Salix L.

willow

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Growth habit, occurrence and use. The willow genus—*Salix*—includes 350 to 400 species (Argus 1996). The majority are in the Northern Hemisphere, from arctic through temperate latitudes (table 1). Three species are native south of Mexico (Dorn 1976) and 67 found in the contiguous 48 United States, where tree and shrub forms predominate. The 39 species found in Alaska are mostly tall to medium shrubs; prostrate growth forms are mostly on the tundra. Shrub and prostrate shrub forms constitute a dominant portion of the vegetation of the circumpolar arctic (defined as north of the treeline) and include about 29 species in the North American Arctic (Argus 1996). These tundra species are segregated into a variety of habitats (Argus 1973; Viereck and Little 1972). General information on the genus worldwide can be found in Warren-Wren (1972) and Newsholme (1992); the taxonomy and distribution of American species is covered by Argus (1973, 1986, 1995), Dorn (1976), MacKinnon and others (1992), and Viereck and Little (1972). General reviews of ecological characteristics and effects of fire on more than 20 species are available in the Fire Effects Information System Database (Fisher 1992). Seed characteristics of poplar (*Populus*, the other North American genus in the Salicaceae) are very similar to those of willows, and information for poplar is applicable to willow (Schreiner 1974; Zasada and Wyckoff 2002). The uniformity in seed characteristics, particularly germination, in the Salicaceae is remarkable considering that the family comprises several hundred species.

The importance of willows as a component of regional vegetation varies geographically and with the mix of habitat types within the region (Fisher 1992). In particular, willows become more important with increasing latitude in North America. In the boreal forests of northern Canada and Alaska, willows are the most common tall and intermediate shrubs; they fill niches occupied by hazel (*Corylus* spp.), maple (*Acer* spp.), and cherry and plum (*Prunus* spp.) in more southern parts of the boreal forest. In the tundra, willows are often the only woody species present; in riparian areas, they are, along with alder (*Alnus* spp.), the largest plants in these important tundra habitats.

Willows have a variety of growth forms (Brinkman 1974; Newsholme 1992; Viereck and Little 1972; Warren-Wren 1972). The tallest attain heights of 30 m, whereas prostrate tundra willows attain heights of a few centimeters to little more than 30 cm. Crown spread and shape is variable; the weeping willow is a popular ornamental tree. "Diamond" willow wood (of various species), named for the diamond-shaped stem lesions that expose the heartwood, is sought after in some areas for making furniture, walking canes, and lamp bases, and for ornamental woodwork.

In natural regeneration, the relative importance of seed versus vegetative propagation varies between species and between locations for a given species (for example, feltleaf willow) (Bliss and Cantlon 1957; Moore 1982; Walker and others 1986). Under appropriate moisture conditions, seeds germinate and seedlings establish in riparian and upland habitats (Densmore and Zasada 1983; Krasny and others 1988; McBride and Strahan 1984; McLeod and McPherson 1972; Walker and others 1986; Zasada and others 1983). Mineral soil is the most suitable substrate because of its water-holding characteristics, but other substrates are adequate if water is available. After seedling establishment, some species (coyote willow and related species) develop clones by suckering from root systems and others by downward bending and layering of stems and branches; however, most species capture space by crown expansion from a multiple-stemmed clump (Douglas 1989; Krasny and others 1988; Ottenbreit and Staniforth 1992). Some species are important colonizers in early stages of primary succession on floodplains, whereas others colonize in later stages of floodplain succession (Argus 1973; Viereck 1970; Viereck and Little 1972; Walker and others 1986).

The majority of species reproduce vegetatively. The most common form of vegetative regrowth is sprouting from buds located at the base of the stem. Other types of vegetative regeneration found in a limited number of species include sprouting from roots, layering of stems, and rooting of broken stem and branch segments. In riparian areas, whole plants are sometimes dispersed by water after being washed out by erosion. Artificial regeneration can be achieved by seeding, and planting seedlings and stem cuttings. Willows regenerate quickly after natural disturbances such as flooding (Krasny and others 1988; Shafroth and others 1994; Viereck 1970); fire (Lyon and Stickney 1976; Viereck and Dyrness 1979; Zasada and others 1983; Zedler and Sheid 1988). They also regenerate on sites disturbed by humans, including mine tailings (Chose and Shetron 1976; Holmes 1982); thermally polluted lands (McLeod and Sherrod 1981); and construction sites (Bishop and Chapin 1989). Willows are used to artificially re-vegetate natural and human disturbance such as those indicated above and for dune stabilization (Fisher 1992; Westoby 1975).

