

# GROWTH AND YIELD OF WILLOWS IN CENTRAL OREGON COMPARED TO REPORTS IN WORLD LITERATURE

Bernard L. Kovalchik

## ABSTRACT

*Willows come in various shapes and sizes and respond in rates of growth and biomass accumulation to factors such as senescence, temperature, frost, flooding, soil nutrients, mineral toxicity, and fertilization. Height growth for naturally growing willows in central Oregon averages less than 1½ feet per year and decreases with age. Accumulated biomass may range from 4,000 to 60,000 pounds per acre dry weight on bogs and well-drained sites.*

## INTRODUCTION

A study describing riparian plant associations on the National Forests of central Oregon was completed in 1987 (Kovalchik 1987). Several of these plant associations were dominated by willows. Unfortunately, many of these willow-dominated sites have been degraded to less stable plant communities in response to improper management activities such as overuse by livestock.

Managers often wish to reestablish willows on degraded sites but lack information on willow establishment and growth responses to environmental factors. This paper summarizes world literature on willow growth and compares the information with willow growth in central Oregon.

## GROWTH RESPONSES TO ENVIRONMENTAL FACTORS

Willow shoot growth varies from year to year, largely in response to the accumulation of resources during the previous year (Wijk 1986). Resource accumulation in turn depends on the length of growing season, which is determined by climatic variables such as length of previous year's snow cover, early season temperature, and drought (Wijk 1986). These conditions may have little visible effect on current season's growth, but may reduce shoot growth and rooting success the following year. Conditions during late-season bud development also affect the following year's shoot elongation (Kozlowski 1984).

## Diurnal Climate

Willow height growth is most rapid during late afternoon and early evening and may be twice that of the rest of the

day (Dowsley 1987). Decreasing temperature and increasing humidity result in lower transpiration stress at this time of day. However, drought conditions and subsequent transpiration stress limit growth at all times of day.

## Air Temperature

Much of the water taken in by a plant is passed through leaves as transpiration (Kramer and Kozlowski 1979). This benefits the plant through cooling of leaves and mineral translocation. However, on hot, dry days transpiration exceeds root absorption, resulting in rapid loss of water from leaves and twigs, increased water stress, stomatal closing, and ceasing of growth (Dowsley 1987; Kramer and Kozlowski 1979; Ogren and Oquist 1985). Exceedingly cold or hot temperatures also affect bud formation, dormancy, initiation, and expansion into shoots (Dowsley 1987). For these reasons, most plants of temperate North America find air temperature between 65 °F and 80 °F optimum for maximum photosynthetic rate (Larcher 1969).

## Soil Temperature

Similarly, cold soil temperature reduces water absorption through roots and can result in transpiration stress and reduced growth, even on days with favorable air temperatures (Dowsley 1987; Fries 1943). Serious desiccation, and even death, of stems and leaves can occur with abnormally warm winter and spring temperatures on frozen or cold ground.

## Frost

Willows are very tolerant of frost. Mature leaves and winter-dormant stems are capable of surviving temperatures of -4 °F and -94 °F, respectively (Sakai 1970). However, frosts during early growing season can cause severe damage to fast-growing shoots of willow (Christersson 1983; Fircks 1983). Temperatures of 28 °F or lower will kill the elongation zone soon after exposure. Frost-injured leaves and stems appear waterlogged and limp after thawing, and dry out rapidly. Exposure to hard frost (<23 °F) results in death immediately after thawing and may kill an entire season's shoot growth. Ice crystals do the actual damage. Lateral buds below the damaged shoot rapidly start to form new shoots.

