore pressure on established Bebb's willow's can be intense. Although the effect of herbivory on establishing plants in Alaska has not been well-studied, it seems likely to be intense, based on severe levels of herbivory on older Bebb's willows (See below).

More work is needed on the impact of herbivory on seedling establishment. However, a recently completed experiment at Fern Mountain, AZ, showed that herbivory had significant effects on Bebb's willow seedling survivorship. Densities of seedlings were significantly higher in plots that were covered with cages that excluded vertebrate and invertebrate herbivores. High densities of grasshoppers, ants and snails were seen at this Fern Mountain site, as well as numerous elk tracks, indicating that many herbivores were present (Waring, pers. obs.).

Heavy mortality of Salix lasiolepis seedlings due to grasshopper herbivory is known to occur in northern Arizona (Sacchi 1987). Herbivory by grasshoppers accounted for over 70% seedling mortality in some experimental plots and no mortality in others. Seedling mortality due to herbivory was variable between years and tended to be greater following dry winters. In another experiment, over 20% of seedlings in plots were grazed by grasshoppers, but only 1-2% died as a result. This study suggests that levels of seedling mortality from invertebrate herbivores can be high although extremely variable.

In a recent survey of western Bebb's willow populations, seedling densities appeared to be lowest at sites that were heavily-grazed by cattle (Waring, pers. comm.). It has been suggested that intense grazing in Utah may limit Bebb's willow community growth because seedlings are unable to establish (Padgett et al. 1989).

Conversely, in southeastern Montana, a Bebb's willow stand that had been protected from grazing pressure for 8 years showed no evidence of recruitment (Atchley 1989). This demonstrates that ultimately grazing has second order effects on Bebb's willow populations, while factors such as water availability and sunlight may be critical for germination and establishment.

Large vertebrates including moose, deer and cattle and small ones including rabbits and hares feed extensively on willows (Padgett et al. 1989, Cannon and Knopf 1984, Chapin et al. 1985). Grazing by large mammals is a major cause of willow mortality in the boreal forest (Chapin et al. 1985, Fox and Bryant 1984, Bryant and Kuropat 1980). Bark stripping of selective plant species by moose can alter relative densities of deciduous and coniferous plants in Alaskan forests (Miquelle and Van Ballenberghe 1989). Over 75% of the aspen and Bebb's willow canopy in an aspen-spruce community in Alaska was debarked by moose, while spruce was not used (Miquelle and Van Ballenberghe 1989). In one study, Bebb's willow was debarked more than any other willow species (Miquelle and Van Ballenberghe 1989). While moose can slow the rate of succession in forests (e.g. Risenhoover and Maas 1987), it appears to be increasing the rate of succession to spruce forest in some parts of Alaska (Miquelle and van Bellenberghe 1989). In the western U.S., cattle grazing has been found to strongly restrict population size in some willow species (Rickard and Cushing 1982).

In Alaska, snowshoe hare feeding on willows during population outbreaks is severe (Chapin 1985). Grazing

by snowshoe hares may be the most significant form of herbivory for Bebb's willow (Bryant, pres. comm.), and plants are commonly reduced to stumps as a result.

Juvenilization of Bebb's willow plants, due to intense herbivory by vertebrates, such as the snowshoe hare, leads to the production of young shoots that are less palatable to herbivores (Chapin et al. 1985). There is no evidence, however, that the chemistry of unbrowsed branches on heavily browsed plants is altered in response to herbivory (Chapin et al. 1985).

In a recent survey of western Bebb's willow, heavily grazed plants of less than 0.5 m in height were found to be up to 15 years old, indicating that vertebrate herbivory can be intense and the plants at this latitude are also tolerant of chronic herbivory, sometimes exhibiting the 'juvenilized form' described for Alaskan plants.

There is little information available on the terrestrial animal fauna, aside from large vertebrates, associated with Bebb's willow. Willows are known to support many animals (e.g. Stevens 1985). Through casual observation, numerous pollinating bees, flower-mining fly and lepidopteran larvae, and leaf galls were found on the Bebb's willows at Fern Mountain, Arizona (Waring, pers. comm.). In general, established plants are remarkably free of herbivore attack except by large species such as elk and cattle (P. Price, pers. obs.).