Hybridization occurs in willows but the extent to which it is present is not well established (Argus 1973, 1974; Mosseler and Zsuffa 1989). Hybridization experiments by Argus (1974), Mosseler and Zsuffa (1989), and Mosseler (1987, 1990) conducted with North American willows have confirmed that hybridization occurs among some native species. Barriers to natural hybridization include phenological differences in flowering times, differences in pollen morphology, and other pre- and post-pollination limitations (Kim and others 1990; Mosseler 1987, 1990; Mosseler and Papadopol 1989).

Uses of willows include wood and fiber production, watershed and soil stabilization, habitat and food for wildlife, environmental restoration, landscaping, basketry and furniture making (MacKinnon and others 1992; Newsholme 1992; Viereck and Little 1972; Warren-Wren 1972). Because of the ease of rooting of stem cuttings, rapid early growth and biomass production, and prolific coppicing following cutting, willows are used in short-rotation forestry (Mitchell and others 1992; Sennerby-Forse 1986; Siren and others 1987; Zsuffa and others 1993). Willows were used by Native Americans and Eskimos for medicinal purposes and construction materials (Fisher 1992; MacKinnon and others 1992; Meeker and others 1993; Viereck 1987; Vogel 1990).

Flowering and fruiting. Willows are dioecious (figure 1). The sex ratio in natural populations is often female-biased, with ratios as high as 4:1 (Alliende and Harper 1989; Begin and Payette 1991; Crawford and Balfour 1983, 1990; Fox 1992; Kaul and Kaul 1984; Kay and

Chadde 1992; Moore 1982). Because of irregular flowering, at least several years may be required to accurately assess the sex of individual shrubs and determine sex ratios in natural populations; this is particularly true on less productive sites. There is no definitive biochemical test or molecular genetics technique available for distinguishing male and female plants.

Mosseler (1987) and Mosseler and Zsuffa (1989) found highly skewed sex ratios resulting from controlled inter- and intraspecific crosses. Sex ratios in naturalized exotic species (for example, *S.* H *rubens* Schronk (pro spp.) and *S. alba* spp. *vitellina* (L.) Arcang. in riparian areas in Colorado) are often highly skewed toward one sex because of vegetative reproduction (Shafroth and others 1994).

There have been reports of differences in vegetative characteristics and growth rate between male and female plants, but these differences are not well-established (Alliende and Harper 1989; Crawford and Balfour 1983, 1990). Male plants usually produce more flowers per unit of crown area than female plants (Kay and Chadde 1992; Zasada 2000).

Although the dioecious trait is universal across the genus, hermaphrodite plants (individuals with separate male and female flowers) and catkins (male and female flowers on the same catkin) have been observed in a number of species (Alliende and Harper 1989; Crawford and Balfour 1983; Mosseler and Zsuffa 1989). Mosseler and Zsuffa (1989) observed hermaphroditic plants in both natural populations and in controlled inter- and intraspecific crosses. Plants that are hermaphroditic initially sometimes become completely male as they mature sexually (Mosseler and Zsuffa 1989).

Seed-bearing age in willows depends on species and site conditions. Following disturbances such as fire and logging, willows of vegetative origin (for example, stump sprouts developing from the basal bud bank) flower sooner than plants of seed origin. Sprouts often produce seeds 1 to 2 years after a fire that kills the mature plant, whereas seedlings of the same species require 5 to 10 years before the first seeds are produced. In controlled environments, Mosseler and Zsuffa (1989) reported that coyote willow plants flowered several months after germination in a controlled environment and Mosseler (1996) found that 6 of 7 native willows flowered within 2 years of germination. Zasada (2000) has also observed flowering in 1-year-old creeping willow seedlings.