## Flooding

Willows are considered to be tolerant of flooding (Knighton 1981; Kozlowski 1984). The level of tolerance varies with the individual species' ability to tolerate various

---

Paper presented at the Symposium on Ecology and Management of Riparian Shrub Communities, Sun Valley, ID, May 29-31, 1991.  
Bernard L. Kovalchik is Riparian Ecologist for eastern Washington, Forest Service, U.S. Department of Agriculture, Colville, WA 99114.

soil and water conditions. Important willow adaptations to flooding include the formation of soft, spongy tissue (aerenchyma) for the transport of gases, enlargement of lenticels in stems to permit more efficient gas exchange, and regeneration of new roots (Kozlowski 1984). Willows tolerate low soil oxygen by their ability to transport large volumes of oxygen to roots through aerenchyma tissue. The roots in turn release oxygen into the soil and water atmosphere, indirectly benefiting plants by reducing toxic compounds, such as iron ions, and reducing the production of harmful gases produced by anaerobic reduction (Kozlowski 1984).

Knighton (1981), in an experiment exposing willow to different levels of permanent flooding, showed willow growth was severely limited when the water level was at or above the root crown. Chlorotic foliage and some dead stems did not appear until the second season. Willow showed some growth if as little as 3 inches of soil was aerated, but was better in 6 inches or more of aerated soil.

The ability to regenerate new roots on the original root or submerged stem is important to willows (Kozlowski 1984). Elevated soil-water tables result in severely restricted root development, and eventual death of the root system. However, adventitious rooting above the flooded soil is abundant in many species of willow (except Scouler willow), and a new root system develops above the soil-water table (Knighton 1981).

## Mineral and Chemical Toxicity in Flooded Soils

Many potentially fatal compounds such as soluble iron and manganese are produced by waterlogged soil (Kozlowski 1984). Ethanol, acetaldehyde, and cyanide compounds are produced by flooded roots. The many products of anaerobic microsoil activity include methane, ethane, propylene, acids, aldehydes, ketones, and diamines. Kozlowski (1984) also reported increases in ethylene, auxins, and abscisic acid in flooded plants, chemicals that variously influence chemical and hormonal processes.

Therefore, wetland plants must have some mechanism for avoiding the toxicity of iron and manganese ions and other chemicals and minerals in flooded soils (Talbot and Etherington 1987). Willows from well-drained riparian soils express toxicity by reductions of growth, accumulation of iron in leaves, and failure to produce new roots when flooded. Roots of flood-tolerant willows immobilize iron and other toxic ions as part of a mechanism to avoid toxicity. This may suggest a site-based ranking of willows in central Oregon by tolerance to both flooding and mineral toxicity:

1. Scouler willow (*Salix scouleriana*), primarily an upland species, is least tolerant of flooded soils.
2. Whiplash willow (*S. lasiandra* var. *caudata*), Pacific willow (*S. lasiandra* var. *lasiandra*), coyote willow (*S. exigua*), and yellow willow (*S. lutea*)—found primarily on well-drained streambanks.
3. Bebb willow (*S. bebbiana*), restricted primarily to moist aspen stands, is never found on sites with long exposure to floods.
4. Geyer willow (*S. geyeriana* vars. *geyeriana* and *meliana*), Lemmon willow (*S. lemmonii*), Drummond willow

(*S. drummondiana*), and Sitka willow (*S. sitchensis*)—found on a wide variety of sites, ranging from well-drained streambanks and floodplains to wet shrub basins, but do poorly on bogs.

5. Booth willow (*S. boothii*) also grows on a wide variety of sites, but grows well in dwarf form on bogs.

6. Eastwood willow (*S. eastwoodiae*) and undergreen willow (*S. commutata*)—restricted largely to peat soils of bogs and higher elevation willow basins, indicating the most tolerance to both flooding and mineral toxicity.

## Soil Nutrients

Walker and Chapin (1986) found higher rates of growth in more advanced successional stages compared to stands on newly colonized silt deposits. Fertilizing the silt soil resulted in an eightfold increase in total biomass, suggesting competition among willow seedlings for limited soil nutrients in early succession stages. The presence of nitrogen-fixing alder in more advanced succession stages results in a sixfold increase of exchangeable inorganic nitrogen compared to the silt deposits, yet the inhibiting effect of alder competition and shade resulted in reduced growth of willow.

