cover by the beginning of June and was fully developed by mid-July or earlier. Its development was faster than that of lady fern or thimbleberry (DeLong 1988). At mid to high elevations, fireweed communities may not reach their maximum height until mid-summer (Douglas 1972). Aerial shoots begin to wither in late July or early August and all have died back by late September or early October (Myersough 1980; Schmidt and Lotan 1980).

The flowering season extends from June to September because the inflorescence begins to flower at the base and continues to elongate during the summer, producing blossoms at the tip of the plant long after the basal fruits have ripened and released their seed (Clark 1976). In the intermountain U.S., seed ripening begins in late July (Schmidt and Lotan 1980). Seeds are released throughout the late summer until after the aerial shoots have withered in autumn.

REPRODUCTION

Seed Production and Dispersal: The plants can flower in their first year of growth from seed. Production of seeds is usually copious in temperate environments. There are an estimated 250–500 seeds in each capsule, and estimates of seed production for each live stem range from 20 000 to 80 000 or higher. The plumed seeds are dispersed by the wind and are very slow to settle (Salisbury 1961; Mosquin 1966; Myersough and Whitehead 1966; Myersough 1980). Seeds often reach high altitudes and commonly are dispersed in the order of 100–300 km (Soltrek and Andersson 1987). Fireweed accounted for 63% of the seed obtained in seed traps 1 year after fire at a northern Saskatchewan site (Archibald 1980). This represented 5.66 million seeds per hectare. At the northern limits of its range, fireweed may not produce ripe seeds regularly (Mosquin 1966; Myersough 1980; Fredskild 1984).

Seed Viability and Germination: Seeds are capable of germinating immediately on release, but best germination rates often occur approximately 3 months after dispersal (Myersough 1980). Most fireweed seeds germinate within a year of dispersal (Granstrom 1987), but germination can continue at reduced rates for up to 18 months (Myersough 1980). Seeds most often germinate in late summer or early autumn following summer fires, or the following spring.

Seeds must be at or near the soil surface to germinate successfully. On the south coast of British Columbia and in the SBS zone, fireweed emerged from mineral soil and from depths of less than 5 mm in the forest floor (McGee 1988b; E. Hamilton, pers. comm., July 1989). Germination is most successful on moist, open sites with few initial plant competitors (van Andel and Rozema 1974). However, Granstrom (1987) noted that fireweed germinates freely in closed vegetation. In the laboratory, germination of fireweed was greater under either 50 or 80% shade levels than under no shade (McGee 1988b). Seed germination may be reduced by leachates from conifer leaves and litter (Jobidan 1986).

Germination is stimulated by light, a chilling period, and treatment of the seed in dilute acid (Myersough 1980). Optimum temperatures for germination are between 15 and 30°C. Fireweed seed does not germinate under dry soil conditions (Myersough and Whitehead 1966). Oberbauer and Miller (1982) found that no germination occurred when soil water potentials were below -3 bars. Increased nutrient availability may improve germination in laboratory experiments (Myersough and Whitehead 1966). However, field experiments have not shown improved germination following nitrogen fertilization of established communities due to competition for water in these populations (van Andel and Rozema 1974).

Archibald (1980) found viable buried seed in soil cores taken immediately following a fire in northern Saskatchewan. He speculates that seed banking may account for the rapid invasion of fireweed on burned sites. In the SBS zone some fireweed seeds seem to work their way down through the soil to a depth where they can survive a burn (E. Hamilton, pers. comm., July 1989).

Vegetative Reproduction: Fireweed relies on large quantities of seed to colonize disturbed areas, but once it arrives on a site, expansion of the population is accomplished by vegetative reproduction. New shoots arise each year from buds located at the base of old stems, and on the horizontally spreading root system 2–8 cm below the soil surface. The root system is perennial and with each year it spreads further outward from the original seedling. New plants are created when they become detached from the parent plant through death of old roots or through disturbance. In an established colony of fireweed, vegetative reproduction occurs much more extensively than does reproduction by seed (Moss 1936; Myersough 1980).
PESTS

Myerscough (1980) provides a comprehensive list of the many insects and diseases found on *E. angustifolium* in Britain.

EFFECTS ON CROP TREES

*Competition:* Fireweed is considered to be a species of low competitive ability because it is a pioneer of recently disturbed sites and will not invade sites with previously established vegetative cover (Mosquin 1966; Watson et al. 1980). However, in the early stages of stand development it can be an important competitor.

Fireweed is of more concern in the interior than on the coast because it is ubiquitous there, it often dominates sites for a decade or longer, and it may overtop slow-growing seedlings for 10 or more years following establishment. On the south coast, fireweed can be outgrown by more competitive woody brush within 1–3 years.  

Fireweed cover establishes early in the growing season. DeLong (1988) found that fireweed had reached 30% of its maximum by May 26, and 90% of its maximum by July 12. In comparison, thimbleberry had attained only 2% of its maximum on May 26 and 68% on July 12. However, although fireweed is at its maximum level for a greater proportion of the growing season than thimbleberry, its narrow-leaved, single stalks do not create the extreme degree of light competition caused by the multi-layered, continuous canopy of well-developed thimbleberry plants.

Dense cover of fireweed may cause substantial reductions in the amount of light received by overtopped conifer seedlings. Light levels of less than 5% of full sunlight have been recorded under dense patches of fireweed (Comeau 1988).

Throughout British Columbia, fireweed can injure young seedlings through snowpress (J. Pollack, pers. comm., Jan. 1985). Douglas-fir and western larch are particularly susceptible because young seedlings are flexible and spindly (D. Lloyd, pers. comm., Nov. 1984). However, widespread snowpress damage has also been observed in Engelmann spruce seedlings on mesic and subhygic sites in the ESSF zone. Reduced light levels beneath dense fireweed canopies results in the development of long spindly conifer stems which are more susceptible to snowpress damage. Physical damage due to fireweed appears to be greatest on wetter hygrotopes in substunes where rainfall and snowfall is high.

Competition between fireweed and conifers for moisture and nutrients has not been demonstrated in British Columbia. However, fireweed grows vigorously and may tie up nutrients. This may limit availability of nutrients, such as nitrogen and phosphorus, to other plants (van Andel and Nelissen 1979).

*Beneficial Effects:* A cover of fireweed may delay development of shrubby vegetation on cleared or burned areas (see, e.g., Stickney 1981), thus allowing planted conifers to gain dominance of a site. Fireweed's extensive root system helps to bind soil and reduce erosion (Watson et al. 1980). Invasion by fireweed undoubtedly increases the organic matter content of severely burned or otherwise disturbed sites. Nutrients are stored by fireweed and become available to conifers in subsequent years as the fireweed declines. This nutrient storage is particularly important on poor sites (T. Lewis, pers. comm., May 1989).

RESPONSE TO DISTURBANCE OR MANAGEMENT

*Forest Canopy Removal:* Fireweed aggressively colonizes logged areas (Mosquin 1966). Colonization is achieved primarily by seeding-in, but where fireweed already exists prior to canopy removal, it is able to expand by means of its spreading root system (McLean 1979; Myerscough 1980; Rowe 1983). The degree of ground disturbance caused by logging or site preparation influences the amount of fireweed invasion. In the ESSF zones in the southern Interior, virtually all summer-logged or site-prepared areas become dominated by fireweed immediately after disturbance. On the other hand, sites logged in the winter, when deep snow prevents disturbance of the ground vegetation and soil, often remain covered with the ericaceous vegetation that typically dominates the understory of Engelmann spruce–subalpine fir forests (J. Mather, pers. observ.).

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130 Ibid.
In Eis' study (1981) of four site types in the SBS zone north of Prince George, fireweed was absent from all sites prior to logging. He observed that fireweed's "first few seeds arrive in the fall of the first year following winter logging and germinate in the spring of the second year. Its presence is most noticeable during the third year after logging and . . . it appears in great numbers during the fourth year." Six years after logging, fireweed accounted for more than 60% of the herbaceous ground cover on the Cornus-Moss site and 50% on the Dryopteris-Aralia site, but it was less than 20% of the cover on the Devil's club site and was not a significant competitor on the Alluvium site. This study demonstrates that fireweed is able to exploit a vacant niche rapidly, but is unable to compete where vegetation is already well established. The Cornus-Moss type had a low diversity and cover of vegetation immediately after logging and fireweed readily became dominant. In contrast, shrubs and herbs were already well established on the Alluvium site and fireweed was unable to move in. Maximum cover of fireweed is usually achieved within 3–5 years of harvesting (Isaac 1940).

Fire: Fireweed is well known in western North America for its ability to invade recently burned areas (Mosquin 1966; Dymness 1973; Watson et al. 1980; Cholewa and Johnson 1983; Foster 1986; Stickney 1986). Its light seeds rapidly colonize vacant ground created by burning. Following fire it can form dense, uniform stands over vast areas. Cover, density, and production of fireweed are usually greatest on areas that suffer the most intense burns (Ahlgren 1960; Mueggler 1965; Morris 1970). Vegetative reproduction is also a prominent means of fireweed invasion and expansion following burning (J. Zasada, pers. comm., Sept. 1989).

Fireweed cover generally increases to a maximum within a few years of burning and may then either decline or remain static (Kellman 1969; Miller and Miller 1974; Tiedmann and Klock 1976; Bartos and Mueggler 1981; Stickney 1986). In a burned western hemlock–Douglas-fir site in the western Cascades in Oregon, fireweed cover averaged 11% after 2 years, 33% after 5 years, 23% after 10 years, 17% after 15 years, and 3% after 20 years (Stickney 1986). Burned sites in the ICH and ESSF zones in the Interior of British Columbia commonly develop much higher fireweed covers; however, overall trends in fireweed development appear to be similar. The longevity of fireweed dominance in seral communities depends on the rate of development of other herb and shrub species (Stickney 1986).

McLean (1969) classified fireweed as moderately susceptible to fire because most of its fibrous roots are located within the upper 5 cm of the mineral soil surface. In some cases, fireweed rapidly loses vigour and will not survive under regimes of frequent burning (Myerscough 1980); however, it has a very low flammability and can suppress fire in early successional vegetation types where it is abundant. The plant acts as a heat sink because of its high moisture content, and because there is little standing dead fuel (Sylvester and Wein 1981).

Cutting and Grazing: There are no published reports describing the response of fireweed to manual cutting. Impact is expected to be short-lived and minimal unless cutting is repeated within a short period of time. Vigorous fireweed that was cut with hoes in late June on two rich mesic sites in the ICH zone near Clearwater was 10–65 cm in height after 60 days (J. Mather, pers. observ.). However, in the McBride Forest District, fireweed cut in early June did not recover at all after 40 days (D. Salaya, pers. comm., July 1989). Fireweed does not survive continued grazing (Myerscough 1980). One year after sheep grazing near Clearwater, fireweed had lost a tremendous amount of vigour and frequency. Plants on grazed plots were only half as tall as plants on the undisturbed control. Sheep can consume a large volume of fireweed before plantation damage occurs (G. Ellen, pers. comm., July 1989). Cattle will graze fireweed throughout the growing season, particularly when plants are in flower (McLean 1979).