There are several pathogens associated with Bebb's willow. The most common foliage pathogen is the rust Melampsora epitea (Hepting 1971). This species attacks most other Salix species in the southwest (Yohem et al. 1985). It is conspicuous in the fall as bright yellow-orange powdery masses of urediospores on leaves. Its basidiospores are produced on fallen willow leaves in the spring, these attack conifers, which produce aeciospores that infest live willow leaves in the summer. Telia are produced on willow leaves in the fall. Infection can spread between willows and it appears that this pathogen can persist on willows without alternate coniferous hosts present (Sinclair et al. 1987). Coniferous hosts include Pinus, Abies and Tsuga (Hepting 1971). The pathogenic effects of Melampsora epitea on willow are not known (Ziller 1974), although a close relative, M. medusae causes premature leaf drop which can lead to a reduction in vigor (Peterson and Stack 1987).

Other pathogens known to be associated with Bebb's willow include Phellinus punctatus. This fungus is associated with canker rot in living hosts and

apparently kills tissue in the stem of living plants (Walla 1984).

Fallen Bebb's willow leaves also provide resources for many aquatic macroinvertebrates such as insects (Short et al. 1980). Bebb's willow leaves are processed faster by macroinvertebrates in streams than alder, aspen or ponderosa pine leaves. In one study, over 30 species of macroinvertebrates were found to be associated with these leaves as they became part of the aquatic environment (Short et al. 1980).

The ideal habitat for colonization by Bebb's willow is probably no different than that for most riparian species: ample water, and less than ample plant competition and herbivory (Fig. 4). This was borne out by germination experiments at Fern Mountain which showed all three of these factors-open habitat, water and herbivory-to be highly important to seedling success. Disturbances such as major flooding or fire stand to open up colonizable habitat for Bebb's willow, reducing competition for resources such as sunlight, space, water and nutrients. And Bebb's willow does establish readily in disturbed sites (e.g. roadway margins), although it also becomes established in sites that are open but not recently disturbed. Such sites include dense knee-high Carex and grass stands fed by seeps. The ability to establish in shaded areas seems unlikely, indicating that major disturbance along drainages or the introduction of water into open and grass stands are two important ways to provide colonizable habitat. As with other willows, this species seems dependent on sun and considerable water for establishment. While Bebb's willow appears tolerant of drier conditions as a mature plant, there is no doubt that seedling recruitment requires ample water. This means that it can persist in habitats that become somewhat drier, but recruitment will cease to occur, such as at Fern Mountain. The seeps it often occurs along may result secondarily from large, mature plants interrupting stream flow patterns (it does get considerably bigger than most other willows it occurs with). By colonizing such habitats as seeps or stream breaches that have already been colonized by species such as grasses and Carex, Bebb's willow is less dependent on major disturbance for recruitment. While established plants are remarkably tolerant of herbivory, herbivory is probably contributing strongly to the low recruitment that characterizes this species in most populations.

APPLICATION: Several studies have examined practical uses of Bebb's willow. Attempts to revegetate borrow pits with Bebb's willow failed because the nutrient

levels of the soil in such habitats was inadequate to meet its nutritional needs (Pregent et al. 1987). Bebb's willow was found to be more tolerant of gamma radiation given off by nuclear power plants than were some other deciduous plants and conifers (Amiro and Dugle 1984).

QUAL-DET

Based on a recent survey of over 20 sites, the population structure of Bebb's willow is typically skewed towards old plants. Consequently, healthy stands of these plants are currently more of a goal than a reality. The quality of a Bebb's willow community will depend on a number of conditions including: (1) adequate habitat size, (2) adequate density, (3) representation of multiple, especially intermediate, age classes, (4) availability of nutritious soils, (5) presence of a stable water source, and (6) the presence of disturbance, such as fire, that periodically creates seedling safe sites and enables older plants to persist (sensu Harper 1977).