Catkins bearing several to many staminate or carpellate flowers (figure 1) appear before or after leaf appearance, depending on the species (Mosseler 1987; Viereck and Little 1972). Each carpellate flower contains 2 carpels. The number of ovules per carpel may vary considerable within and among species. Argus (1996) observed the following variation in ovules per carpel: feltleaf willow, 6 to 9; peachleaf willow, 8 to 11; arctic willow, 6 to 7; Bebb willow, 3 to 8; Booth willow, 6 to 9; pussy willow, 3 to 9; coyote willow, 6 to 15; Geyer willow, 3 to 6; Pacific willow, 16 to 20; yellow willow, 3 to 9; meadow willow, 3. Hand-pollination can significantly affect seed production (it increases the number of flowers producing seeds and the number of fertilized ovules per flower), suggesting that insufficient pollination is common in natural populations (Fox 1992). Species vary in their dependence on insect- or wind-pollination, though the former predominates across the genus (for example, Argus 1974; Mosquin 1971; Vroege and Stelleman 1990). The female catkin, when adequately pollinated, produces several to many capsules (fruits) with multiple seeds (figures 2 and 3; table 2). Moore (1982) observed that 24, 38, 67, and 62% of the capsules (flowers) matured and produced viable seeds in feltleaf willow. Zasada (2000) found that between 80 to 90% of the capsules in creeping willow produced seeds. Jones (1995) found that between 28 to 88% of capsules on arctic willow catkins produced seeds.

Primary dispersal of willow seeds is by wind. The hairs or "cotton"—which give the seed great buoyancy—develop on the seedcoat as opposed to being a modification of the seedcoat, as is the case with the wings and other structures that facilitate dispersal in other species (Bewley and Black 1994). The seed separates easily from the hairs. Although willows have the potential to travel great distances (many kilometers), depending on wind and weather conditions, large quantities are deposited under the plant (Zasada 2000). Seeds can also be carried long distances over water, either by the wind or by the water itself. Measuring seed-rain for willows is not as easy as in other species because of the nature of the dispersal unit and short life of the seeds. Various sized containers filled with water or a soil mix in which germination occurs have been used successfully (Walker and others 1986; Zasada and Densmore 1979) and sticky traps are also effective in catching and hold seeds. Water or wet soil appear to be a particularly good medium for catching and holding the dispersal unit.

Flowering and fruiting can be reduced significantly by biotic and abiotic factors. Zasada (2000) observed mortality due to frost of 0 to 38% for female flowers and 0 to 68% for males. Herbivores—for example, moose (*Alces alces*) and elk (*Cervus elphus*)—can reduce flower production by browsing twigs and birds such as ptarmigan (*Lagopus leucurus*) specifically eat flower buds. Kay and Chadde (1992) found essentially no catkins outside of exclosures protected from elk browsing, whereas inside exclosures there were an average of 1,445 (137/ft²), 583 (55/ft²), 694 (66/ft²), and 1336 (126/ft²) catkins/m² of canopy for Bebb, Booth, yellow, and Geyer willows, respectively. Insect galls in arroyo willow reduced reproductive bud production by 43% compared to unaffected stems and seed production potential of individual clones by 10 to 50% (Sacchi and others 1988).

Collection of fruits and seeds. There are 2 broad groups of willows relative to seed dispersal patterns—those with seeds that are dispersed in late spring or summer and those with seeds that are dispersed in the fall, mainly after leaves have been shed (Chmelar and Meusel 1979; Densmore and Zasada 1983; Junttila 1976; Lautenschlager 1984; Poptsov and Buc 1957; Toepfer 1915; Viereck and Little 1972; Zasada and Densmore 1980; Zasada and Viereck 1975). Fall-dispersers comprise about 11% and about 20% of the species in North America and Alaska, respectively. Fall-dispersers are most common in the tundra regions of Alaska and Canada, but some species occur in the boreal forest (Argus 1973; Densmore and Zasada 1983; MacKinnon and others 1992; Viereck and Little 1972).