Herbicides: Glyphosate severely injures fireweed, but the plant is not effectively killed and reductions in cover are not long-lasting. Broadcast applications of 1.4–2.1 kg a.i./ha in August and September have typically reduced fireweed cover by 60 to 100%. Pretreatment cover is almost always regained after 2 or 3 growing seasons. Initial regrowth may be stunted or deformed, but by the time the original cover is regained, plants tend to be healthy and vigorous with many thick, branched stalks (D. Barron, pers. comm., May 1989; B. Raymer, pers. comm., June 1989; J. Wright, pers. comm., July 1989).131,132,133,134 Near Grand Forks,

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131 Dyke 1987.
133 Ladd 1989.
D. Barron (pers. comm., May 1989) found significant differences in fireweed control between spring and fall applications of glyphosate. Spring applications resulted in complete recovery of fireweed after 1 year, while fall applications gave good control for at least 3 years.

Broadcast applications of hexazinone have resulted in poor to excellent control of fireweed after one growing season. Rates of about 1 kg a.i./ha of undiluted liquid hexazinone have tended to cause little damage (less than 20% defoliation). Rates of about 2 kg a.i./ha have also tended to give unsatisfactory control, though in Saskatchewan, an application rate of 2.2 kg a.i./ha caused 82% defoliation after one growing season. Rates of 3–4.3 kg a.i./ha often result in good control; best control is achieved at the highest application rates.

Spot applications of hexazinone have resulted in variable control of fireweed. Best control has tended to result from a rate of 8 ml per spot and 2-m spacing. Information is lacking on the length of control provided by spot or broadcast applications of hexazinone; however, fireweed has completely recovered two seasons after low rates of application. Hexazinone is ineffective on sites with deep organic matter. Humus depths greater than about 8 cm have greatly reduced the effectiveness of the herbicide.

Laboratory experiments have been carried out to investigate the impact of several other herbicides on fireweed. Soil-acting compounds which were found to kill fireweed include: bromacil, cyanazine, ethofumesate, lenucil, oxadiazon, oxyfluorfen, propachlor, and simazine. Foliar applications of 2,4-D amine, mecoprop, trichlopyr ester, paraquat, and pentschior + chlorophan have been found to give effective control of fireweed (Turner and Richardson 1979; Bailey and Hoogland 1984).

Soil Disturbance: Fireweed rapidly seeds-in to exposed mineral soil (Watson et al. 1980). It also reproduces vegetatively from plant parts that have become detached from the parent plant during disturbance. Fireweed tends to reach higher densities on disturbed sites in the interior than on the coast.

Severe mechanical disturbance involving complete removal of the forest floor and compaction reduces the height and density of fireweed but is likely to be detrimental to conifer regeneration. In the Gaspé Region of Quebec, Mosquin (1966) observed that fireweed was growing poorly on exposed subsoil but had very good vigour on adjacent sidecast mounds of humus and topsoil.

Fertilization: Fireweed may increase in abundance where fertilizers are used in silviculture (Reinikainen 1964, cited by Myerscough 1980). Germination is improved on fertilized sites lacking vegetation (Myerscough and Whitehead 1967), but when plant cover is well established on a site, fertilization may not increase germination of fireweed (van Andel and Rozema 1974).

Other: Areas seeded to grass can have lower cover and frequency of fireweed than unseeded areas (Hernandez 1973, cited by Watson et al. 1980; Crane et al. 1983).

WILDLIFE AND RANGE

Food: Fireweed has low to moderate importance for many wildlife species in British Columbia. Browsing is seldom heavy or extensive. However, this plant can be an important browse for deer in the province (Singleton 1976; Rue 1978; Wills et al. 1980; Harvey 1981). It has moderate to low importance in summer and fall for moose (Singleton 1976; Harestad 1983) and Roosevelt elk. Fireweed is often grazed by elk in Montana (McLean 1979). Simpson and Woods (1987) found that caribou use fireweed in the spring near Revelstoke. Wolff (1978) observed that fireweed shoots made up 11% of snowshoe hares' diet in May but accounted for less than 3% of their diet the rest of the year.

Cattle will graze fireweed throughout the growing season, particularly when plants are in flower. Sheep can also be used to control fireweed (McLean 1979).

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135 Teskey and Masterson 1984b.
136 Fahlman and Herring 1985.
137 Teskey and Masterson 1984a,c; 1985b,c,d; 1986b,c.
138 Teskey and Masterson 1986b.
139 Teskey and Masterson 1985a.
140 Smith et al. (undated).
141 Balfour 1989.
Other Resources: The flowers are noted for their nectar production and are sought out by hummingbirds, bees, butterflies, and other insects. The fireweed complex provides habitat for many small mammals including deer mice, Oregon and Townsend voles, shrews, and chipmunks (T. Sullivan, pers. comm., April 1989).
Gaultheria shallon
(salal)

Distribution of G. shallon in British Columbia.
**Gaultheria shallon** Pursh.  

**Salal**

**DESCRIPTION**

Salal is an erect to nearly prostrate evergreen shrub, loosely to densely branched, and up to 2.5 m tall, sometimes forming impenetrable thickets. It has an extensive root system with spreading rhizome-like structures. The leaves are thick, leathery, and ovate, often with finely toothed margins. The pinkish, bell-shaped flowers are borne in terminal and subterminal, one-sided racemes. The fruit is a round, hairy, purplish-black, berry-like capsule (Szczawinski 1962; UBC Bot. Garden 1970).

**Variation:** No subspecies or varieties of salal are described in British Columbia (Taylor and MacBryde 1977). The presence of altitudinal ecotypes is possible but not probable, and the species apparently does not hybridize (Pojar 1974).

**DISTRIBUTION AND ABUNDANCE**

Salal occurs along the entire length of the B.C. coast in the CWH and CDF biogeoclimatic zones, seldom penetrating far inland. A single isolated population of the species is recorded from the Kootenay Lake area, but otherwise all records are from west of the Coast Mountains (Szczawinski 1982). It is extremely abundant in south coastal British Columbia but becomes less important on the mainland and inner islands of the north coast where it is rarely found at any distance from the shoreline.

**Altitudinal Range:** Salal is primarily a low-elevation species, becoming more restricted in elevation with increasing latitude. On the south coast it ranges from sea level to approximately 800 m (Lyons 1952), but on the north coast it rarely occurs above 100–200 m elevation.

**HABITAT**

**Climatic Relations:** The restricted range of salal suggests that it requires a humid to perhumid coastal climate with mild temperatures, little snow, and unfrozen soils in winter. In British Columbia, salal is most vigorous and abundant on Vancouver Island and adjacent coastal areas.

**Site and Soil Conditions:** Salal is a dominant understory plant in lowland coniferous coastal forests and is very abundant in open, shoreline habitats such as bluffs and rocky knolls (Calder and Taylor 1968). It grows on a wide variety of mineral and organic substrates including shallow rocky soils, sand dunes, glacial till, and peat. Soils supporting salal are most often Podzols, frequently with deep mor humus forms, but salal is also found on Brunisolic, Folicolic, and organic soils (see, e.g., Klinka et al. 1979).

On poor, shallow soils the plants often exhibit a low mat-forming habit, while on better deeper soils they become vigorous upright shrubs (UBC Bot. Garden 1970; M. Newton, pers. comm., Dec. 1984). Best growth in cultivation occurs on moist sandy or peaty soil. Salal frequently grows on decaying wood, particularly old stumps, and in extremely humid environments it can be found as an epiphyte on living trees (UBC Bot. Garden 1970).

**Nutrient Relations:** Salal can survive and grow under a wide range of nutrient conditions (Sabhasri 1961). Throughout its range, it is noted for its abundance on nutrient-poor sites (see, e.g., Klinka 1977a). Its abundance on these sites reflects a tolerance for nutrient-poor conditions but should not be construed as a preference for a low-nutrient environment. In fact, salal shows a definite growth response to additions of macronutrients, particularly of nitrogen (Sabhasri 1961; UBC Bot. Garden 1970). It does not grow well in limy soils (UBC Bot. Garden 1970).

**Water Relations:** Salal will survive and grow under a variety of soil moisture conditions but growth is most vigorous in moist conditions and the plant has poor vigour on shallow, droughty soils (Sabhasri 1961; Allen 1969; UBC Bot. Garden 1970; McMinn et al. 1976). In the Vancouver Forest Region, salal is found on soil moisture regimes ranging from very xeric to hygic sites. However, it tends to occur on the wetter sites in the driest CDF subzones, and it is most abundant on the driest sites in wet subzones of the CWH (Klinka 1977b).

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142 Banner et al. 1983.
143 Yole et al. 1982.
144 Banner et al. 1983.
Light Relations: Salal grows well in partial shade but is uncommon and has very low vigour under dense forest canopies. Increasing light intensity by reducing overstory shade increases the vigour and growth rate of salal (Sabharsi 1961; Stanek et al. 1979; Koch 1983), but in most cases best growth is in light shade rather than in full sunlight (UBC Bot. Garden 1970; USDA 1974; Koch 1983). This may reflect evaporative stresses rather than an intolerance of sunlight (Koch 1983). Sabharsi (1961) reports that germination and survival of salal seedlings is not affected by low light intensities, but Schopmeyer (1974) found that partial shade is needed to successfully establish salal seed.

Although these field observations indicate that salal is at least a moderately shade tolerant species, Sabharsi's (1961) laboratory research suggests that the photosynthetic and respiration characteristics of salal are similar to those of plant species classed as shade intolerant. Actively growing plants are very sensitive to light conditions and significantly increased in photosynthetic activity and seedling growth with increased light intensities up to the maximum level tested (400 ft-candles). At low light intensities (100 ft-candles) respiration appears greater than photosynthesis. Maximum growth occurs under red light.

Messier et al. 145 found dramatic differences in salal leaf morphology under different light intensities. At 1.8% full sunlight (80% canopy cover), leaves were almost 3 times larger in area than they were in a clearing. However, in deep shade (0.3% full sunlight) leaves were similar in size to those in the clearing. Leaves growing in 0.3% full sunlight were less than half the weight and about half the thickness of those in the clearing.

Temperature Relations: The geographic range of salal suggests that it may be sensitive to frost. This suggestion is supported by Sabharsi's (1961) observation that a short period of freezing temperature in the middle of May killed nearly all germinants.

GROWTH AND DEVELOPMENT

In nature, early growth of salal seedlings is very slow (M. Newton, pers. comm., Dec. 1984). Once established, the plant adds considerable biomass each growing season, but actual height increment is slower than for many other shrub species. Vigorous salal may grow to a height of over 2.5 m (Szczezawinski 1962), but most plants average 60–120 cm in height (Clark 1976). The average new shoot increment during a growing season in western Washington was 5 cm (Sabharsi 1961).

Leaves of salal normally live for 2–4 years and occasionally last as long as 6 years. Twigs survive for 16 years or more but only bear leaves during the first few years (Koch 1983). Individual plants survive for an indefinite period because of continued resprouting.

The root system of salal is very extensive. Plants expand outward by means of rhizome-like root structures. Shoots consisting entirely of new growth were found up to 2 m from the parent plant (Koch 1983).

The total weight of new leaves added to a site in western Washington during the growing season averaged 900 kg/ha, while the total weight of salal biomass was approximately 36 000 kg/ha. Total root biomass exceeded the weight of above-ground parts (Sabharsi 1961).

Phenology: Phenological development of salal is highly variable (Stewart 1974a). In Washington, vegetative buds burst in early April. Most rapid vegetative growth occurred from late April onward, peaking in early June (Sabharsi 1961).

Flowering can occur any time between March and July (USDA 1974) but commonly occurs during May and June in Alaska (Viereck and Little 1972). Near Vancouver, flowering took place between June 12 and July 4 in 1971 (Pojar 1974), while in western Washington, fruit set began by the third week of June (Sabharsi 1961). Fruits ripen between August and October and remain on the stem until December (USDA 1974).