EATS

Bebb's willow populations face several threats, a lack of replacement by younger age classes and accelerated successional replacement. Several studies have reported on populations that are in 'decadent' or declining condition (e.g. Atchley 1989, Dorn 1970, Froiland 1962). Another study verified the latter, reporting that Bebb's willow populations in interior Alaska are being replaced at a faster rate by spruce (Miquelle and Van Ballenberghe 1989). The longevity of Bebb's willow needs to be determined to evaluate the importance of its current demographic structure. These conditions have probably resulted from an interruption of natural processes, including the following:

Water

A decline in water availability will limit recruitment in Bebb's willow populations. This can result from diversion of stream channels or water-table drawdown. The community at Fern Mountain, AZ, appears to have experienced a decline in water availability, possibly due to both of these factors, and the structure of the Bebb's willow population was strongly skewed towards old individuals. This apparent decline in water availability probably relates to increased use of available water by an expanding nearby community and also to drought-like conditions in the area, especially during the last five years. The rarity of intermediate sized plants at this site suggests, however, that water has probably been limiting for an even longer period of

time. Soils that were once wet enough to allow establishment of the existing population of adult plants are now too dry to support further seedling establishment.

However, a recent survey of soil moisture levels at over 20 Bebb's willow sites suggests that water may not currently be a limiting factor at many sites. The Fern Mountain site seems somewhat exceptional in this regard.

Excessive water may occasionally pose a threat to Bebb's willow. Excess water, resulting from beaver dams, appeared to have negative effects on a Bebb's willow population studied in southern Idaho. This was evidenced by considerable dieback in sapling-sized plants.

Disturbance

Flooding: While major flooding does not appear to play a major role in Bebb's willow establishment (See Biology section), it can and has created habitats suitable for colonization by this species, by wetting soils and clearing away overstory vegetation.

Fire: The suppression of fire is a common occurrence in the western U.S. today and many plant communities are undoubtedly affected by this. Bebb's willow is known to respond positively to fire, as seedling survivorship and growth are greater on severely burned soils, and established plants in Alaska are known to survive intense burns. Bebb's willow is also more tolerant of fire than spruce, a species that often invades Bebb's willow stands in the western U.S. Consequently, fire, as a form of disturbance and nutrient recycling, can provide direct benefits to this species. It will create sites for recruitment and promote the persistence of older individuals, by altering successional processes. Prolonged suppression of fire in Bebb's willow habitat may pose a threat to the persistence of this species.

Grazing: Grazing of Bebb's willow by wild and domesticated herbivores can be intense. This is particularly true in Alaska, where feeding by snowshoe hare and moose commonly reduce plants to stumps. According to a recent geographical survey of Bebb's willow sites in the western U.S., heavily grazed sites tended to have the smallest frequencies of young plants. Cattle can have the same juvenilizing effect on Bebb's willows that wild Alaskan herbivores do, as plants as old as 15 years and reaching only .25 m in height were found on this survey. Negative impacts of

cattle grazing on recruitment in riparian ecosystems have been found elsewhere (Glinski 1977). Insect herbivores such as grasshoppers have been shown to devour large numbers of Salix lasiolepis seedlings (Sacchi 1987), indicating that small herbivores also pose a threat to seedling establishment in some willow species.

LAND-PROT-SPECS

The area required for a healthy stand of Bebb's willows should include adequate area for large, sprawling older individuals and open area for colonization of seedlings. Most populations of Bebb's willow visited during the recent geographical survey were small, comprised on average of around 120 individuals, with over 70% of these being old plants. If the objective is to replace existing mature plants in populations, then one way to estimate area needed might be to measure the area covered by mature plants, multiply that by the number of adults at sites and set aside that amount of land. Colonizable area for Bebb's willow seeds must include wet soil, as well as open area.

While a relationship exists between population size and genetic variability in some species, it does not exist in others and much more work is needed to evaluate this relationship and its importance to patchily distributed plant populations such as Bebb's willow populations (Ledig 1986).

RECOVERY-POT

The recovery potential for these populations, including Fern Mountain, AZ, seems high. The factors that appear to be limiting recruitment appear to be few, straightforward and reconcilable. In essence, the amount of colonizable habitat in some Bebb's willow populations needs to be increased and grazing pressure needs to be reduced, at least long enough to enable seedlings and juveniles to outgrow susceptibility to grazing damage. Creation of colonizable habitat will require opening up land that has high soil moisture content and considerable sunlight. Fire may be one option for this. An alternative would be to divert enough water from an existing drainage to create new stream or seep habitat. Ultimately, creation of habitat colonizable by seedlings will be essential, as vegetative propagation of stems has been unsuccessful.