The seeds of the summer-dispersers live up to about 8 weeks; the rate at which seeds lose viability differs among species and is related to ambient temperature and relative humidity. No seeds in this group have been observed to overwinter and germinate the year after dispersal (Densmore 1979; Densmore and Zasada 1983; Ebersole 1989; Martens and Young 1992; Moss 1938). The rapid loss of viability is a critical consideration when collecting and handling fruits and seeds.

Catkins should be collected as close to the time of seed dispersal as possible. Timing of collection can be based on catkin color and condition of the capsule. Catkin color changes from green to yellow or yellow-brown at maturity. It is best to wait until the capsules begin to open (figure 3), as collection at this stage usually results in the most rapid opening of capsules and the most efficient seed extraction. One note of caution: insect-damaged capsules may *appear* to be dispersing seeds but are often still green and capsules are not opening normally (figure 3). There can be variation of a month or more in timing of dispersal for a species with a wide altitudinal or elevational range (table 3). Once capsules are ripe and begin to open, the rate of seed dispersal is determined by weather conditions: under warm, dry, windy conditions all seeds may be

dispersed within a few days. Under wetter, cooler conditions, dispersal may be spread out over a month. If only a limited amount of seeds is required, stems with immature catkins can be collected and placed in a greenhouse in water; seeds are collected when the capsules open (Marten and Young 1992).

After catkins have been removed from the plant they should be placed in a paper bag that allows the catkin-drying process to continue during transport. Catkins should not be packed tightly because air circulation may be restricted. Bags containing catkins must be kept out of direct sunlight.

To obtain seeds from a specific inter- or intraspecific cross, dormant stem cuttings (50 cm or less in length) with reproductive buds should be obtained from female and male plants in late winter (Mosseler 1987). These cuttings should then be placed in a greenhouse or growth chamber, where they will flower within 2 weeks. Male clones are often forced to flower before females and the pollen stored until the females are ready for pollination. This avoids pollination from unwanted sources. Willow pollen may be frozen for 1 to 2 months without losing its viability. There is a period of 3 to 6 days, depending on species, during which flowers can be pollinated (Mosseler 1987). Catkins will produce viable seeds within 3 to 5 weeks using these procedures. It may be necessary to remove some catkins from the branch in order to assure that enough water and other resources are available for complete development of some catkins. Stems can be kept in aerated or unaerated water; water should be changed 2 to 3 times per week. At each change of water, 1 to 2 cm of stem should be trimmed from the base to expose fresh xylem to assure efficient water uptake. Stems of some species will root readily under these conditions (Densmore and Zasada 1978; Haissig 1970; Mosseler 1987). Mosseler (1987) reported that stem cuttings that rooted were more likely to produce seeds.

The seeds of the fall-dispersers are not as short-lived as summer-dispersers and thus there is more leeway in collecting catkins and handling seeds (Zasada and Densmore 1977). Seeds of fall-dispersers may disperse quickly during warm weather in September, but it is often possible to find seeds in late fall after the first snowfall.

To estimate the number of catkins necessary for a desired quantity of seed, it is important to know the seed yield per catkin (table 2). As in other genera with multiple-seeded fruits, seed yield per catkin varies among species, among sites for a species, among years, and with condition of the catkin (for example, amount of insect infestation or disease).

Although willows generally produce seeds annually, the variation among years is not well-documented. Moore (1982) found that some female feltleaf willows produced relatively large numbers of catkins (200 to 500) over a 2-year period, whereas others of the same age and stature produced no catkins in either year. Within Moore's 3 study areas, 22 of 66% of the mature shrubs did not produce flowers. Jones (1995) found that annual variation in seed production occurred on both wet and dry sites during 2 years of study and that no seeds were produced on their wet site in one of the years. Walker and others (1986) observed similar levels of willow seed production on riparian sites in Alaska during a 2-year period. In addition to genetic and physiological factors that control flowering and seed production, animal browsing, insects, and disease can significantly affect annual variation in seed availability (Kay and Chadde 1992). Though some level of variation in seed production should be expected among years, it is usually possible to find some individuals of a species with a collectible seedcrop in a given year on most sites.