REPRODUCTION

Seed Production and Dispersal: Pollination of salal flowers is by insects, primarily bumblebees and flies (Pojar 1974). The fruit is a many-seeded capsule with a fleshy outer calyx that forms a pseudo-berry. Fruits have

an average of 126 seeds each. Heavy crops of fruit are produced on a regular basis, but fruiting was not observed by Koch (1983) under canopies with greater than 30.3% closure. Dispersal of the seeds is by birds and mammals that feed on the sweet fruit (Sabharsi 1961; USDA 1974).

Seed Viability and Germination: The fruits of salal are persistent and seeds remaining on the plant are viable for a considerable time following ripening. In cold, dry storage, the seed will remain viable for several years, but viability diminishes more rapidly under most natural conditions. The seeds do not appear to require chilling to induce germination. Schopmeyer (1974) reported that moist, acid conditions under partial shade are needed for the successful propagation of salal from seed. A germination rate of 27–35% has been obtained from fresh seed under lighted conditions (Sabharsi 1961; USDA 1974). Germination rates of about 60% were obtained in a British Columbia nursery (C. Messier, pers. comm., July 1989).

Even though large quantities of seed are produced and numerous germinants may appear, very few seedlings survive due to limitations of dispersal, seedbed conditions, and sensitivity to environmental extremes. Best germination was observed on decaying wood, but survival and seedling development on this seedbed was poor. In Oregon, salal is reported to germinate well both in clearcuts and under mature Douglas-fir stands, but establishment is most successful in the understory of young Douglas-fir stands. Seedling production is insignificant as a means of reproduction on most sites where salal is already established (Sabharsi 1961; Stewart 1978; Koch 1983; McGee 1988a; Nuszdorfer and Nuszdorfer 1988).

Vegetative Reproduction: Once salal is present on a site, further expansion is almost exclusively by vegetative means (Sabharsi 1961; Koch 1983; McGee 1988a) including layering and sprouting or suckering from roots and stem bases. Vegetative respouting was an important mechanism for re-establishment of salal on the southern coast of British Columbia (McGee 1988b). Cuttings made from roots or stems readily form new roots and sprouts (Sabharsi 1961; Pojar 1974; Stewart 1974b; USDA 1974).

PESTS

Of the numerous diseases known to occur on salal, the most common and serious is the leaf spot fungus (Mycosphaerella gautheriae). The grey weevil also causes severe leaf damage to salal in southern British Columbia (UBC Bot. Garden 1970).

EFFECTS ON CROP TREES

Competition: Salal is a common and often serious competitor with coniferous tree species in low-elevation coastal British Columbia. Barker et al. suggest that the understory of 100 000 ha of cedar–hemlock forests in coastal British Columbia is dominated by salal. Over most of its range, salal is a competitor primarily on mesic and drier ecosystems, but it may occasionally become abundant on moister and richer ecosystems. Salal is capable of gaining nearly complete occupancy of a site and, unlike most other brush species, is relatively insensitive to nutrient or water levels (Sabharsi 1961). Competition is most severe during the early stages of stand development (Long 1977) but may continue through the rotation, particularly if the canopy is open enough to allow a well-developed understory of salal to persist (Stanek et al. 1979)

Several studies have shown that salal can be successfully controlled with herbicides, burning, or mechanical treatments, and that conifers typically show a positive response to salal eradication by the second year after treatment. Two years after a herbicide application, the average diameter of Douglas-fir seedlings was 37% larger where salal was removed than on an untreated control. On eastern Vancouver Island, reduction of salal cover by moderate and severe burns increased Douglas-fir height growth by about 40% while light burns increased height growth by only 12.5% (Vihanek 1985).

Salal is believed to provide serious competition for moisture on dry sites (Sabharsi 1961; Stanek et al. 1979). Price et al. (1986) showed that salal removal in the CDF zone increased Douglas-fir growth because of the higher soil water potential. However, salal is unlikely to compete with seedlings for water in the wetter CWH zone where soil water deficits are rare. During a typical summer drought, mechanical

146 Barker et al. 1987.
147 Wellman and Harrison 1987.
removal of salal provided Douglas-fir with 14% more water than on adjacent areas without salal removal, and it increased conifer growth (Kellihan 1985). Douglas-fir stem diameter growth and colour were enhanced in the second growing season following salal eradication in the CWH-dm subzone on southern Vancouver Island. The improved performance of Douglas-fir is likely due to greater soil moisture availability (B. D'Anjou, pers. comm., July 1989). Dunsworth obtained a 56% increase in stand volume in a 12-year-old Douglas-fir stand on eastern Vancouver Island 3 years following salal cover removal. He attributed some of the growth increase to lower moisture stress. Removal of salal had no significant impact on a 25-year-old Douglas-fir stand.

Salal can have an impact on the nutrient budget of conifers (Germain 1985; G. Weetman, pers. comm., Nov. 1984). Barker and Weetman found that 2 years after salal eradication on northern Vancouver Island there was a modest increase in nitrogen and phosphorus uptake in Sitka spruce, western hemlock, and western redcedar, and a modest increase in hemlock and cedar height growth (spruce growth response was not measured). The authors considered that effects of salal removal on nutrients are likely to be gradual, and that nutrient-stressed trees may respond particularly slowly to salal eradication.

Dense salal can lower soil temperatures and thereby reduce conifer growth by reducing root growth and mycorrhizal infection (Parke et al. 1983) or by reducing the activity of the microflora. On northern Vancouver Island, however, temperature differences under different salal covers were small and may not be biologically significant.

**Allelopathy:** A western Washington study (del Moral and Cates 1971) found no evidence of allelopathic chemicals in extracts of salal foliage and litter. Further research on the possibility of salal allelopathy is under way in British Columbia (L. Montigne, pers. comm., Feb. 1989).

**Beneficial Effects:** Sahasari (1961) could not demonstrate any negative impact of salal on Douglas-fir growth in his test plots in western Washington. In fact, control plots had significantly better growth than those plots where salal was manually removed. He noted that salal roots could make an important contribution to the organic matter content of the soil, and speculated that the loss of organic matter and associated nutrients caused by removal of the salal may have contributed to the poor growth of the seedlings.

**RESPONSE TO DISTURBANCE OR MANAGEMENT**

**Forest Canopy Removal:** Several studies indicate that salal biomass is inversely related to overstory cover, and salal will increase in cover, vigour, and height when the overstory cover is either reduced or totally removed (Sahasari 1961; Long and Turner 1975; Long 1977; Stanek et al. 1979; Black et al. 1980; Koch 1983; Gholz et al. 1985; Vales and Bunnell 1986, cited by Vales 1986). However, salal does not grow as rapidly as many other shrub species, and may take many years to become dominant above ground following clearcutting. Salal establishes itself relatively quickly below ground (C. Messier, pers. comm., July 1989).

Re-invasion of salal after logging occurs from rhizomes that were present in the undisturbed forest. Salal can only dominate clearcuts if it is not shaded out by the developing overstory. Salal cover and height were measured under four coniferous stand densities. Very open stands had 85% salal cover, open stands 75%, closed stands 45%, and very closed stands 1%. Differences in cover were caused by differences in light intensity. Salal height decreased with decreasing stand closure (increasing light). D. Harrison (pers. comm., May 1989) has also observed that overstory removal on northern Vancouver Island tends to increase cover and lead to reduced height of salal. Spacing on southern Vancouver Island in the CDF and CWH zones caused salal to increase in height after 1–2 years (R. Muller, pers. comm, July 1989). Messier et al. report that thinning practices that reduce the overstory canopy to below 80% may create conditions favourable for salal growth.
Fire: Light fires tend to increase salal cover above pre-burn levels. Fire stimulates resprouting from roots and stem bases (Sahsarsi 1961). In the Fraser Valley, salal cover increased from less than 10% before burning to 35–50% after 3–4 years and 85% after 9 years (Lafferty 1980). Similar results have been obtained on northern Vancouver Island (C. Messier, pers. comm., July 1989).

However, even on lightly or moderately burned areas, above-ground parts of salal can be slow to recover to pre-burn levels (G. Dunmore, pers. comm., Dec. 1984; B.M. Geisler, pers. comm., Jan. 1985). For example, moderate severity burns led to salal covers of 3% after 2 years, 1% after 5 years, 10% after 20 years, and 18% after 30 years (Schoonmaker and McKee 1988). Despite slow above-ground recovery, the below-ground environment is usually fully occupied by salal within 8 years of burning in cedar–hemlock sites in the CWH zone.154

Severe burns can reduce salal cover only if fire penetrates sufficiently deep to kill the roots. High severity burns on dry sites on eastern Vancouver Island have decreased salal cover by 80% compared to adjacent unburned areas. In contrast, low and moderate severity burns have decreased cover by only 40% compared to unburned areas (Vihanek 1985). In the CDF and CWH zones on southern Vancouver Island, severe burns have reduced sprouting of salal, while light burns have resulted in more intense sprouting (R. Muller, pers. comm, July 1989).

Cutting: Manual or mechanical cutting of salal can be expected to stimulate sprouting; the response may be similar to that following burning.

Herbicides: Conard and Emmingham (1984a) report that glyphosate causes light damage to salal. Salal was not damaged by glyphosate applied in September at 2 kg a.i./ha in the CWHwmb subzone on Vancouver Island.155 Moderate damage occurred 1 year after glyphosate was applied at 4 kg a.i./ha by backpack sprayer in late summer in the drier CWH subzone on eastern Vancouver Island (B. D'Anjou, pers. comm., July 1989).

Results from hexazinone applications are inconsistent. It is often described as ineffective at controlling salal (Newton and Knight 1981; Boateng and Herring 1990). However, an April ground application of 2 kg a.i./ha granular hexazinone for site preparation resulted in good control of salal near Chilliwack. Two years after herbicide application, salal biomass on the treated areas was about half that on the control.156 A backpack application of 4 kg a.i./ha hexazinone in February–March on southern Vancouver Island in a dry CWH subzone caused a 45% reduction in salal cover.

Conard and Emmingham (1984a) report that spring and summer applications of amitrole caused no visible injury to salal and that 2,4-D caused light damage.

Triclopyr ester (Garlon®) has been more successful than other herbicides in controlling salal.

Triclopyr ester in diesel applied at 4 kg a.i./ha using backpack sprayers reduced salal cover by 78%.157 Garlon® in diesel provided at least three seasons of salal control in a Douglas-fir–salal ecosystem on the east coast of Vancouver Island near Nanaimo.158 Application of 4 kg a.i./ha triclopyr ester in diesel oil at 100 L/ha in early spring or late summer reduced salal cover by 60–90% in the dry CWH subzone on Vancouver Island. Salal cover was reduced by only 40% when 100 L/ha mineral oil were used as the carrier instead of diesel oil. Reducing the concentration of chemical by using 150 L/ha diesel instead of 100 L/ha had no effect on results. Although above-ground parts of salal were well controlled, living root dry weight was 89% of that in an untreated control, indicating that roots continue to survive despite good foliar control (B. D'Anjou, pers. comm., July 1989).

Soil Disturbance: Any form of soil disturbance that causes mechanical damage to salal but does not physically remove it from the site can be expected to stimulate resprouting. Pieces of stems and roots that are detached from the parent plant and buried in soil will root and form new plants (Sabhrasi 1961). Backhoe

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156 Wellman and Harrison 1987.
158 Dunsworth 1996.
SALAL

site preparation (i.e., mixing organic and mineral soil layers) on a mesic CWH-wh site in the Queen Charlotte Islands initially reduced salal cover, but within 3 years it was rapidly invading (S. Craven, pers. comm., June 1989). Heavy scarification in the CDF and CWH zones on Vancouver Island has resulted in very slow re-invasion of salal (R. Muller, pers. comm., July 1989).