The situation at Fern Mountain is different from most sites in the West because there is currently no water in the existing drainage to divert. Hydrological studies currently underway should determine the basis for this situation and possibly some solution. Studies

currently examining the potential for establishing seedlings in the small amount of moist soil available at Fern Mountain will determine if some level of recruitment is possible without supplementing water levels from some source. It may be that this site was colonized long ago during much wetter conditions and the existing lack of recruitment is an unavoidable consequence of drier times.

It will be important to determine, if possible, how old individual plants live to be. If they are short lived, then it would be desirable to promote a great deal of recruitment soon.

BIOL-MONIT-NEEDS

Factors in need of monitoring include: (1) Age structure and recruitment rates in Bebb's willow populations; (2) determination of the importance of water availability, disturbance and herbivory to recruitment; (3) interactions with later successional species, including aspen and spruce; (4) interactions with associated species, including other willows and alder; (5) interactions with associated understory species; (6) soil nutrient conditions.

BIOL-MONIT-PROCS

BIOL-MONIT-PROGS

Current research/monitoring efforts in Bebb's willow populations include the following:

1. Historic and current status of hydrological conditions at Fern Mountain Ranch (Fern Mountain Ranch, AZ, Charles Avery, NAU).

2. Seedling establishment and over-wintering survivorship in Fern Mountain Creek (Fern Mountain Ranch, AZ, Gwen Waring, MNA, short-term monitoring).

3. Geographic survey of Bebb's willow populations western states to determine population structure and site conditions (Gwen Waring, MNA, short-term monitoring).

RSRCH-NEEDS Y

RSRCH-NEEDS-COMM

1. Germination and recruitment requirements of Bebb's willow, including soil moisture and nutrients, light requirements, and susceptibility to plant competition and herbivory.

2. Determine longevity in Bebb's willow.

3. Response of mature Bebb's willow to fire.

4. Determination of fire history at Fern Mountain, AZ.

5. Construct a water budget for Fern Mountain, AZ, to determine water availability.

6. Interactions between Bebb's willow and associated understory species to determine if the latter are dependent on Bebb's willow for more than shade.

7. Determine grazing history at Fern Mountain, AZ.

8. Influence of associated rust, Melampsora epitea, on seedling survivorship

RSRCH-PROGS

RSRCH-PROGS-COMM

1. Bebb's willow germination response to several levels of light and soil moisture (Joyce Maschinski, The Flagstaff Arboretum).

2. Bebb's willow germination and short-term survival in multifactorial field experiment examining water, plant competition (alleviation of it by manual clearing and fire) and herbivory (Fern Mountain Ranch, AZ, Gwen Waring, MNA).

3. Responses of adult Bebb's willow to fire at Fern Mountain (Fern Mountain Ranch, AZ, Bob Coons and USFS, Flagstaff, AZ).

4. Determine the fire history of the Fern Mountain area (Planning stage, TNC).

5. Assess xylem water potential status of Bebb's willow on a seasonal basis at Fern Mountain Ranch as a measure of seasonal patterns of water availability (Planning stage, TNC).

MGMT-NEEDS Y

MGMT-NEEDS-COMM

Successful management and enhancement of the Bebb's willow population at Fern Mountain, AZ, seems highly feasible. The factors that appear to be limiting recruitment appear to be few, straightforward and reconcilable. In essence, the amount of colonizable habitat needs to be increased and grazing pressure needs to be reduced, at least temporarily, to enable seedlings and juveniles to outgrow susceptibility to

grazing damage. Creation of colonizable habitat will require opening up land that has high soil moisture content and considerable sunlight. Fire may be one option for this. An alternative would be to create new stream or seep habitat.

Studies currently examining the potential for establishing seedlings in the small amount of moist soil available at Fern Mountain will determine if some level of recruitment is possible without supplementing water levels from some source. It might be possible to open up habitat along the aquifer-fed wet portions of the Fern Mountain Creek to promote recruitment there, although this would be a limited and short-term solution to the recruitment problem. It is clear that more water must come into the system. Hydrological studies currently underway should determine the basis limited surface water at Fern Mountain and thus, how reconcilable the situation is.