Extraction and storage of seeds. Simak (1980) stated that the following conditions were key for extraction and storage of Salicaceae seeds: (1) placement in proper conditions as

soon as possible (catkins cannot necessarily be stored at ambient air or room temperatures and be expected to have viable seeds); (2) separation of seeds from the cotton using methods that minimize mechanical damage to seeds; (3) pre-drying to about 6 to 10% of dry weight and storage in sealed containers that will maintain a constant humidity; and (4) storage of seeds at subfreezing temperatures to maintain seed viability for time periods of 6 months or more.

There is some difference of opinion regarding the need to separate seeds from the cotton (figure 4) (Martens and Young 1992; Simak 1980). We agree with Simak (1980) that seeds should be separated because doing so reduces the bulk of the material to be stored. There is some indication that storage with the cotton may reduce viability, particularly in the summer-dispersing species (Simak 1980).

Small- to medium-sized lots of seeds can be cleaned according to the following steps:

- Catkins should be placed in a single layer in screen-covered boxes in a relatively warm, dry area, with temperature 20 to 24 EC and relative humidity at 25 to 35%. Air should be able to circulate around the catkins to allow rapid drying. If capsules are beginning to open when collected, opening will be completed in 2 to 3 days. Green catkins open more slowly and incompletely and seed recovery is low.
- Then, the catkins and cotton-containing seeds should be placed in a container so that material can be shaken or tumbled in an airstream or tumbled as in a cement mixer (Einspahr and Schlafke 1957; Fung and Hamel 1993). The seeds separate easily from the cotton (figure 4) under these conditions.
- Seeds can be separated from coarser and finer residue by passing the mixture through a screen or sieve.
- Seeds extracted in this way have a moisture content very close to the 6 to 8%, as recommended by Simak (1980).

Seeds should be stored at temperatures from ! 5 to ! 40 EC immediately after cleaning. They can be stored for up to 6 months at 1 to 5 EC but not for longer time periods. Storage in containers with a dessicant such as calcium chloride (CaCl₂) does not appear to prolong seed life (Martens and Young 1992; Simak 1980). However, storage with a dessicant appears to provide long-term benefit for poplar (*Populus* spp.) (Zasada and Wyckoff 2003) and additional work is needed on use of desiccants for storing willow seeds. The longest periods of successful storage reported are 44 months at ! 20 EC (Simak 1980) and 36 months at ! 10 EC (Zasada and Densmore 1980). Viability of poplar seeds with characteristics similar to summer-dispersing willows has been maintained for 10 to 12 years when stored at ! 10 to ! 20 EC (Wyckoff and Zasada 2003). The small seed size (figure 5 & table 4) makes it easy to store very large quantities of seeds in a limited space.

Germination tests. Willow seeds are very small, usually 1 to 2 mm long and less than 1 mm wide (figures 5 and 6). The seedcoat is transparent and the green cotyledons are readily visible. Seeds appear to contain a functional photosynthetic system [chlorophyll a, 1.45 mg/g; chlorophyll a:b, about 2.4 mg/g for dormant seeds of white willow, a fall-disperser (Zasada and Coyne unpublished data]. Green color is an indicator of potential seed viability.

Germination requirements differ for summer and fall dispersers (figure 7) (Densmore and Zasada 1983; Juntilla 1976; Poptsov and Buch 1957; Zasada and Viereck 1975). Under natural conditions, seeds of summer dispersers germinate in 12 to 24 hours after dispersal with adequate moisture (figure 7). Seeds will germinate under water (Densmore and Zasada 1983; Moore

1982). Germination may be reduced on substrates with a substantial content of salt (Jackson and others 1990; Krasny and others 1988). All tested species—from climates as different as the Arctic, coastal rain forest, and plains areas of the western United States—appear to exhibit a similar response to temperature and do not exhibit any signs of dormancy (Densmore and Zasada 1983; Juntilla 1975; Krasny and others 1988; Martens and Young 1992; Zasada and Viereck 1975). Germination is complete between 5 to 30 EC but declines rapidly at temperatures above 30 EC. Temperatures of 20 to 25 EC appear to be optimum (figure 7). Germination may be tested on a variety of substrates (Brinkman 1974). Seeds germinate completely in the dark, but rate of germination may be higher in the light (Densmore and Zasada 1983; Zasada and Viereck 1975). Official seed testing recommendations call for a 14-day test on moist blotter paper with alternating temperatures of 20 to 30 EC, and light during the 8 hours at 30 EC; no pretreatments are needed (ISTA 1993).