Fertilization: Salal responds to applications of fertilizer, particularly nitrogen, with increased above- and below-ground growth and vigour (Sabhrasi 1961; UBC Bot. Garden 1970). However, while Osmocote® substantially increased hemlock growth, it had no effect on salal 2 growing seasons after it was applied to western hemlock seedlings at the time of planting in the CWH zone on northern Vancouver Island (Nuszdorfer and Nuszdorfer 1988). In forest stands, applications of fertilizer that result in an increase in the density of the tree canopy may cause a decline in vigour and cover of the salal understory (Long and Turner 1975; Stanek et al. 1979).

WILDLIFE

Food: Salal is an important wildlife food in British Columbia. It is valuable to black-tailed deer year-round but is particularly important in winter (McTaggart-Cowan 1945; Brown 1961; Jones 1975; Singleton 1976; Rue 1978; Harvey 1981; Nyberg et al. 1986; Chambers 1988). Stems, leaves, blossoms, and fruit are consumed. Salal has been described as one of the 10 most important foods of black-tailed deer and has made up about 10% of its total diet (Brown 1961; Jones 1975). Salal is an important winter and spring browse for Roosevelt elk (Bailey 1966; Singleton 1976). It has made up 36–47% of the February diet of Roosevelt elk. Salal sprouts well after ungulate browsing (T. Lea, pers. comm., Feb. 1989).

Salal is browsed by some small mammals and birds. Its leaves and twigs are fairly important foods for mountain beaver (Banfield 1974), although this mammal has very limited distribution in British Columbia. King (1969) found that leaves and buds were important to ruffed grouse from March to late May at a Vancouver Island site and Zwickel and Bendell (1972) noted that incubating female blue grouse also consume salal.

Animals that consume salal berries play an important role in seed dispersal (Halverson (compiler) 1986). The berries are commonly eaten by grouse and other birds (Viereck and Little 1972). Adult blue grouse have shown strong selection for salal berries even when the plant has been available only in relatively minor amounts (King and Bendell 1982). The berries are an important food for blue grouse chicks from May to September on northern Vancouver Island. Salal berries have made up 19% of the early August diet and 45% of the late August diet of juvenile ruffed grouse on Vancouver Island (King 1969). Other animals eating the fruit include black bear, black-tailed deer, and red squirrel (USDA 1974).

Other Resources: Mountain beaver often use salal for the central portion of their nests (Martin 1971, cited by Chapman and Feldhamer (editors) 1983).

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159 Blower 1982.
160 Ibid.
161 Smith et al. (undated).
162 Ibid.
Lonicera involucrata
(black twinberry)

Distribution of *L. involucrata* in British Columbia.
**Lonicera involucrata** (Richards.) Banks

*Black twinberry*

(twinberry, honeysuckle)

**DESCRIPTION**

Black twinberry is a straggling to ascending deciduous shrub 1–3 m tall. Stems have opposite branching and are four-sided when young. The leaves are elliptic to obovate, and untoothed. The yellow, tubular flowers occur in pairs above conspicuous green or purple bracts. The "twin" fruits are black to reddish round berries with few seeds (Viereck and Little 1972; Hultén 1974).

**Variation:** There are several forms of *L. involucrata*. The form occurring in British Columbia is the typical var. *involucrata* (UBC Bot. Garden 1979).

**DISTRIBUTION AND ABUNDANCE**

Black twinberry occurs throughout British Columbia to approximately 57°N latitude. It is common on the coast and in the Interior and is found in all forested biogeoclimatic zones, but it is absent from northern subzones of the BWBS. It is also present in the Peace River valley and scattered in specialized habitats in the Stikine–I skut drainage, but it is apparently absent from the Fort Nelson and Liard River areas in the extreme north of the province (A. Ceska, pers. comm., Nov. 1984). As well, it is common in lowland areas of the Queen Charlotte Islands (UBC Bot. Garden 1979).

**Altitudinal Range:** Black twinberry is present from sea level to at least 1525 m in British Columbia (UBC Bot. Garden 1979).

**HABITAT**

**Climatic Relations:** The distribution of black twinberry suggests that it tolerates a wide range of climatic extremes but is not adapted to the extremely short growing season and harsh winter temperatures found in northern British Columbia and at high elevations. In various parts of its range, however, black twinberry appears to be prevalent in frost pockets or areas of cold air drainage (R. Coupé and A. Ceska, pers. comm., Nov. 1984).

**Site and Soil Conditions:** Black twinberry is a species of swamps, riparian habitats, alluvial soils, and moist woods (Lyons 1952; Viereck and Little 1972; Marchant and Sherlock 1984).

**Nutrient Relations:** Clark (1976) observes that black twinberry favours rich soil. Ecosystem associations in which black twinberry appears as a characteristic understory species typically have a medium to very rich nutrient status (Comeau et al. 1982; Pojar et al. 1982).

**Water Relations:** Black twinberry is described as being a species of moist or wet soils (Lyons 1952; Viereck and Little 1972; Marchant and Sherlock 1984). In climatically humid areas such as the Interior Wet Belt it occurs on submesic to subhydric hygrotopes, whereas in climatically drier areas it tends to be restricted to hygic and subhydric sites (Comeau et al. 1982; Angove and Bancroft 1983).

**Light Relations:** Black twinberry will tolerate semi-shade (Marchant and Sherlock 1984) but is most vigorous in open situations where sufficient moisture is available.

**Temperature Relations:** No information.

**GROWTH AND DEVELOPMENT**

**Phenology:** Black twinberry breaks bud in April in the Kimsquit Valley on the central British Columbia coast and between early and late May on the east slope of the U.S. Rocky Mountains (Schmidt and Lotan 1980). In the Rockies, leaves are fully grown by mid-June, and leaf-fall occurs between late August and late September. In contrast, at Kimsquit some leaves are fully expanded by mid-April. In early August, the first leaves begin to turn yellow and most shrubs retain some leaves until October.

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164 Ibid.
165 Hamilton 1984.
BLACK TWINBERRY

Flowering begins after the leaves open. In the Rocky Mountains, flowering occurs between late May and early July (Schmidt and Lotan 1980). On the British Columbia coast flowering can begin in April\textsuperscript{166} and some plants can continue to flower until the end of August even as the fruits ripen (Clark 1976). Fruits ripen from mid-July to late August at low elevations in coastal British Columbia (Marchant and Sherlock 1984)\textsuperscript{167} and throughout July only in the eastern Rockies (Schmidt and Lotan 1980).

REPRODUCTION

Seed Production and Dispersal: Each fruit has four to five seeds. Dispersal is primarily by birds and mammals (USDA 1974; UBC Bot. Gardens 1979); cedar waxwings are especially fond of the berries (Marchant and Sherlock 1984).

Seed Viability and Germination: Air-dried seeds can be stored for up to 15 years at 1–3°C without loss of viability, and for several years at warmer temperatures (USDA 1974; Marchant and Sherlock 1984). The lengthy period of viability suggests that black twinberry may be a seed banker; seeds remain buried in the forest floor until conditions become conducive to germination. The seeds have some embryo dormancy and require a chilling period of 45–60 days for satisfactory germination to occur. A scarification treatment of the seed coat also improves germination. High germination percentages (56–80\%) have been obtained under artificial conditions (USDA 1974; Marchant and Sherlock 1984).

Vegetative Reproduction: Several Lonicera species sucker from a spreading root system (Jackson 1974), but there are no reports of this for *L. involucrata*. Artificial cuttings taken during the dormant season rooted well when a rooting hormone was applied (Marchant and Sherlock 1984).

PESTS

Marchant and Sherlock (1984) report that young plants are susceptible to leaf miner and that a leaf-deforming fungus which slows growth is prevalent in the southern Interior. The following diseases have been identified on *L. involucrata* in the wild in British Columbia: *Kabatia lonicerae* var. *involucrata* (leaf spot), *Microsphaera penicillata* (powdery mildew), *M. alni*, *Leptophaeia dumetorum*, and *Ophiobolus minor* (UBC Bot. Garden 1979).

EFFECTS ON CROP TREES

Black twinberry is a competitor of moderate, but not major, importance throughout most of its range in the province. It is primarily found as a component of a complex, vigorous brush community on moist productive ecosystems in many biogeoclimatic zones (C. Delong, R. Coupé, and D. Lloyed, pers. comm., Nov. 1984; J. Pollack, pers. comm., Jan. 1985). Very little is known about its competitive ability or any negative or beneficial effects that it may have on coniferous tree growth.

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: Eis’ study (1981) in the SBS zone north of Prince George showed that black twinberry was present and numerous on both the Devil’s Club and Alluvium site types prior to logging. Six years after logging, black twinberry had become common on the *Aralia–Dryopteris* site type, had greater than 25\% cover on the Devil’s Club site type, and was the dominant species (40\% cover) on the Alluvium site type. Twinberry had produced a small quantity of seed and had almost reached a mature height on the Alluvium site by the end of the first season following logging. Shrub density increased for several years following logging and was 120 cm high within 2.5 years. It took the shrubs 7 years to reach this same height on the Devil’s Club site type.

Fire: On boreal sites, severe burns often eliminate twinberry, but light burns stimulate vigorous resprouting (Ahlgren 1960). In the oak fern community in seral SBSwk ecosystems, black twinberry was consistently present after burning. In the Queen’s Cup ecosystem, it was more commonly killed by burning and resprouting and growth of the species was fairly slow. Black twinberry reached a maximum height of about 1.5 m after burning in the SBSwk subzone. Twinberry was 1.2 m tall within 2 years on burned SBSmk

\textsuperscript{166} Hamilton 1984.
\textsuperscript{167} Ibid.
BLACK TWIJBERRY

Horsetail sites and after 7 years on burned SBSmk Devil's Club sites. Burned sites in the SBSwk and SBSmk subzones with the greatest cover of twinberry were in the Horsetail association. Re-establishment from buried seeds did not occur during the first 10 years after burning in the SBSwk subzone (Hamilton and Yearsley 1988).

Cutting: No information.

Herbicides: Broadcast applications of glyphosate applied from mid-July to the fall have caused very severe injury to twinberry in British Columbia (J. Pollack, pers. comm., Jan. 1989; D. Barron, pers. comm., May 1989; Boateng and Herring 1990). Broadcast applications of 1.5–2.1 kg a.i./ha have been effective. Spot or broadcast applications of hexazinone have caused variable injury to twinberry in British Columbia (Boateng and Herring 1990). A fall application of 3.6 kg a.i./ha hexazinone in the SBS zone in the Prince Rupert Forest Region resulted in moderate control of twinberry in the third growing season. Third-year canopy cover and height of twinberry were near or greater than pre-treatment levels following several methods of hexazinone application (granular and liquid; spot and broadcast; 2 and 4 kg a.i./ha) carried out in mid-April in the CWH zone near Chilliwack.

Soil Disturbance: Twinberry increased in cover after intense mechanical site preparation in the SBSmk2 variant in the Mackenzie Forest District (D. Greenley, pers. comm., May 1989).