BIBLIOGRAPHY

Amiro, B.D. and J.R. Dugle. 1984. Temporal changes in boreal forest tree canopy cover along a gradient of gamma radiation. Can. J. Bot. 63:15-20.

Argus, G.W. 1957. The willows of Wyoming. Wyo. Univ. Pub. 21:1-63.

Argus, G.W. 1974. An experimental study of hybridization and pollination in Salix (willow). Can. J. Bot. 52:1613-1619.

Argus, G.W. 1986. The genus Salix (Salicaceae) in the southeastern United States. Syst. Bot. Monogr. 9:1-170.

Atchley, J.L. 1989. Temperature, light and soil effects on the establishment of Bebb's willow (Salix bebbiana). M.S. Thesis, Montana State Univ., Bozeman, Montana.

Brinkman, K.A. 1974. Seeds of woody plants of the United States. USDA Handbook No. 450.

Brown, D.E. 1982. Biotic communities of the American Southwest-United States and Mexico. Desert Plants 4:1-4, Special Issue.

Brunsfeld, J. and F.D. Johnson. 1985. Field guild to the willows of eastcentral Idaho. Forest, wildlife and Range Exp. St., Univ. Idaho, Moscow, Idaho. 95pp.

Bryant, J.P. and P.J. Kuropat. 1980. Selection of winter forage by subarctic browsing vertebrates: The role of plant chemistry. Ann. Rev. Ecol. Syst. 11:261-285.

Cannon, R.W. and F.L. Knopf. 1984. Species composition of a willow community relative to seasonal grazing histories in Colorado. Southwestern Nat. 29:234-237.

Chapin, F.S., J.P. Bryant and J.F. Fox. 1985. Lack of induced chemical defense in juvenile Alaskan woody plants in response to simulated browsing. Oecologia 67:57-459.

Chmelar, J. 1974. Propagation of willows by cuttings. N.Z. J. For. Sci. 4:185-190.

Covington, W. and S. Sackett. 1990. Fire effects on ponderosa pine soils and management implications. In J.S. Crammes (ed.), Effects of fire management of southwestern natural resources. USDA Tech. Rept. No. RM-191.

Covington, W. and L. De Bano. 1990 Effects of fire on pinyon-juniper soils. In J.S. Crammes (ed.), Effects of fire management of southwestern natural resources. USDA Tech. Rept. No. RM-191.

Densmore, R. and J. Zasada. 1978. Rooting potential of Alaskan willow cuttings. Can. J. For. Res. 8:477-479.

Densmore, R. and J. Zasada. 1982. Seed dispersal and dormancy p dormancy patterns in northern willows: evolutionary significance. Can. J. Bot. 61:3207-3216.

Dorn, R.D. 1970. Moose and cattle food habits in southwest Montana. J. Wild. Manage. 34:559-564.

Dorn, R.D. 1977. Willows of the Rocky Mountain States. Rhodora 79:390-429.

Fox, J.F. and J.P. Bryant. 1984. Instability of the snowshoe hare and woody plant interaction. Oecologia 63:128-135.

Froiland, S.G. 1962. The genus Salix (willows) in the Black Hills of South Dakota. USDA-USFS Tech. Bull. No. 1269.

Glinski, R.L. 1977. Regeneration and distribution of sycamore and cottonwood trees along Sonoita Creek, Santa Cruz County, AZ. In R.R. Johnson and D.A. Jones (Tech. Coords.), Importance, preservation and management of riparian habitat: a symposium. USDA-FS Gen. Tech. Rept. RM-43, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.

Goodrich, S. 1983. Utah flora: Salicaceae. The Great Basin Natur. 43:531-550.

Harper, J.L. 1977. Population biology of plants. Academic Press, New York.

Hepting, G.H. 1971. Diseases of forest and shade trees of the United States. USDA-FS Agric. Handbook No. 386.

Holloway, P. and J.C. Zasada. 1979. Vegetative propagation of eleven common Alaska woody plants. USDA USFS Res. Note PNW-334.

Hosner, J.F. and L.S. Minckler. 1963. Bottomland hardwood forests of southern Illinois: regeneration and succession. Ecology 44:29-41.

Krasny, M.E. 1988. Establishment of four Salicaceae species on river bars in interior Alaska. Hol. Ecol. 11:210-219.