Willows do not express good height growth on peat bogs. The soil is wet, pH 4 or below, and the mineral nutrient availability poor (Elowson and Rytter 1986). Bog soil contains considerable nitrogen, largely in unavailable organic form, and little or no P or K (Hytonen 1985). Soil bulk density is low and, coupled with high hydraulic conductivity, results in increased water and nutrients leaching out of the thin zone where roots do grow (Elowson and Rytter 1986). However, willows tolerate these low nitrogen levels by enhanced root growth and reduced height growth. Thus the plant may exploit a greater soil volume to sustain healthy dwarfed shoots (Good and Williams 1986).

Vesicular arbuscular mycorrhizae (VAM) occur on the roots of willows (Backhaus and others 1986). VAM fungi increase nutrient uptake by functioning as extended root systems. The benefits would be especially important in nutrient-poor soils such as peat and sand. However, Gray (1979) felt low pH associated with peat soils would inhibit VAM development on willows. VAM benefits would be less in clay and loam soils, which have large amounts of available nutrients and soil structure favorable for water storage, soil aeration, and nutrient exchange.

## Fertilization

Europeans have considerable experience with fertilizing willow energy plantations. Plantations utilize draining, irrigating, and fertilizing to increase biomass production in planted willow stands. Growth of willows on unfertilized peat and sand soils is slow (Christersson 1986; Hytonen 1985). The application of wood ash increases soil pH from 4.9 to 5.5, which results in increased microbial activity, organic nitrogen mineralization, and nitrogen availability (Weber and others 1985) with a subsequent increase in the willow harvest of 65 to 70 percent. Adding ammonium nitrate to peat soils results in increased shoot growth, leaf weight, shoot-to-root ratio, and aboveground biomass (Good

and Williams 1986). However, treatment with urea increases the acidity of peat soils, counteracting any beneficial effects (Hytonen 1985).

## GROWTH RESPONSES TO NONENVIRONMENTAL FACTORS

### Ungulate Browsing

Ungulate browsing and beaver cutting immediately reduce height growth of willows by damaging and killing stems. Smith (1980) and Kindschy (1990) found that less than half of heavily clipped or browsed willow stems survive into the following year, even with protection from browsing. Of the survivors, regrowth was half the growth of ungrazed stems. Therefore, it may take 3 or more years for heavily browsed willows to recover from browsing by domestic or wild ungulates.

### Insects

Managers often overlook damage done by willow insect pests. The following types of willow damage are caused by insects (West 1985):

- *Defoliating*. Leaf-eating is done by grasshoppers, spanworms, the larvae of moths, butterflies, and larval and adult beetles. Defoliation of a plant reduces the photosynthetic capacity of the plant. The effect of normal infestations on a willow's growth may be negligible.

- *Mining*. Leaf miners include a diverse group of insects such as flea beetles, leaf miners, and casebearers. The tiny larvae of these insects live in the leaf epidermis, causing irregular blotches or tunnels as they consume the leaf tissue. Damage is usually minor.

- *Wood boring*. Borers cause damage by slowing growth or killing attacked portions of the willow. In addition, the tunnelling activity weakens shoots so that wind or snow breaks them. Attack often stimulates the growth of lateral branches, thus compensating for the destruction of shoots.

- *Leaf and stem galling*. Gall-forming insects cause immature leaf and stem tissues to form swollen structures that provide the insect with food and shelter at the expense of the rest of the plant. Stem galls may girdle stems and result in the direct death of the shoot. Damage from leaf galls is minimal.

- *Sapsucking*. Sapsucking insects include the psyllids, aphids, scale insects, and mites. Sapsucking reduces the carbohydrate reserves of the willows. Injury due to sapsucking is usually minor.