Fall-dispersers exhibit seed dormancy (figure 7). Under natural conditions, seeds overwinter and germinate quickly following snowmelt (Densmore 1979; Densmore and Zasada 1977). Germination of unstratified seeds occurs between 5 to 30 EC, with the highest germination at the warmest temperatures. Stratification widens the range of temperatures over which seeds germinate and increases the rate of germination (Densmore 1979; Densmore and Zasada 1977; Juntilla 1976; Zasada and Viereck 1975; Zasada and Densmore 1983). After 30 days of stratification, the germination pattern at all temperatures resembles that of summer dispersers (Densmore and Zasada 1983). The length of stratification required for complete germination increases prior to the onset of dispersal, reaching a maximum as dispersal begins in the fall, and declining in seeds dispersed late in the fall (Densmore 1979; Densmore and Zasada 1983; Zasada and Viereck 1975). The International Seed Testing Association (1993) did not consider fall-dispersed seeds in their testing rules.

Willow germination, though epigeal, does not follow the usual pattern. Hypocotyl hairs attach the seedling to the substrate and the radicle shows delayed development. Simak (1980) has proposed appropriate criteria for evaluating willow germinant quality (figure 7).

Nursery practice. Contrary to earlier beliefs (Brinkman 1974), seeds can be sown after being stored. Although seed viability may decline during 3 to 4 years of storage, vigorous seedlings can be produced with seeds stored for at least this long. Seedlings can be produced as bareroot stock or in containers and much of the information for *Populus* applies to willows (Schreiner 1974; Wyckoff and Zasada 2002). Although opened capsules containing seeds and cotton can be broadcast on well-prepared beds, seedling density and distribution can be better controlled if the cotton is removed.

After sowing, seeds can be gently pressed into the soil. Seeds should not be buried, however, as a soil covering of 2 to 4 mm (0.09 to 0.2 in) will significantly reduce seedling emergence (McDonough 1979; Zasada 2000). Seedbeds must be kept moist until the seedlings are well-established; a fine spray of water is preferable. To conserve moisture and maintain a high relative humidity near the bed surface, close shading often is provided with slats and burlap. These covers should be removed as soon after germination as possible, for willows grow best under full light. Seedling growth is relatively rapid, and plantable container seedlings can be produced in 1 growing season.

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Figure 1—*Salix bebbiana*, Bebb willow: male and female catkins, which consist of a varying number of flowers depending on sex of the flower and species.

The mature female flower produces a capsule (Fig. 3) containing variable numbers of seeds depending on species, pollination success, and post-pollination predation.

Figure 2—*Salix glauca*, white willow: catkin just beginning to open.

Figure 3—Salix, willow: capsule at various stages of opening (**A–E**) and the dispersal unit at different stages; $\mathbf{F} = \text{hairs}$ in capsule; $\mathbf{G} = \text{hairs}$ fully deployed and separated from the seed. When seeds land on water, hairs may remain attached to the seed, giving the seed buoyancy. [based on Lautenschlager (1984) and Lautenschlager and Lautenschlager (1994)].

Figure 4—*Salix alaxensis*, feltleaf willow: seeds, divisions on scale each = 1 mm.

Figure 5—*Salix*, willow: seed; there is no endosperm and the seed is attached to the hairs at the radicle end. Viable seeds are green due to the presence of chlorophyll; the shade of green is determined by the species, seed water content, and length of time in storage (Simak 1980), H70.

Figure 6—*Salix*, willow: generalized patterns of temperature and stratification effects on germination of seeds of summer- and fall-dispersing willows (see germination section of text for sources); numbers indicate germination temperatures.