Lafleur, P. 1988. Leaf conductance of four species growing in a subarctic marsh. Can. J. Bot. 66:1367-1375.

Larcher, W. 1975. Physiological plant ecology. Springer-Verlag, Berlin.

Ledig, F.T. 1986. Genetic structure and the conservation of California's endemic and near endemic conifers. In T.S. Elias, ed., Conservation and management of rare and endangered plants. California Native Plant Society, Sacramento, CA.

McLeod, K.W. and J.K. McPherson. 1973. Factors limiting the distribution of Salix nigra. Bull. Torrey Bot. Soc. 100:102-110.

Miquelle, D.G. and V. van Ballenberghe. 1989. Impact of bark stripping by moose on aspen-spruce communities. J. Wildlife Manage. 53:577-586.

Mosseler, A. 1990. Hybrid performance and species crossability relationships in willows (Salix). Can. J. Bot. 68:??-??.

Mosseler, A. and C.S. Papadopol. 1989. Seasonal isolation as a reproductive barrier among sympatric Salix species. Can. J. Bot. 67:2563-2570.

Mosseler, A. and L. Zsuffa. 1989. Sex expression and sex ratios in intra- and interspecific hybrid families of Salix L. Silvae genetica 38:12-17.

Mosseler, A., L. Zsuffa, M.U. Stoehr and W.A. Kenney. 1988. Variation in biomass production, moisture content and specific gravity in some North American Willows (Salix L.). Can. J. For. Res. 18:1535-1540.

Ng, F.S.P. 1978. Strategies of establishment in Malayan forest trees. In P.B. Tomlinson and M.H. Zimmerman (eds.), Tropical trees as living systems. Cambridge Univ. Press, Cambridge, Mass.

Padgett, W.G., A.P. Youngblood and A.H. Winward. 1989. Riparian community type classes in Utah and southeastern Idaho. USDA USFS Inter. Mount. Reg. R4-Ecol-89-01. 191pp.

Pregent, G., C. Camire, J.A. Fortin, P. Arsenault and J.G. Brouillette. 1987. Growth and nutritional status of green alder, jack pine and willow in relation to site parameters of borrow pits in James Bay Territory, Quebec. Reclam. and Reveg. Res. 6:33-48.

Rickard, W.H. and C.E. Cushing. 1982. Recovery of streamside woody vegetation after exclusion of livestock grazing. J. Range Manage. 35:360-361.

Risenhoover, K.L. and S.A. Mass. 1987. The influence of moose on the composition and structure of Isle Royale forests. Can. J. For. Res. 17:357-364.

Richardson, J. 1823. No. VII. Botanical Appendix. In J. Franklin. Narrative of a journey to the shores of the Polar Sea, in the years 1819-1822. London.

Sacchi, C.F. 1987. Reproductive ecology of the arroyo willow, Salix lasiolepis. Ph.D. Dissertation, Northern Arizona University, Flagstaff, Az.

Short, R.A., S.P. Canton and J.V. Ward. 1980. Detrital processing and associated marcoinvertebrates in a Colorado mountain stream. Ecology 61:727-732.

Sinclair, W.A., H.H. Lyon and W.T. Johnson. 1987. Diseases of trees and shrubs. Cornell Univ. Press, Ithaca, New York.

Stevens, L.E. 1985. The influence of herbivory on plant competition. M.S. Thesis. Northern Arizona University, Flagstaff, Az.

Stevens, L.E. 1989. Mechanisms of riparian plant community organization and succession in the Grand Canyon, Arizona. Ph.D. Dissertation, Northern Arizona University, Flagstaff, Az.

Sudworth, G.B. 1934. Poplars, principal tree willows and walnuts of the Rocky Mountain region. USDA Tech. Bull No. 420.

Szaro, R.C. 1989. Riparian forest and scrubland community types of Arizona and New Mexico. Desert Plants 9:70-138.

Walker, L.R. and F.S. Chapin III. 1986. Physiological controls over seedling growth in primary succession on an Alaskan floodplain. Ecology 67:1508-1523.

Walker, L.R., J.C. Zasada and F.S. Chapin III. 1986. The role of life history processes in primary succession on an Alaskan floodplain. Ecology 67:1243-1253.