### Age

All plants experience decreases in height growth with age (Kozlowski 1984). Yearly decreases in shoot growth are partially due to nutrient and water deficiencies arising from restricted root growth, or may be due to reductions in xylem and phloem formation with age. Additionally, respiration burden and translocation resistance increases with the height and spread of the plant, thus requiring larger

energy expenditures (Wijk 1986). An increase of 5 years in age may correspond to a reduction in average shoot growth of 50 percent.

## GROWTH AND YIELD FROM PUBLISHED REPORTS

### Height Growth

Height growth is dramatic in the controlled, enhanced environments of energy plantations. Christersson (1983) reported 9 to 12 feet total height growth in a 2-year-old energy plantation in Sweden. In another Swedish study, Dowsley (1987) reported willow heights of 5½ to 6½ feet at the end of the first growing season. Robertson (1986) did not report height growth for energy plantations in Newfoundland, but photographs of a first-year plantation showed 6 to 8 feet of growth. Hybrid clones may grow 50 percent faster than either parent (Hathaway 1987). Data are not available for natural stands.

### Radial Growth

The ultimate size of willow stems depends on the willow species and the characteristics of the site. Walker (1987) showed strong correlation between summer temperature regimes and growth ring width on floodplains along the north slope of Alaska. Elevation, soil moisture, wind, and nutrients also affect radial growth. Radial growth decreases with age and beyond 10 years cannot be strongly correlated with any environmental factor. In bog and tundra environments, cold soil temperatures and low nutrient availability are likely more limiting to radial growth than air temperature (Walker 1987). Data were not available for energy plantations.

### Biomass Distribution

Thilenius (1990) reported unbrowsed twigs of Alaska willow (*Salix barclayi*) growing as gently tapering cylinders along the coast of Alaska. The distal one-half of the twigs contained only 35 to 41 percent of the total weight of the current year's growth. Implications are that a browsed willow with one-half of its twigs used to one-half of their length would look heavily used. Yet, less than 20 percent of the weight of the current year's growth is used. His study did not account for browsed twigs dying back to the next lower stem bud, as I have observed them to do.

Cannell and others (1988) reported willow biomass distributed 24 percent to leaves, 42 percent to stems, and 33 percent to roots on well-drained soils. At the beginning of the growing season, 40 to 50 percent of the dry matter production went into leaves, setting the stage for later biomass production through apical elongation and meristematic expansion. Dry, aboveground biomass for Alaska willow was proportioned 25 to 30 percent in the leaves and 70 to 75 percent in the stems (Thilenius 1988). Reader and Stewart (1972) reported 75 percent of the yearly net above- and belowground production for bog willows was in roots,

indicating a high root ratio for willows in bogs compared to well-drained soils typical of tall willow stands.

## Biomass Production

Cannell and others (1987) reported daily increments of 380 pounds aboveground biomass per acre per day during peak production periods (mid-June through mid-August) and an average of 176 pounds per acre per day for the entire growing season in an energy plantation in Scotland. Total seasonal biomass production was 9,700 pounds per acre aboveground, of which 7,300 pounds occurred in stems and 2,400 pounds in leaves.

Eckersten and others (1987) found considerable variation in the biomass production of willow clones planted in energy plantations in Sweden. The mean annual production of aboveground biomass averaged 6,961 dry pounds per acre for all sites. Variation between locations reflected variability in temperature and radiation climate. The coastal sites had less variation due to the buffering effect of coastal climate. Even higher production of 23,100 pounds per acre dry aboveground matter was reported for a first-year plantation in Newfoundland (Robertson 1986). Another Swedish energy plantation yielded a total aboveground biomass of 11,700 dry pounds per acre, of which 7,770 pounds was for stems and 3,400 pounds for leaves in the first season after planting (Nilsson and Ericsson 1986). The second year yielded 17,500 pounds, with 10,800 pounds of stems and 6,700 pounds of leaves. Production was higher the second year due to larger root systems, larger initial nutrient stores, and buds ready to sprout.