WILDLIFE

Food: Black twinberry is not a common browse species in British Columbia (T. Lea, pers. comm., Feb. 1989) but is a moderately important winter food for Roosevelt elk and moose. The berries are the most common part of the plant eaten and provide summer food for birds, black bears, grizzly bear, and other mammals on the coast (USDA 1974; UBC Bot. Garden 1979; Marchant and Sherlock 1984; National Wildlife Foundation 1987; Lofroth 1988). However, it can be unpalatable to snowshoe hares in Alberta (Keith et al. 1984, cited by Carreker 1985).

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168 Herring 1984a.
169 George 1989.
170 Newhouse 1988b.
171 D'Anjou 1988b.
172 Blower 1982.
173 B.C. Min. Environ. (undated).
Menziesia ferruginea
(false azalea)

Distribution of *M. ferruginea* in British Columbia.
Menziesia ferruginea Sm.

False azalea
(Rusty menziesia, Pacific menziesia)

DESCRIPTION

False azalea is an erect, spreading, deciduous shrub to 2 m tall with slender, widely forking, opposite branches. Young twigs are finely pubescent and older branches are smooth or have loosely shedding bark. Leaves are thin, oblong to obovate, up to 6 cm long, and slightly toothed along margins. Branches are opposite, but leaves appear to be arranged in whorls. Leaves sometimes have a distinct bluish colouration. The small, yellowish-red, bell-shaped flowers are borne in small terminal clusters on shoots of the previous year. The fruit is a thin-walled, reddish-brown ovoid capsule that splits along four partitions at maturity. The opened dry capsules often persist throughout the winter (Szczawinski 1962; Viereck and Little 1972).

Variation: Two subspecies of false azalea are found in British Columbia. Menziesia ferruginea ssp. ferruginea is found along the coast and in the central Interior, while ssp. glabella is found in southeastern B.C. only. The latter subspecies is differentiated from the former by its more rounded leaves and greater pubescence (Szczawinski 1962; Taylor and MacBryde 1977).

DISTRIBUTION AND ABUNDANCE

False azalea occupies coastal and mountain areas throughout the moist regions of British Columbia. It extends along the entire length of the province on the west side of the Coast Mountains and is also present in the Interior Wet Belt. It is rare, however, in the Interior Plateau and all of northern British Columbia east of the Skeena Mountains (Szczawinski 1962; Hickman and Johnson 1969). False azalea is present in many biogeoclimatic zones except the PP, BG, IDF, BWBS, and SWB, but it is abundant in only the CWH, MH, andESSF zones.

Altitudinal Range: Along the coast, false azalea is common from sea level to the alpine tundra, although it is generally absent in the CDF and drier CWH zones of the south coast. East of the Coast Mountains, it tends to be found only at higher elevations, above approximately 900 m in the ICH and ESSF zones.

HABITAT

Climatic Relations: False azalea appears to require a fairly humid environment where only minor climatic moisture stresses are experienced during the growing season. This would explain why it occurs to sea level along most of the coast but retreats to more moist mountainous areas inland and along the Strait of Georgia. The dry central Interior of the province is described as "climatically unsuitable" for Menziesia ferruginea by Hickman and Johnson (1969). These authors report that throughout western North America it becomes dominant in areas of high rainfall or persistent fog or mist. False azalea is also apparently unable to tolerate the extremely cold boreal climate of northeastern British Columbia. Evidence from other species suggests that adequate snow cover may be a critical factor in protecting false azalea from desiccation (Bowers 1960b).

Site and Soil Conditions: False azalea is well developed in mesic habitats but can occur on a wide variety of sites including shallow rocky and deep wet soils (Hickman and Johnson 1969). Soils on which false azalea is typically found are predominantly Humo-Ferric or Ferro-Humic Podzols with a mor humus (see, e.g., Pajar (editor) 1983; Haussler et al. 1984).

Nutrient Relations: In British Columbia, ecosystem associations on which false azalea is a significant understory component often have very poor to medium nutrient status (see, e.g., Klinka 1977b), but it can occur over a wide range of nutrient regimes. False azalea is typically found on sites with low pH (Brooke et al. 1970; Haussler et al. 1984). In the cedar-hemlock forests of northern Idaho, it is associated with soils low in potassium and with a high organic matter content (Mueggler 1965).

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174 Banner et al. 1964.
175 Ibid.
176 Banner et al. 1983.
177 Lloyd (compiler) 1984.
FALSE AZALEA

Water Relations: In moist climates, false azalea is most abundant on well- to moderately well-drained soils with a more-or-less mesic moisture status (Hickman and Johnson 1969; Viereck and Little 1972; Klinka 1977b). In very wet climates, both in the Interior and on the outer coast, false azalea can be very abundant on xeric sites (Angove and Bancroft 1983). The species is also abundant in poorly drained coastal bogs (Hickman and Johnson 1969).

Light Relations: False azalea is a common species of deeply shaded climax western hemlock forests (Szczawinski 1962; Viereck and Little 1972). Its ability to persist in these heavily shaded forest understories in which light intensities are typically 5% of full light (P. Alaback, pers. comm., Dec. 1984) indicates that it is very shade tolerant. However, the species usually displays its best vigour in the partially shaded conditions of forest openings among the tree clumps characteristic of the mature subalpine forests of the ESSF and MH zones (Brooke et al. 1970; Caza, pers. observ., 1987).

Temperature Relations: No information.

GROWTH AND DEVELOPMENT

False azalea can reach heights of 3 m at maturity (Viereck and Little 1972), but it is usually no more than 2 m tall (Clark 1976). The longevity of false azalea plants is not known, but other co-occurring ericaceous species may live over 100 years and Alaback’s (1982) study indicates that plants survive at least 30 years in northern forests.

Phenology: In Alaska, false azalea flowers from late May through July. Leaves expand in early June at the time flowers open; they begin to senesce in mid-August and September at high elevations in the province (C. Caza, pers. observ., 1987). The capsule matures in July or August (Viereck and Little 1972).

REPRODUCTION

Seed Production and Dispersal: Numerous tiny seeds are produced in capsules, which open through natural dehiscence at maturity (Szczawinski 1962). Seed is dispersed by gravity and wind.

Seed Viability and Germination: No information.

Vegetative Reproduction: False azalea sprouts from root crowns and adventitious stem buds after destruction of above-ground stems (Miller 1977; Coates 1987). The species also appears to be capable of layering by forming roots from adventitious buds along stems (C. Caza, pers. observ., 1987). Layering is an effective means of growth and expansion at high elevations where heavy snow loads keep branches close to the ground. False azalea does not spread by means of rhizomes (Miller 1977).

EFFECTS ON CROP TREES

Competition: There have been no reports of dense, pure populations of false azalea, and the shrub is rarely the most abundant or aggressive member of shrub complexes (Miller 1977; Stickney 1980; Coates 1987). Nevertheless, false azalea is a member of the ericaceous shrub complex that is abundant on well-drained, usually more-or-less mesic sites along the coast of British Columbia and in moist mountainous areas of the Interior. The complex, common in the MH and ESSF zones, commonly includes Rhododendron albilorum and Vaccinium spp. In coastal British Columbia, the Vaccinium-Menziesia shrub community is rarely a specific target of vegetation management efforts because it is perceived as having much less impact on the regeneration of conifers than the brush communities on productive low elevation sites. In contrast, in some areas of the southern Interior, such as the ESSF zone in the Kamloops Forest Region, the Rhododendron albilorum-Vaccinium spp.–Menziesia ferruginea complex is considered a major brush problem.

Although the complex in which false azalea occurs is very abundant and often dominates logged sites, research on its effects on the establishment and growth of crop trees is limited. Coates (1987) found that regrowth of false azalea after manual cutting or mechanical scarification is slow, indicating that conifer

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178 Banner et al. 1983.
179 Delong et al. 1984.
seedlings planted promptly after shrub reduction treatments are unlikely to be overtopped by the shrub. This suggests that it is relatively easy to maintain control of above-ground competition from false azalea. On ESSF sites where false azalea and its associates are left untreated, Coates (1987) suggests that shading is the most important mechanism of above-ground competition. Shading reduces light available to conifer seedlings and also reduces soil temperature throughout the growing season.

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: The response of false azalea to overstory removal depends on the degree of ground disturbance. Logging on snow causes little destruction to mature false azalea in subalpine fir–Engelmann spruce forests. Summer logging damages false azalea, at least in patches, and commonly results in very slow recovery of the shrub and invasion of perennial herbs including Epilobium angustifolium and Valeriana sitchensis. In the cedar–hemlock forests of northern Idaho, there was no significant difference between the cover and frequency of false azalea on logged and unlogged sites (Mueggler 1965). On the central Oregon Coast, Alaback and Herman (1988) found that the percent cover of false azalea was greatest on heavily thinned plots and least in the undisturbed forest. Biomass of false azalea in early successional stands (up to 30 years) in southeastern Alaska was 3 times greater than the biomass in climax western hemlock–Sitka spruce forest (Alaback 1982).

Fire: False azalea is a fire-sensitive species (Stickney 1981). Miller (1977) speculates that it will sprout from the root crown after a burn but will not produce suckers. Fire appears to have totally removed this species from experimental plots in Washington and Oregon for up to 16 years (Morris 1970). In the ESSF zone in British Columbia, burning provides very effective control of false azalea for at least 10 years even though it is not completely killed (J. Wright, pers. comm., July 1989). In western Montana, Stickney (1981) found that survival of false azalea was low and it was very slow to develop after fire, especially on areas which had been severely burned. On the other hand, Mueggler (1965) reported no significant difference in cover and frequency between burned and unburned areas in northern Idaho.

Cutting: False azalea does not respond vigorously to cutting. Stems cut in June on sites in the ESSFwc subzone regrew 2–75 cm by August of the same year. Average regrowth was 30 cm, or about 19% of the original height (C. Caza, pers. comm., July 1989). False azalea sprouted 40 cm in 1 year following a manual cutting treatment in the Penticton Forest District. After false azalea was cut in early July at another ESSFwc site, new shoots averaged 1.3 cm in height by the end of the second growing season (Coates 1987). This represents slower growth on this site than that of associated shrubs (Rhododendron albiflorum, Vaccinium membranaceum, Vaccinium ovalifolium). Almost all new shoots arose from buds on existing stems rather than as sprouts or suckers from the soil. Height growth of false azalea was more an average of 5.6 shoots per stem, twice as many as any of the associated shrubs. A second cutting 1 year after the first did not affect regrowth vigour (Coates 1987).

Herbicides: False azalea was very susceptible to broadcast applications of 2.1 kg a.i./ha glyphosate applied in the ESSF and ICH zones in September near Revelstoke, Salmon Arm, Blue River, and Penticton (J. Wright, pers. comm., July 1989). Control was effective for at least 2 years. Lower application rates are reported to cause partial control and more vigorous resprouting. For example, Simard reported that September applications of 0.7 and 1.4 kg a.i./ha glyphosate resulted in 70% control after 2 years, with vigorous sprouting 2 years after the lowest application rate. In the same study, application of 2.1 kg a.i./ha provided 90% control and only weak sprouting after 2 years.

1 Mather 1986.
3 Dyke 1987.
4 Simard 1986.
5 Ibid.
FALSE AZALEA

Soil Disturbance: In the ESSFwc subzone near Clearwater, scarification that removed tops or uprooted entire false azalea plants caused severe damage. Few new shoots were produced by surviving plants. Two growing seasons after treatment, there was no sign of new sprouts from the soil (Coates 1987).