Walla, J.A. 1984. Incidence of Phellinus punctatus on living woody plants in North Dakota. Plant Disease 68:252-253.

White, K.L. 1965. Shrub-carr of southeastern Wisconsin. Ecology 46:286-303.

Yohem, K.H., G.B. Cummins and R.L. Gilbertson. 1985. Revised list and host index of Arizona rust fungi. Mycotaxon 22:451-4468.

Zasada, J.C., R.A. Norum, R.M. van Veldhllluizen, and C.E. Teutsch. 1983. Artificial regeneration of trees and tall shrubs in experimentally burned upland black spruce/feather moss stands in Alaska. Can. J. For. Res. 13:903-913.

Ziller, W.G. 1974. The tree rusts of western Canada. Can. For. Serv. Publ. No. 1329, Dept. of the Environ., Victoria, B.C.

FIGURE 10.—North American distribution of *Salix bebbiana* Sarg., Bebb willow.

Fig. 1. From Froiland (1962).

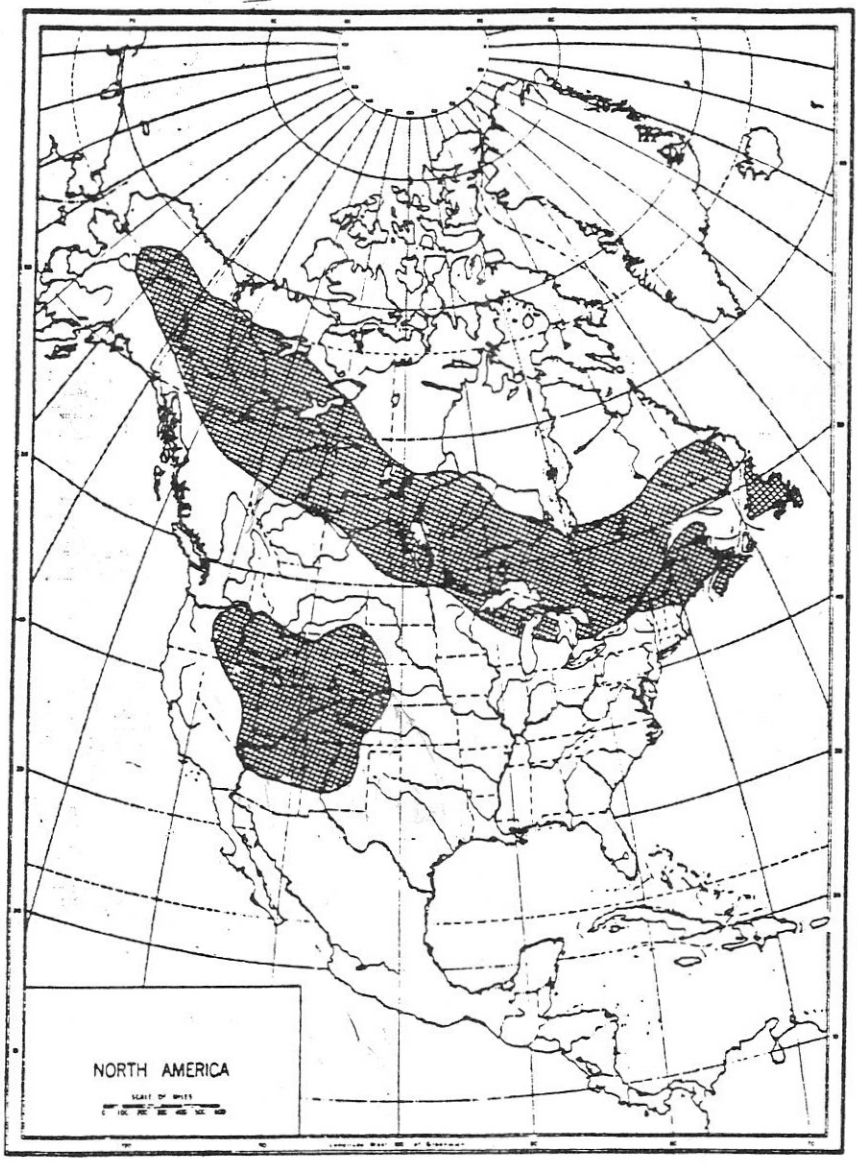

FIGURE 13.—North American distribution of *Salix bebbiana* var. *perrostrata* (Rydb.) Schneid., smooth Bebb willow.