Biomass production in natural willow stands is lower than in energy plantations. Accumulated aboveground biomass ranged from 10,000 dry pounds per acre in a bog to 30,000 pounds in a tall willow stand in Alaska (Reader and Stewart 1972). Shrub biomass in mixed willow, alder, and birch wetlands in Minnesota ranged from 446 to 59,000 pounds per acre (Connolly-McCarthy and Grigal 1985). Total biomass averaged 5,442 pounds per acre on bogs and 12,000 pounds per acre on well-drained peat, while marshes with mineral soil averaged 9,900 pounds per acre. Thus production differences between strikingly different soil classes were not that great, indicating factors other than soil classification have a greater effect on shrub biomass production. For instance, soils with lower water tables support much greater biomass than similar soils with high water tables. Elsewhere, estimated accumulated biomass for alder-willow stands on alluvial soil in central Alaska ranged from 9,000 pounds per acre for 5-year-old stands to 43,000 pounds for 20-year-old stands (Van Cleve and others 1971).

## GROWTH AND YIELD OF NATURAL WILLOW STANDS IN CENTRAL OREGON

Stems of willows were destructively sampled in conjunction with the development of the riparian plant association classification for central Oregon (Kovalchik 1987). One prominent, healthy stem was selected from the center of a willow clump and cut into 1-foot sections. Diameters

and ages were measured in the office and used to develop height/age curves for the common willows of central Oregon. Results are discussed here.

## Growth Form

Willows in central Oregon vary considerably in size and shape. Geyer, Lemmon, Booth, Sitka, Eastwood, and undergreen willows all form broadly rounded, many-stemmed shrubs on well-drained soils. Booth, Eastwood, and undergreen willows also form dwarf (less than 2 feet tall), few-stemmed shrubs on bogs. Yellow, Pacific, whiplash, Bebb, and Scouler willow grow as tall, several-stemmed shrubs or small trees with one or more trunks.

## Root Growth

The numerous stems of Geyer willow arise from a single root caudex (author's observation). Several main roots branch off this caudex into numerous horizontal roots that extend considerable distances from the plant. New root systems may develop by adventitious rooting of stems forced into contact with the ground by snow loading. The root caudex may grow for at least 50 years.

Total age of Geyer and similar willows may be many centuries because of the ability of willows to regenerate new root systems in response to disease, injury, or changing soil-water tables. Coyote willow is the only willow in central Oregon that forms large clones by sprouting from root runners.

## Height Growth

Height/age comparisons from sectioned stems of common willows are shown in figure 1. Curves are for well-drained sites, except Eastwood willow is shown for both well-drained peat and poorly drained bog soils. Annual rate of height growth ranged from several inches to 1½ feet per year in the first 10 years of growth. Lemmon willow shows the fastest height growth, averaging 15 feet at 10 years and 17 feet maximum height at 15 years. Geyer willow is slightly slower in growth, averaging 12 feet at 10 years and 15 feet at 18 years. Booth willow averages 8 feet at 10 years and 10 feet at 16 years on well-drained soils. Eastwood willow height growth reflects higher elevations and cold soils. Mature shrubs are about 6½ feet tall at 10 years and 7 feet at 13 years on well-drained peat, but average only 2 feet in height at 10 years on bogs. Undergreen willow grows similarly to Eastwood willow on well-drained peat. Both undergreen and Booth willows grow like Eastwood willow on bogs.

## Basal Diameter

Basal diameter for willows in central Oregon ranged from:

- 0.8 to 2.25 inches for 11- to 21-year-old Lemmon willow.
- 0.5 to 2.05 inches for 10- to 21-year-old Geyer willow.
- 0.8 to 1.7 inches for 10- to 20-year-old stems of Booth willow.