WILDLIFE

Food: False azalea is seldom browsed and is generally considered unimportant to ungulates in British Columbia. However, it can be a moderately important browse for Columbian black-tailed deer and Roosevelt elk. 186 Although it is considered relatively unpalatable to Sitka black-tailed deer, the overpopulation of these ungulates on the Queen Charlotte Islands has depleted the species in many places. 187 In Alaska, false azalea was much more abundant outside deer enclosures than where deer were allowed to feed (Hanley 1987).

186 Blower 1982.
Polystichum munitum
(sword fern)

Distribution of P. munitum in British Columbia.
Polystichum munitum (Kauf.) Presl.

Sword fern

DESCRIPTION

Sword fern is a large fern with stiff, erect fronds up to 1.8 m tall, rising from a stout, woody rhizome. The blades are evergreen, linear to lanceolate, with numerous toothed, sharp-pointed pinnae. The pinnae have a characteristic hilt-like projection near the base (Taylor 1973a; Wagner 1979).

Variation: Size and frond shape vary widely, particularly in response to environmental conditions (Taylor 1973a). A type of sword fern with a very narrow linear blade and closely crowded overlapping pinnae is common in exposed locations. There is some disagreement as to whether this fern represents an ecological form of P. munitum (forma imbricans) produced in response to extreme environmental conditions (Frye 1934; Taylor 1973a; Taylor and MacBryde 1977), or whether it is a distinct taxon (Wagner 1979).

DISTRIBUTION AND ABUNDANCE

Sword fern is widespread and common west of the Coast Mountains along the entire length of British Columbia, including the Queen Charlotte Islands. It is also found in the moist forests of the west Kootenays. In the U.S., the species extends inland to northern Idaho and Montana (Wagner 1979). Sword fern is abundant in the CDF and CWH biogeoclimatic zones and uncommon in the MH and ICH zones.

Altitudinal Range: Sword fern is primarily a low elevation species in British Columbia. In southwestern British Columbia it is rarely found at elevations above 900 m (Brooke et al. 1970). On the north coast it is even more restricted in elevation, rarely found more than 100 m above sea level.

HABITAT

Climatic Relations: The geographic and altitudinal range of this species suggests that it requires a humid coastal climate with mild winters. It also occurs in areas of moist, relatively mild continental climate in Idaho and Montana and adjacent areas of British Columbia, but in these areas it tends to favour the shaded, moist northern aspects (Mueggler 1965). The evergreen frond of sword fern may be a limiting factor in its ability to survive in areas with cold winters.

Site and Soil Conditions: Sword fern will grow on a wide variety of parent materials including exposed bedrock, but the most luxuriant growth is found on deep loamy soils, especially those developed on fluvial parent materials (see, e.g., Klinka and Carter 1980).

Nutrient Relations: Sword fern grows best and is most abundant on fertile soils (Taylor 1973a; McMinn et al. 1976). Ecosystem associations with this species as a characteristic understory species are usually medium to very rich in nutrients (see e.g., Klinka 1977a). When abundant and vigorous, sword fern is often considered to be an indicator of nutrient-rich sites.

Water Relations: Sword fern is characteristically found in moist or shaded locations, where drainage is good but little moisture stress is encountered. In the CDF zone of southern Vancouver Island, where summer moisture deficits are common, it is found only where seepage water augments the soil moisture supply (McMinn et al. 1976). In wetter climates it is less restricted by soil moisture supply. Ecosystem associations in which sword fern is abundant typically have a mesic to hygric moisture status (see e.g., Klinka 1977a).

Light Relations: Sword fern is apparently shade tolerant since it typically occurs in the understories of mature forests and favours shady sites or north aspects (Mueggler 1965; Taylor 1973a). In clearcut areas it often prefers protected, shaded locations. This probably reflects sensitivity to high evapotranspirative losses rather than intolerance of light itself. When plants of P. munitum are subjected to increased insolation through removal of overstory shade, the fronds become dwarfed and more erect and the pinnae become crisped (Frye 1934; Taylor 1973a; Wagner 1979).

Temperature Relations: The evergreen frond of sword fern is presumably at least moderately resistant to frost.

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188 Yole et al. 1982.
189 Brand 1984.
Sword fern

GROWTH AND DEVELOPMENT

See Athyrium filix-femina for a simplified explanation of the fern life cycle. The growth and development of sword fern is probably quite similar to that of lady fern except that sword fern fronds are evergreen and thus persist for several years. At maturity the frond is 60–180 cm in length and approximately 25 cm wide (Taylor 1973a; Wagner 1979).

Phenology: Stewart (1976) reported that, in Oregon, sword fern fronds were partially unfurled on May 26. By July 28, the fronds were mature and spores were nearing maturity.

REPRODUCTION

Spore Production and Dispersal: Most medium-sized forest ferns begin to produce spores at between 1 and 5 years of age and spore production takes place very regularly from year to year. The vigour of the plant, as influenced by its habitat, is an important determinant of plant fertility. Most ferns similar in size to sword fern produce tens of millions of spores on each frond. The tiny spores are ejected into the air when mature and are carried away by gravity, wind, water, or animals. Evergreen ferns like Polystichum can retain some spores on the fronds over winter for dissemination the following spring. Fern spores are capable of travelling thousands of miles, but in forests there may be a lack of air currents to carry them aloft. Airborne spores are often brought to earth during rainstorms (Page 1979).

Spore Viability and Germination: Fern spores in a dry, resting state are resistant to physical extremes and can withstand intense radiation and very low temperatures. They are reportedly very sensitive to temperatures above 55°C (Kato 1963; Miller 1968). Under ideal conditions, fern spores remain viable for 2–4 years, but their viability and the speed of germination deteriorates with age (Page 1979). Spores usually germinate only after being soaked in water. Like most fern spores, the spores of sword fern germinate best when exposed to light, but sword fern is one of only a few fern species in which some germination will occur in darkness (Weinberg and Voeller 1969).

Vegetative Reproduction: Vegetative reproduction of sword fern can occur through division of its perennial, woody rhizome. The rhizome becomes somewhat branched with age (Wagner 1979) but is apparently not creeping. Although the species often occurs in pure, uniform stands, these stands probably represent populations of individual sporophytes rather than clones.

PESTS

No information.

EFFECTS ON CROP TREES

Competition: Sword fern is a dominant species of understory vegetation on some of the most productive growing sites for Douglas-fir and other conifers in British Columbia (Wagner 1979; Klinka and Carter 1980). However, it is not considered a serious or major competitor on the Coast since it interferes significantly with the regeneration and growth of conifers only in localized areas where it is extremely abundant or vigorous (Stewart 1976; M. Scott, pers. comm., Nov. 1984). Reduction or elimination of sword fern from conifer plantations may reduce competition for moisture and light and may reduce the desirability of these plantations as habitat for tree-damaging mammals (Stewart 1976), but the magnitude and exact nature of the competitive effect have not been studied.

Allelopathy: del Moral and Cates (1971) studied the allelopathic potential of sword fern in western Washington; they found no evidence of inhibitory chemicals under either laboratory or field conditions.

Beneficial Effects: No information.

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: Limited evidence suggests that sword fern initially decreases in cover following logging (M. Scott, pers. comm., Nov. 1984; B.M. Geisler, pers. comm., Jan. 1985), but that it slowly

190 Brand 1984.
Sword Fern

recovers (Lafferty 1972). Following logging of moist, productive sites in the CWH zone near Vancouver, sword fern, previously an important understory species, could only be found in shady spots under a protective canopy of bigleaf maple.\(^{191}\) In contrast, 17 years after thinning of a spruce–hemlock stand on the central Oregon Coast, sword fern attained higher percent covers on heavily thinned blocks than on lightly thinned blocks (Alaback and Herman 1988). It seems likely that sword fern, like lady fern, is able to maintain its cover on sites where soils remain moist after logging, and that its cover is diminished on exposed and drier sites where evapotranspirative stresses are severe. The fronds often become dwarfed in size following exposure to dry air and strong light (Frye 1934; Wagner 1979).

Fire: Slashburning studies in the CWH zone near Vancouver show that sword fern is capable of surviving even a severe fire (Lafferty 1972), but on some sites it may be absent for the first few years following a fire or restricted to unburned patches only.\(^{192}\) In the western Cascades of Oregon, Schoonmaker and Mcgee (1988) found that sword fern averaged 8% cover in undisturbed forests, 2% cover on 2-year-old burns, 10% cover on 5-year-old burns, and 19% cover on 30-year-old burns. Morris (1970) found that sword fern was equally abundant on burned and unburned clearcut areas from the third to the sixteenth seasons following burning in western Washington and Oregon.

Cutting: No information.

Herbicides: In western Washington and Oregon, glyphosate causes very severe injury when applied in late summer and moderate injury when applied in the fall (Conard and Emmingham 1984a). In British Columbia, glyphosate is reported to cause very severe injury to sword fern (Boateng and Herring 1990). Sword fern was significantly controlled but not eliminated one growing season after an early September broadcast application of 1.4 kg a.i./ha glyphosate near Campbell River on Vancouver Island (J. McLamon, pers. comm., May 1989).

Broadcast applications of hexazinone have caused moderate injury to sword fern in British Columbia (Boateng and Herring 1990). D’Anjou (pers. comm., June 1989) found a 45% decrease in sword fern cover following a 4 kg a.i./ha hexazinone application.

Applications of 2,4-D in the winter or amitrole in the spring are reported to provide poor control of sword fern in western Washington and Oregon (Conard and Emmingham 1984a).

In Oregon, dicamba and bromacil effectively controlled sword fern when applied at any time between mid-May and mid-July (Stewart 1976).

Soil Disturbance: No information.

WILDLIFE

Food: Extensive use of sword fern is generally limited to periods when animal populations reach high densities (e.g., introduced Sitka deer on the Queen Charlotte Islands) and preferred foods are limited in distribution (Klein 1965).

Sword fern is a moderately important food for black-tailed deer year-round (Singleton 1976). Leslie et al. (1984) found that sword fern made up 13% of the annual diet and 70% of the winter diet of this deer at a site in Washington (Jones 1975).

Sword fern is an important winter food for mountain beaver in Oregon (Stewart 1976). In British Columbia, mountain beaver has a very restricted range and therefore consumption of sword fern by this mammal is limited to a small geographic area in the southwest of the province.

Black bears sometimes forage on this fern (Frye 1934; Pojar et al. 1984).

\(^{191}\) Brand 1984.
\(^{192}\) Ibid.
*Populus balsamifera* ssp. *balsamifera*
(balsam poplar)

Distribution of *P. balsamifera* in British Columbia. The dashed line indicates the approximate boundary between ssp. *balsamifera* (balsam poplar) to the north and east, and ssp. *trichocarpa* (black cottonwood) to the south and west. Specimens intermediate between the two subspecies are common where their ranges overlap.
**Populus balsamifera** L. ssp. *balsamifera*  
Balsam poplar

**DESCRIPTION**

Balsam poplar is a deciduous tree with a long straight trunk and an open crown, reaching 35 m in height and 60–80 cm in diameter. The bark is grey and deeply furrowed. The twigs are stout with large, pointed, resinous buds. Leaves are broadly lanceolate to ovate and untoothed. The fluffy seeds are produced on long drooping catkins (Hosie 1973; Hultén 1974).

**Variation:** No geographic varieties of balsam poplar are described in British Columbia (Taylor and MacBryde 1977). Balsam poplar hybridizes extensively with the closely related black cottonwood (*P. balsamifera* ssp. *trichocarpa*) and may hybridize with *P. tremuloides* in some areas (Hosie 1973; Hultén 1974).