Fig. 2. From Froiland (1962).

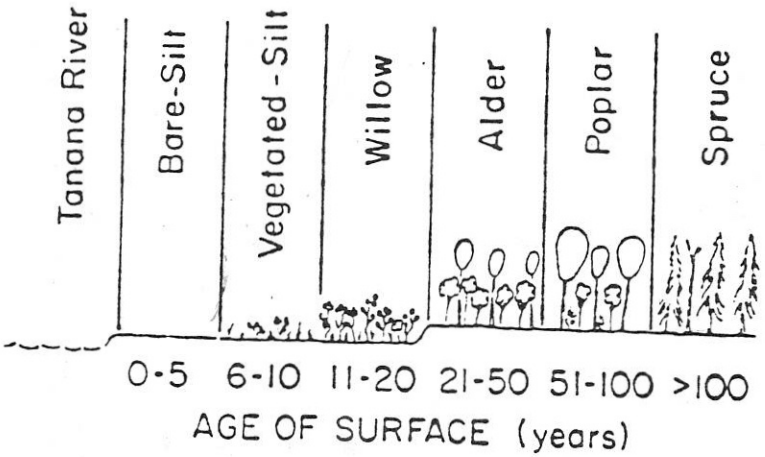

FIG. 1. Primary successional stages on the Tanana River floodplain in interior Alaska (modified from Viereck 1970).

Fig. 3. From Walker et al. 1986.

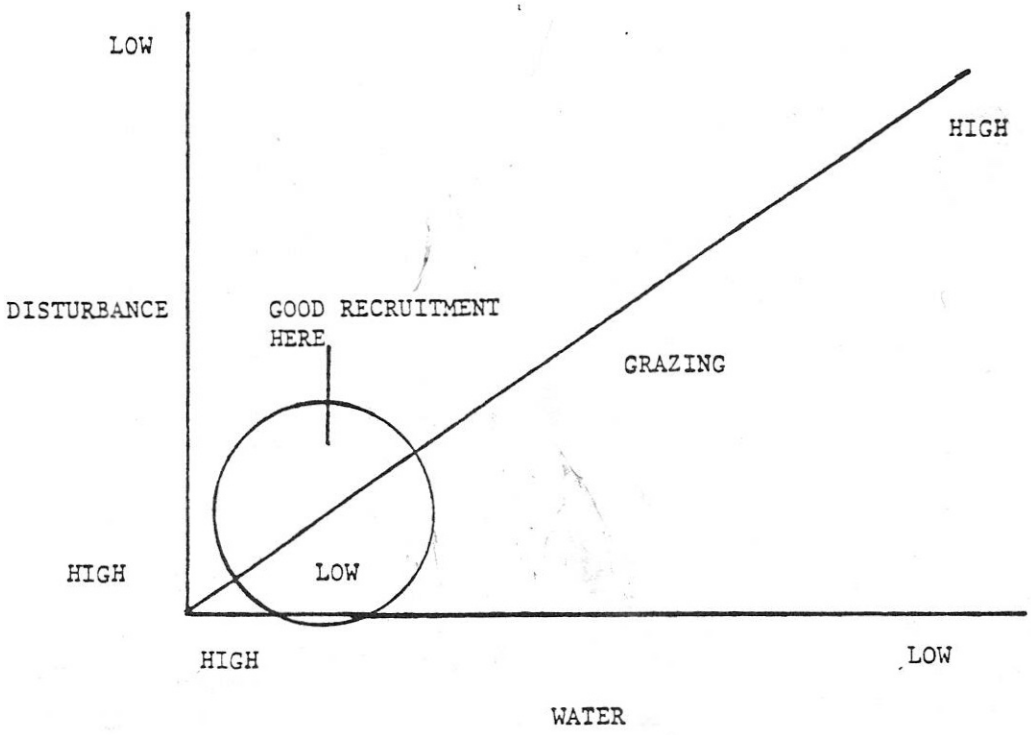

Fig. 4. A model predicting maximum recruitment in Bebb's willow populations based on interactions among levels of disturbance, water availability and herbivory.