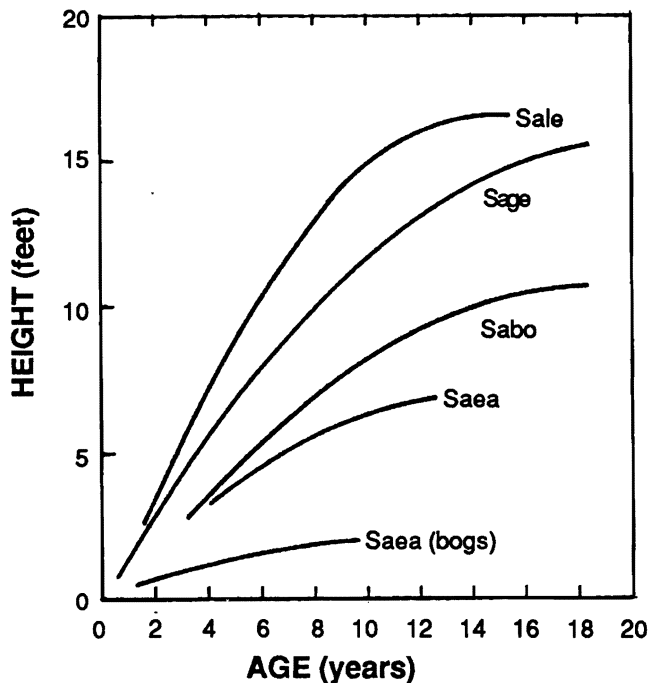


Figure 1—Height/age comparisons for some important willows in central Oregon. Sale = *Salix lemmonii* on well-drained sites ( $n = 35$ ,  $R^2 = 0.97$ ,  $Y = 2.211X - 0.074X^2$ ); Sage = *Salix geyeriana* on well-drained sites ( $n = 234$ ,  $R^2 = 0.87$ ,  $Y = 1.534X - 0.078X^2$ ); Sabo = *Salix boothii* on well-drained sites ( $n = 103$ ,  $R^2 = 0.77$ ,  $Y = 1.126X - 0.030X^2$ ); Saea = *Salix eastwoodiae* on well-drained sites ( $n = 67$ ,  $R^2 = 0.79$ ,  $Y = 0.984X - 0.035X^2$ ); Saea (bogs) = *Salix eastwoodiae* on peat bogs ( $n = 9$ ,  $R^2 = 0.15$ ,  $Y = 0.414X - 0.022X^2$ ).

- 0.2 to 0.9 inches for 5- to 13-year-old Eastwood willow on well-drained peat.
- 0.2 to 0.4 inches for 5- to 10-year-old Eastwood willow on bogs.

## Stem Age

Maximum stem ages vary considerably between species of willows. Stems of Geyer, Lemmon, and Booth willows on well-drained soils approach senescence between the ages of 15 to 20 years and die due to attacks by insects or disease (author's observation). Dead stems often resprout from adventitious buds from near the base of the stem, and grow to replace the dead stem. The same age pattern occurs for Eastwood and undergreen willows on well-drained peat soil, but at 10- to 15-year intervals. On bogs, stem ages for Eastwood, undergreen, and Booth willows were not observed to exceed 10 years. Total shrub age is much greater due to

continuous regeneration of roots and stems (author's observation). All age classes should be present on healthy, vigorous willows.

## Biomass Distribution

Biomass distribution information was not collected for central Oregon willows, but is probably similar to information shown in figure 2.

## CONCLUSIONS

Rates of growth for willows in central Oregon are much less than reported for energy plantations in Eurasia and Newfoundland. Willows on bogs grow only a few inches in height per year and mature plants average less than 2 feet tall. Basal stem diameters are less than 0.4 inches. Willows on well-drained soils average less than 1½ feet annual height growth. Depending on species, mature shrubs grow to 7 to 17 feet with basal diameters of 0.9 to 2.15 inches. For comparison, willows on energy plantation grew 4½ to 8 feet the first year (Christersson 1986; Dowsley 1987; Robertson 1986).