Figure 7—*Salix*, willow: seeds; note development of hypocotyl hairs (**arrow**) from the hypocotyl ring (figure 6) [adapted from Simak (1980)].

 Table 1—Salix, willow:
 nomenclature and occurrence

Species	Common name	Occurrence
S. alaxensis (Anderss.) Coville	feltleaf willow	Throughout Alaska, Yukon Territory, & N British Columbia; scattered E across Canadian Arctic & S in Rocky Mtns. to Jasper National Park
S. amygdaloides Anderss.	peachleaf willow	S Quebec, W to SE British Columbia, S to E Washington, Nevada, & Arizona, E to Kentucky & Pennsylvania
S. arctica Pallas	arctic willow	Alaska E to Quebec, S to California,, N Europe, & Asia
S. babylonica L.	weeping willow	China; naturalized from s Quebec, S Ontario, & s Vermont SW to Missouri, Georgia, & South Carolina
S. bebbiana Sarg.	Bebb willow	Newfoundland, W to Hudson Bay & Alaska, S to New Mexico, N to Montana & E to Iowa, Maryland, & New England
S. boothii Dorn.	Booth willow	British Columbia to Alberta, S through Washington & Montana to New Mexico, Arizon, & California
S. caroliniana Michx.	coastal plain willow	Maryland to E Kansas, S to E Texas & E to S Florida; also in Cuba
S. discolor Muhl.	pussy willow	Labrador W to central British Columbia, S to Idaho, E to Delaware & in mtns. S to E Tennessee
S. eriocephala Michx. S. cordata Muhl. S. rigida Muhl.	cordate willow	S Newfoundland to E Saskatchewan & Montana, S to Kansas, E to Virginia
S. exigua Nutt.	coyote willow	Montana, Alberta to British Columbia &Washington, S to S California, E to W Texas & W South Dakota
S. geyerana Anderss.	Geyer willow	Montana W to British Columbia, S to California & Arizona; also Colorado & Wyoming
S. glauca L.	white willow	Alaska, S to British Columbia & in Rocky Mtns to New Mexico & w Texas; also N Mexico
S. interior Rowlee	sandbar willow	E Quebec, W to central interior Alaska, S to E Colorado and New Mexico, E to Louisiana, Tennessee, & Maryland; also N Mexico
S. lasiolepis Benth.	arroyo willow	Idaho & Washington, S to S California, SE Arizona & W Texas; also N Mexico
S. lucida Muhl. [incl. S. lasiandra Benth.]	Pacific willow	Saskatchewan to interior Alaska, S to S California; scattered E to New Mexico & N to Wyoming & Idaho
S. lutea Nutt.	yellow willow	Manitoba & Saskatchewan, w to Yukon & British Columbia, S to E Washington & E Oregon & to S California, Arizona, & New Mexico; also E Nebraska &

North Dakota

S. nigra Marsh.	black willow	Maine to E Minnesota, S to E Kansas & S Texas, E to N Florida; also in N Mexico, Arizona, & California
S. petiolaris Sm.	meadow willow	New Brunswick W to Alberta; scattered S to Colorado & E to New Jersey
S. planifolia Pursh.	diamondleaf willow	Throughout Alaska & Yukon Territory, N British Columbia
S. repens L.	creeping willow	Wet areas in Europe & Asia
S. scouleriana Barratt ex Hook.	Scouler willow	E Manitoba to S Alaska, S to S California; scattered E to New Mexico & N to Montana

Sources: Argus (1973, 1975), Brinkman (1974), Cooper and Van Havern (1994), Hillier and sons (1989), Little (1979), MacKinnon and others (1992), Newsholme (1972, 1992), Viereck (1987), Viereck and Little (1972), Vogel (1990).