**DISTRIBUTION AND ABUNDANCE**

Balsam poplar is found across Canada but is replaced by black cottonwood through most of British Columbia. In this province, it is restricted to areas adjacent to or east of the Rocky Mountains in the Peace River and Fort Nelson lowlands (Hultén 1974) and east of the Rocky Mountain Trench (Krajina et al. 1982). It extends westward in northern British Columbia to the Stikine Plateau. Balsam poplar is abundant in the BWBS zone, less common in the SWB zone, and occurs sporadically in some eastern subzones of the SBS, IDF, and ICH (Krajina et al. 1982).

**Altitudinal Range:** Balsam poplar grows from sea level in Alaska to 1650 m elevation in the Rocky Mountains (Fowells (compiler) 1965). It is primarily a lowland species (Hosie 1973; Zasada et al. 1981).

**HABITAT**

**Climatic Relations:** Balsam poplar is primarily a species of boreal climates, although it occurs in arctic to temperate climates. The boreal climate is characterized by frozen ground and snow cover for 6 or more months duration with the average temperatures below -3°C during the coldest month and rarely above 10°C in the warmest month (Krajina et al. 1982).

**Site and Soil Conditions:** Balsam poplar is most commonly found on moist upland and alluvial bottomland sites. It exhibits its best growth on moist, rich, bottomlands with deep soil. Where balsam poplar occurs together with black cottonwood, the cottonwood generally inhabits the alluvial sites, and balsam poplar the uplands. Balsam poplar rarely grows on dry, exposed sites. Soils supporting balsam poplar vary widely and include gravels, deep sands, clay loams, silts, silt loams, and shallow organic soils, but not deep peats (Fowells (compiler) 1965; Hosie 1973; Brayshaw 1978; Zasada et al. 1981).

**Nutrient Relations:** The nutrient requirements of balsam poplar are high; it does not tolerate acid or humus forms in which nutrients are slowly released. Balsam poplar requires a good supply of calcium and magnesium and prefers nitrates to ammonium as a supply of nitrogen (Krajina et al. 1982). In the BWBS zone of northeastern British Columbia, it is most abundant on river terraces described as having a rich nutrient status.

**Water Relations:** An abundant supply of soil moisture is critical for good growth of balsam poplar (Fowells (compiler) 1965), but it does not tolerate brackish water. It is most often found on sites with a subhygric to hygric moisture status. Flood resistance of balsam poplar is possibly the highest among the trees growing in British Columbia (Krajina et al. 1982).

**Light Relations:** Balsam poplar has very low shade tolerance (Krajina et al. 1982). Best growth and development occurs in full sunlight; it will not grow in competition with other species unless it is in a dominant position (Fowells (compiler) 1965). Growth of shaded balsam poplar seedlings was significantly less than that of unshaded seedlings in a greenhouse experiment in Alaska (Walker and Chapin 1986).

**Temperature Relations:** The frost resistance of balsam poplar is very high; it can become established in areas of permafrost (Krajina et al. 1982). In the taiga of interior Alaska, balsam poplar grows on sites with low soil temperature, where surficial soil layers do not completely thaw until well into the growing season and frosts are common well into June (Foote 1983).
BALSAM POpLAR

GROWTH AND DEVELOPMENT

Balsam poplar is characterized by rapid early growth that allows it to establish and maintain dominance above other vegetation. Rapid growth can be maintained for the first 40–50 years of life by which time it can reach heights of 25 m and diameters of 45 cm. Mature trees in southern Alaska average 35 m in height and 66 cm in diameter (Foote 1983); however, trees in eastern North America are typically smaller (Fowells (compiler) 1965; Hosie 1973). Balsam poplar is relatively short-lived in southern parts of its range but can live as long as 200 years in Alaska (Fowells (compiler) 1965; Foote 1983). It normally has a shallow root system (Hosie 1973), especially on wet soils or where permafrost is present at shallow depths.

On good sites, balsam poplar will outgrow aspen. The dominance of balsam poplar over aspen on some newly formed alluvial sites in Alaska may be more related to flood tolerance than to growth relations.

Phenology: Catkins flower between April and June before the leaves appear. The seed matures very early, from mid-May to mid-June when the leaves are about two-thirds grown. Seed dispersal occurs immediately after the seeds are mature. Flowering and seed maturation times appear to be regular from year to year within ecotypic ranges (Fowells (compiler) 1965; USDA 1974).

REPRODUCTION

Seed Production and Dispersal: Balsam poplar first flowers between 8 and 10 years of age (USDA 1974); it subsequently produces a good seed crop every year (Lutz 1955). The seeds have downy plumes and are readily distributed by wind (Fowells (compiler) 1965; Brayshaw 1978), but seed deposition is greatly reduced at distances greater than 100–200 m from the seed source (Zasada et al. 1981).

Seed Viability and Germination: Balsam poplar seed remains viable for only a few days following dispersal (Fowells (compiler) 1965). The seeds will germinate over a broad range of temperatures (J. Zasada, pers. comm., Sept. 1989), often immediately after arriving on a suitable seedbed (Lutz 1955). Thus, most germinants appear in mid-summer. In an Alaska study, more than 80% of total germinants appeared within 2 weeks of artificial seeding and seedlings continued to appear for 3–4 weeks (Zasada et al. 1983).

Young balsam poplar seedlings are extremely susceptible to drying, rain damage, and soil fungi. They require at least 1 month of abundant moisture to ensure survival (USDA 1974). Zasada et al. (1981) observed no seedlings establishing on organic and gravel surfaces at an alluvial site in Alaska following harvesting of a balsam poplar overstory, but regeneration by seed is very common on these river bottom sites (Zasada 1971). Lutz (1955) reports abundant balsam poplar seedlings wherever mineral soil is exposed and a seed source is available. Walker et al. (1986) found that, on a Alaskan floodplain, a litter-floored seedbed strongly inhibited germination and/or initial establishment of balsam poplar. Seedling density was increased by 5- to 10-fold once the litter and forest floor were removed. On upland sites, J. Zasada (pers. comm., Sept. 1989) found no germination except on severely burned microsites.

Vegetative Reproduction: Balsam poplar will regenerate vegetatively from root suckers as well as from stump sprouts and buried branch pieces (Lutz 1955; Zasada et al. 1981). Stump sprouts originate from either dormant buds or from callus tissue. Callus sprouts usually originate at the top of a cut stump, or form where a stump has been damaged during logging. Most root suckers grow from roots of approximately 1 cm in diameter that occur within the top 2 cm of the soil. Suckers also develop from exposed roots. Suckering is significantly less in gravely soil than in silty soils and is greatest where the organic layer has been removed, exposing mineral soil. Branch parts must be well buried in the soil to produce aerial shoots (Zasada et al. 1983). Sucker regeneration is probably more important than regeneration from seed for balsam poplar in Alaska (Lutz 1955).

PESTS

Primary disease and insect pests of balsam poplar are discussed in Fowells (compiler, 1965).

EFFECTS ON CROP TREES

Competition: There are no quantitative data on the effect of balsam poplar competition on conifers. Its growth easily outstrips the growth rates of young conifers, especially when it is of sucker origin. White spruce
is the primary crop species occurring in association with balsam poplar, and many of the most productive alluvial growing sites in the boreal forest are occupied by fairly pure stands of balsam poplar (Neiland and Viereck 1977; Foote 1983).

**Allelopathy:** Balsam poplar has been shown to have an allelopathic effect on the germination and early growth of green alder (Jobidan and Thibault 1981).

**Beneficial Effects:** There are no reports in the literature of beneficial effects of balsam poplar on the growth of coniferous trees. It plays an important role in stabilizing river banks and maintaining river islands, and it may be a valuable crop tree in northern British Columbia.

**RESPONSE TO DISTURBANCE OR MANAGEMENT**

**Forest Canopy Removal:** Trees cut or damaged during logging will sprout from the stump or sucker from the roots; seedling germination will likely occur on areas of exposed mineral soil (Lutz 1955; Zasada et al. 1981). Removal of the overstory canopy from a site in Alaska resulted in very large increases in balsam poplar growth (Walker and Chapin 1986).

**Fire:** Of the tree species in the northern boreal forest, balsam poplar is perhaps the most resistant to destruction by fire (Lutz 1955). Like aspen, balsam poplar is stimulated to produce root suckers following fire. In Alberta, the majority of balsam poplar suckering occurred during the second season following spring burning of a 15-year-old stand (Bailey and Anderson 1979). Density after 5 years was greater on burned areas than on unburned areas.

**Cutting:** In an Alaskan study (Zasada et al. 1981), more than 50% of mature balsam poplar cut during the summer, fall, and winter produced sprouts from callus tissue and dormant buds. Many stumps had more than 25 sprouts after the first growing season. Sprout survival on trees cut in the fall and winter was high, but less than 15% of the trees cut in the summer had surviving sprouts after 4 years. Stump sprouting was most pronounced on winter-logged areas, and sprouts originating from dormant buds were most common after winter logging. Cutting also stimulates suckering from the roots, but there are no studies documenting suckering response. In the Fort St. John Forest District, the response of balsam poplar to girdling has been similar to the response of aspen to this treatment. Girdling is apparently effective in all seasons (P. Wadey, pers. comm., June 1989).

**Herbicides:** Glyphosate applied either by backpack spray or aerially at 2.4–3.0 kg a.i./ha has provided good to excellent control of balsam poplar.\(^{193}\)

Hexazinone applied as a liquid spray, by soil injection, or in granular applications also provides good control of balsam poplar. This herbicide is ineffective in areas with deep organic layers. Liquid hexazinone resulted in 100% control of balsam poplar 1 year after application of 2.2, 3.2, and 4.3 kg a.i./ha in late May in Saskatchewan.\(^{194}\) Similarly, excellent control of balsam poplar occurred in Alberta 2 years after mid-August and late October applications of undiluted hexazinone liquid at rates of both 4 and 8 mL per spot and either 1.5- or 2-m grid spacing.\(^{195}\) Liquid hexazinone applied around stem bases at 0.24 to 0.48 g/cm of dbh gave effective seed tree control of balsam poplars that were 70 cm in diameter and 30 m tall.\(^{196}\) Hexazinone gridballs aerially applied at 4 kg a.i./ha in late May to a mesic BWBSmw site near Dawson Creek provided extremely good control of balsam poplar for at least five growing seasons. Less than 1000 stems per hectare emerged on the treated plots compared with over 32 000 stems per hectare on the controls.\(^{197}\)

Balsam poplar is resistant to 2,4-D and was less sensitive than aspen when sprayed with 2,4-D in the dormant season. Rates of 2.2 kg a.i./ha had virtually no effect and a rate of 4.4 kg a.i./ha provided only marginal control (Bowes 1981). Similarly, increasing the concentration of 2,4-D from 0.25 to 6.75 \% did

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194 Teskey and Masterson 1986e.
195 Teskey and Masterson 1986a.
196 Newhouse 1988b.
197 Herrin 1988b.
BALSAM POPLAR

not significantly increase the damage to balsam poplar in northeastern Saskatchewan (Waddington and Bittman 1987). In Alberta, mortality was high on first-year suckers sprayed with 2.2 kg a.i./ha as a mid-summer foliage spray, but spraying did not prevent further suckering from taking place the following year (Bailey and Anderson 1979).

Soil Disturbance: Exposure of mineral soil favours germination of balsam poplar seed and may promote root suckering by increasing soil temperatures. Branch fragments buried as a result of soil disturbance have a high likelihood of regenerating. (Lutz 1955; Zasada et al. 1981). Following heavy flooding, balsam poplar quickly sends out new roots into the freshly deposited silt layers (Neiland and Viereck 1977).