Total shrub biomass in central Oregon may be similar to that reported for natural stands in Alaska and Minnesota (Connolly-McCarthy and Grigal 1985; Van Cleve and others 1971). If so, they would accumulate about 4,000 to 6,000 pounds per acre dry weight on peat bogs and 40,000 to 60,000 pounds per acre on well-drained soils. The general distribution of aboveground biomass should approximate 25 to 30 percent in the leaves and 70 to 75 percent in the stems (Thilenius 1988). Roots should comprise about one-third of the total shrub biomass (Cannell and others 1988) on well-drained soils and 75 percent on bogs (Reader and Stewart 1972).

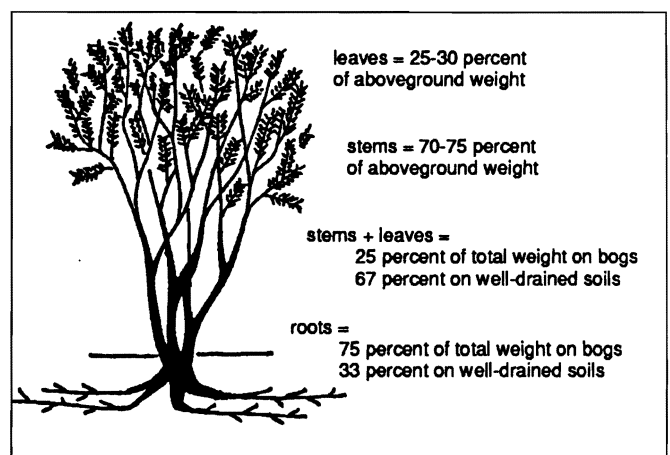


Figure 2—Biomass distribution on shrubby willow (Cannell and others 1988; Reader and Stewart 1972; Thilenius 1988).