Table 2—Salix, willow: seed quantity in catkins

Species	Location	Capsules in catkin w/seeds	Seeds/capsule	Seeds/catkin
S. alaxensis	Alaskan Arctic Slope			
	Site 1	45 (35-61)	8 (7-8)	333 (245-427)
	Site 2	71 (61–80)	9 (8-10)	673 (488–800)
	Site 3	119 (92-137)	10 (8-11)	1,174 (736–1,280)
	Site 4	98 (82-109)	7 (6-8)	600 (492-763)
S. amygdaloides	Ontario, Canada	- '	16 (14–18)	
S. arctica	Canadian high Arctic—Ellesmere Island			
	Dry site (year 1)	24 (8-40)	18 (10-25)	432
	Dry site (year 2)	65 (60-70)	9 (8-10)	595
	Wet site (year 1)	7 (2–12)	12 (5–18)	84
S. bebbiana	Yellowstone National Park	37 (24–48)	6 (5-7)	218 (144-311)
S. boothii	Yellowstone National Park	64 (43-79)	6	400 (286-427)
S. discolor	Ontario, Canada	-	10 (8-12)	_
S. exigua	Ontario, Canada	_	25 (15-36)	_
S. geyeriana	Yellowstone National Park	18 (12-29)	5 (4-6)	81 (42-171)
S. lucida	Ontario, Canada	_	17 (12-20)	_
S. lutea	Yellowstone National Park	74 (69–78)	11 (11-12)	841 (754-925)
S. petiolaris	Ontario, Canada	_	3 (2-5)	_
S. repens	Newborough, Warren, North Wales	4 (3-4)	22 (19–25)	82 (50-110)

Sources: Jones and others (in press), Kay and Chadde (1992), Moore (1982), Mosseler (1987), Zasada (2000). **Note:** Values are means with ranges in parentheses.

Table 3— Salix: phenology of flowering and fruiting

Species	Location	Flowering dates	Fruit ripening dates	Seed dispersal dates
S. alaxensis	Alaska—Brooks Range	May-June	June-July	July-Aug
	Alaska—Tanana River	Apr-May	May	May-June
	Alaska—Central Interior*	May-June	June-July	July-Aug.
S. amygdaloides	NE Minnesota	May-June	_	_
S. arctica	Canadian high Arctic—			
	Ellesmere Island	July	Aug-Sept	
	Interior Alaska	June-July	July-Aug	Aug-Sept
S. bebbiana	_	Apr-June	May-June	May-June
S. caroliniana	North & South Carolina	Mar-April	Mar-Apr	_
S. discolor	N Ontario & British	May	_	_
	Columbia			
	Rocky Mtns, USA	Mar-April	Apr-May	Apr-May
S. eriocephala	NE Minnesota & N Ontario	Apr-June	June	June-July
(as S. rigida)				
S. exigua	_	May-July	June-July	June-July
S. fragilis	US & Europe	Apr-May	May-June	May-June
S. glauca	Alaska—Brooks Range	June-July	July-Aug	Sept-Nov
	Alaska-mid-boreal forest	May-June	July-Aug	Sept-Nov
	Alaska—Denali National Park	June-July	July-Aug	Sept-Nov
S. interior	N Ontario		Aug 13	_
S. lucida†	Idaho	Apr-May	June-Aug	June-Aug.
S. nigra	In north	Feb-April	Apr-May	Apr-May
	In south	May-June	June-July	June-July
S. petiolaris	General	May-June	June-July	June-July
S. scouleriana	General	Apr-June	May-July	May-July

Sources: Brinkman (1974), Densmore and Zasada (1983), Jones and others (in press), Viereck and Little (1972). * High elevation.

[†] As S. lasiandra.

Table 4—Salix, willow: cleaned seeds

	Place of	Cleaned seeds H 1,000/weight		
Species	collection	/kg	/lb	Samples
S. amygdaloides	Minnesota	5,720	2,600	1
S. bebbiana	Idaho (770 m)	5,500	2,500	2
S. caroliniana	South Carolina	18,260	8,300	1
S. exigua	Washington (615 m)	22,000	10,000	1
S. fragilis	Minnesota	7,040	3,200	1
S. lasiandra	Idaho (770 m)	25,300	11,500	1
S. petiolaris	Minnesota	1,100	500	1
S. scouleriana	Idaho (770 m)	14,300	6,500	1

Source: Brinkman (1974).