## REFERENCES

- Backhaus, G. F.; Haggblom, P.; Nilsson, L. O. 1986. The influence of vesicular-arbuscular mycorrhizae on biomass production in willow. *Canadian Journal of Forest Research*. 16(1): 103-108.
- Cannell, M. G. R.; Milne, R.; Sheppard, L. J.; Unsworth, M. H. 1987. Radiation interception and productivity of willow. *Journal of Applied Ecology*. 24: 261-278.
- Cannell, M. G. R.; Sheppard, L. J.; Milne, R. 1988. Light use efficiency and woody biomass production of poplar and willow. *Journal of the Institute of Chartered Foresters*. 61(2): 125-136.
- Christersson, L. 1983. Frost damage during the growing season. In: *Plant production in the north workshop: proceedings*; September 4-9; Tromso, Norway: 191-198.
- Christersson, L. 1986. High technology biomass production by *Salix* clones on a sandy soil in southern Sweden. *Tree Physiology*. 2: 261-272.
- Connolly-McCarthy, B. J.; Grigal, D. F. 1985. Biomass of shrub-dominated wetlands in Minnesota. *Forest Science*. 31(4): 1011-1017.
- Dowsley, B. 1987. Study of the correlation of diurnal growth patterns to climatic variables in a *Salix* energy plantation. Newfoundland Forest Research Center Information Report N-X-260. Canadian Forestry Service. 28 p.
- Eckersten, H.; Lindroth, A.; Nilsson, L. 1987. Willow production related to climatic variations in Southern Sweden. *Scandinavian Journal of Forest Research*. 2: 99-110.
- Elowson, S.; Rytter, L. 1986. Soil characteristics of raised sphagnum bog in relation to intensively grown deciduous species. *Scandinavian Journal of Forest Research*. 1(1): 95-111.
- Fries, N. 1943. On the winter water regime of broadleaved trees. *Svensk Botan Tidskrift*. 37: 241-265.
- Good, J. E. G.; Williams, T. G. 1986. Growth responses of selected clones of birch (*Betula pendula* Roth., *B. pubescens* Ehrh.) and willow (*Salix caprea* L., *S. cinerea* L.) to nitrogen in solution culture. *Plant and Soil*. 92(2): 209-222.
- Graw, D. 1979. The influence of soil pH on the efficiency of vesicular-arbuscular mycorrhizae. *New Phytology*. 82: 687-695.
- Hathaway, R. L. 1987. Willows for the future. *New Zealand Soil Conservation Centre* 53. 4 p.
- Hytonen, J. 1985. Stability of various phosphorus and nitrogen fertilizers for fertilizing willow stands on cut-over peatlands. In: *Bioenergy 84: the proceedings of an international conference on bioenergy*. Goteborg, Sweden: Elsevier Applied Science. 2: 114-118.
- Knighton, M. D. 1981. Growth response of speckled alder and willow to depth of flooding. *Res. Pap. NC-198*. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station. 5 p.
- Kovalchik, B. L. 1987. Riparian zone associations: Deschutes, Ochoco, Fremont, and Winema National Forests. R6-ECOL-TP-279-87. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region. 171 p.
- Kozlowski, T. T. 1984. Plant responses to flooding of soil. *BioScience*. 34(3): 162-167.
- Kramer, P. J.; Kozlowski, T. T. 1979. *Physiology of woody plants*. London: Academic Press.
- Larcher, W. 1969. The effect of environment and physiological variables on the carbon dioxide gas exchange of trees. *Photosynthetica*. 3: 167-198.
- Nilsson, L. O.; Ericsson, T. 1986. Influence of shoot age on growth and nutrient uptake patterns in a willow plantation. *Canadian Journal of Forest Research*. 16(2): 185-190.
- Reader, R. J.; Stewart, J. M. 1972. The relationship between net primary production and accumulation for a peatland on southeastern Manitoba. *Ecology*. 53(6): 1025-1037.
- Robertson, A. 1986. Boreal plantation R & D with *Salix* species: Proceedings of the sixth international workshop on forest regeneration. Gen. Tech. Rep. PNW-194. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station: 27-30.
- Sakai, A. 1970. Freezing resistance in willows from different climates. *Ecology*. 51: 485-491.
- Shaver, G. R. 1986. Woody stem production in Alaskan tundra shrubs. *Ecology*. 67(3): 660-669.
- Smith, B. H. 1980. Riparian willow management: its problems and potentials, within the scope of multiple use management. Presented to: University of Wyoming—Shrub Ecology Workshop. 1980 June 5-6; Lander, WY. 15 p. Unpublished report.
- Talbot, R. J.; Etherington, J. R. 1987. Comparative studies of plant growth and distribution in relation to water-logging. *The New Phytologist*. April: 575-583.
- Thilenius, J. F. 1988. Weight distribution in the current annual twigs of Barclay willow. *Res. Note PNW-472*. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 10 p.
- Thilenius, J. F. 1990. Dimensional weights and forage quality of Barclay willow and sweetgale on moose ranges in the wetlands of the Copper River Delta, Alaska. *Forest Ecology and Management*. 33/34(1-4): 463-483.
- Van Cleve, K.; Viereck, L. A.; Schlenker, R. L. 1971. Accumulation of nitrogen in alder (*Alnus*) ecosystems near Fairbanks, Alaska. *Arctic and Alpine Research*. 3: 101-114.
- Walker, L. R.; Chapin, F. S. 1986. Physiological controls over seedling growth in primary succession on an Alaskan floodplain. *Ecology*. 67(6): 1508-1523.
- Walker, D. A. 1987. Height and growth rings of *Salix lanata* ssp. *richardsonii* along the coastal temperature gradient of northern Alaska. *Canadian Journal of Botany*. 65(5): 988-993.
- Weber, A.; Karsisto, M.; Leepanen, R.; Sundman, V.; Skujins, J. 1985. Microbial activities in a histisol: effects of wood ash and NPK fertilizers. *Soil Biology and Biochemistry*. 17(3): 291-296.
- West, A. 1985. A review of insects affecting production of willows. Newfoundland Forest Research Center Information Report N-X-232. Canadian Forestry Service. 82 p.
- Wijk, S. 1986. Influence of climate and age on annual shoot increment in *Salix herbacea*. *Journal of Ecology*. 74(3): 685-692.