Fertilization: On a floodplain site in interior Alaska, balsam poplar fertilized with NPK had significantly higher dry mass and stem growth (in some plots) than unfertilized seedlings. However, balsam poplar seedlings were less responsive to fertilization than willow. An NPK fertilization in the greenhouse raised the shoot:root ratio of balsam poplar seedlings from about 2 to 4 (Walker and Chapin 1986).

WILDLIFE

Food: Balsam poplar is a moderately important winter food for mule deer and Rocky Mountain elk in British Columbia.\(^{196}\) Snowshoe hares browse heavily on balsam poplar in Alaska (Walker et al. 1986), and the tree is a preferred food of beavers (Denney 1952, cited by Allen 1982). Squirrels feed on flowers and leaf buds in the spring (Harestad 1983). Balsam poplar sprouts after browsing (T. Lea, pers. comm., Feb. 1989).

Other Resources: Eagles use balsam poplar for perching, and cavity nesters make their home in this tree.

\(^{196}\) Blower 1982.
*Populus balsamifera* ssp. *trichocarpa*  
(black cottonwood)

Distribution of *P. balsamifera* in British Columbia. The dashed line indicates the approximate boundary between ssp. *balsamifera* (balsam poplar) to the north and east, and ssp. *trichocarpa* (black cottonwood) to the south and west. Specimens intermediate between the two subspecies are common where their ranges overlap.
**Populus balsamifera L.**
ssp. *trichocarpa* (Torr. & Gray) Brays
(P. *trichocarpa*)

**Black cottonwood**

**DESCRIPTION**

Black cottonwood is a deciduous tree, up to 40 m high and 150 cm in diameter. The grey bark of mature trees is deeply furrowed; young bark is smooth. Twigs are stout and hairless, with large, resinous, pointed buds. Separate male and female flowers form long, drooping catkins which split to release seeds bearing cottony down. Black cottonwood differs from balsam poplar in having wider leaves and a three-valved rather than a two-valved fruit (Hosie 1973; Brayshaw 1978).

**Variation:** There are many intermediate forms between this subspecies and ssp. *balsamifera* where the ranges of the two overlap in northern British Columbia (Brayshaw 1978).

**DISTRIBUTION AND ABUNDANCE**

Black cottonwood is found throughout southern and central British Columbia to the edge of the Rocky Mountains. It is absent along the outer coast including northern Vancouver Island and the Queen Charlotte Islands. In northern British Columbia, it is present adjacent to the Alaska panhandle but is replaced by balsam poplar inland (Brayshaw 1978; Krajina *et al.* 1982). Throughout the province it is abundant in major river valleys. It is found in all biogeoclimatic zones except the SWB and AT.

**Altitudinal Range:** Although black cottonwood primarily grows in valley bottoms, it occurs from sea level to the lower limits of the MH zone on the British Columbia coast (Packee 1976) and has been recorded as high as 2100 m in elevation in the Selkirk Mountains of the Interior (Fowells (compiler) 1965).

**HABITAT**

**Climatic Relations:** Black cottonwood grows in climates ranging from relatively arid to humid, but it achieves its best development in areas of humid climate (Fowells (compiler) 1965). It is absent from the cool, perhumid areas of the outer British Columbia coast and is replaced by balsam poplar in the severe boreal climate of the northeastern province (Brayshaw 1978). It occurs marginally in subalpine climates (Krajina *et al.* 1982).

**Site and Soil Conditions:** Black cottonwood is characteristically associated with river banks, gravel bars, or low-lying land, but it also grows on the loams, clays, and rich humic soils of upland sites. Typical soils are young with little soil development. The largest trees grow at low elevations on deep alluvial soils, while the poorest growth is on newly deposited gravel (Lyons 1952; Roe 1958; Fowells (compiler) 1965).

**Nutrient Relations:** Nutritional requirements of black cottonwood are high. Like balsam poplar it requires a good supply of calcium and magnesium and does not grow well on acid mor humus forms where nutrients are released slowly (Krajina *et al.* 1982). A pH of 6–7 is required for optimum growth (Smith 1957, cited by Packee 1976). Black cottonwood commonly grows on deep alluvial soils that are among the richest, most productive growing sites in British Columbia.

**Water Relations:** Black cottonwood requires abundant, well-oxygenated water for optimum growth (Smith 1957, cited by Packee 1976). It is highly tolerant of flooding, and grows abundantly on sites that receive regular flooding, but it does not tolerate the brackish water that forms near the ocean or in stagnant pools following flooding. Fine sediment deposited by flooding tends to reduce soil aeration and inhibit cottonwood growth, whereas fast-moving water, rich in oxygen, speeds growth (Fowells (compiler) 1965; Krajina *et al.* 1982). Black cottonwood apparently has low tolerance of drought, and throughout most of its range is restricted to sites receiving supplemental moisture. There are reports (Shulte *et al.* 1987) that black cottonwood is incapable of closing its stomata, which would make it very poorly adapted to drought. In Washington, however, Pezeshki and Hinkley (1988) observed that while a long drought period during the growing season may significantly reduce red alder's growth, it may have less of an effect on black cottonwood's growth. In climatically dry areas it survives in protected valleys and canyon bottoms, where the roots can reach a permanent supply of soil moisture (Fowells (compiler) 1965).
BLACK COTTONWOOD

Smith (1988) found that in a low-oxygen environment, rooted cuttings that were flooded for 6 weeks grew slower than unflooded seedlings. In a greenhouse experiment (Harrington, 1987), black cottonwood seedlings that were flooded in a low-oxygen environment for 20 days exhibited no differences in height growth in comparison to non-flooded seedlings. However, during the 20-day recovery period after flooding, the flooded seedlings had significantly slower height growth and put on significantly less root and leaf biomass than the non-flooded seedlings.

Light Relations: Black cottonwood is a shade intolerant species (Fowells (compiler) 1965; Krajina et al. 1982) that grows best in full sunlight. It does not survive in a forest understory.

Temperature Relations: While dormant, black cottonwood is one of the most frost-resistant trees in the northwestern U.S. (Minore 1979) although it can be killed or damaged by late fall frosts (Fowells (compiler) 1965). It is presumably less tolerant of cold temperatures than balsam poplar (Krajina et al. 1982).

GROWTH AND DEVELOPMENT

Black cottonwood exhibits rapid juvenile growth that outstrips that of its competitors, allowing it to establish and maintain a dominant position in a stand (Packee 1976). In Washington, Heilman and Stettler (1985) recorded average heights of 4-year-old pure black cottonwood stands at 10 m and average heights of black cottonwood grown with alder at 11 m. Exceptional trees can reach 13.7 m in height and 18 cm diameter in 7 years. By age 27, black cottonwood can exceed 36 m in height and 80 cm in diameter. It is the largest-growing deciduous tree in British Columbia. Maturity is normally reached in 60–70 years, but good growth can be maintained for as long as 200 years. Black cottonwood outlives red alder in mixed stands. Best growth occurs on coastal sites, with growth decreasing towards the north and in interior locations (Fowells (compiler) 1965; Hosie 1973).

The tree develops a long straight bole and is normally free of branches for most of its length. Young trees have a narrow, conical crown with upswept branches (Lyons 1952). The root system is shallow and widespread (Hosie 1973).

In cutover areas, large numbers of sprouts are produced from cut stumps. With the possible exception of red alder, vigorous cottonwood sprouts are the fastest growing plants on recently logged coastal alluvial sites on the Skeena River (J. Pollack, pers. comm., Jan. 1985). Observations from the Pacific Northwest suggest that if black cottonwood can establish a deep root system it can outgrow all other species (Heilman and Stettler 1985; Hinkley et al. 1988, cited by Pezeshki and Hinkley 1988). According to Pezeshki and Hinkley (1988), if soil moisture is adequate, first-year growth of black cottonwood and red alder will be about the same.

Phenology: The flowers of black cottonwood appear from late March or early April through to late May on the coast; they can appear as late as mid-June in some areas of the Interior. Leaf emergence follows flowering. Fruits are ripe within a month of flowering, and seed dispersal is as early as late May and early July. Seed is shed between April and June on the coast (D. McLennan, pers. comm., July 1989). Trees of northern and inland provenances cease growth earlier in the growing season than provenances from south coastal areas (Fowells (compiler) 1965).

REPRODUCTION

Seed Production and Dispersal: Black cottonwood first produces seed at approximately 10 years of age. Good seed crops are produced annually. The downy seed is light and buoyant and can be transported for long distances by wind and water (Fowells (compiler) 1965; USDA 1974). The timing of seed dispersal coincides with the timing of flooding in many coastal rivers. Sandbars along rivers may be covered by seedlings in May and June (D. McLennan, pers. comm., July 1989).

Seed Viability and Germination: The viability of fresh seed is high but of short duration (Fowells (compiler) 1965). Cottonwood seed will readily germinate on a variety of favourable sites (Beals 1966), particularly where bare soil has been exposed or new soil laid down. Moist seedbeds are essential for high germination rates and seedling survival depends on favourably moist conditions for at least the first month (Roe 1958; USDA 1974). Mortality of seedlings is extremely high because precise moisture requirements must be met. Roots of developing seedlings must not dry out, thus successful growth depends on the
ability of seedlings to follow retreating subsurface water levels as they subside after the summer flood (D. McLennan, pers. comm., July 1989). Seeding establishment is the primary means of reproduction of black cottonwood in the Cariboo Forest Region199 and probably throughout British Columbia.

Vegetative Reproduction: Sprouting from the stump is the most common form of vegetative reproduction in black cottonwood, although minor root suckering also occurs (Roe 1958). Sprouts arise primarily from suppressed buds on the stump but can also originate in wound callus (DeBell and Alford 1972). Black cottonwood is also known to regenerate from broken stem or root fragments incorporated in moist mineral soil. An unusual form of vegetative reproduction has been reported by Galloway and Worral (1979). Small shoots, complete with green leaves, abscise naturally and either root where they fall, or are transported some distance by water before taking root.

Artificial regeneration can be successfully obtained using stem cuttings of various lengths. For best results the cuttings should be collected from mid-December to mid-February from young saplings 2–3 m tall. Cuttings should average 1–2 cm in diameter and 25 cm to 3 m in length depending on the application (D. McLennan, pers. comm., July 1989). Early spring planting is recommended to capture soil moisture. Stine et al. (1981) report that survival of unrooted cuttings is as good as, or better than, survival of artificially rooted cuttings. However, other researchers (e.g., D. McLennan, pers. comm, July 1989) have observed the opposite effect. Rooted cuttings have exhibited more rapid juvenile growth than unrooted cuttings.

PESTS

Principal disease and insect pests are described by Fowells (compiler, 1965).

EFFECTS ON CROP TREES

Competition: Black cottonwood is a severe competitor with conifers because of its rapid height growth and early dominance of forested sites. Competition is most severe on extremely productive bottomland sites and will continue for the length of the rotation. Early competition comes from plants of both sprout and seed origin. Cottonwood plants may be extremely dense in the first few years of growth, but self-thinning will normally take place by age 5 as weaker trees are quickly suppressed by the more dominant plants (Roe 1958).

Beneficial Effects: D. McLennan (pers. comm., July 1989) described the following beneficial effects of black cottonwood on alluvial floodplains in British Columbia:

1. Black cottonwood can be a valuable crop tree. The short (20–30 year) rotation reduces the risk of losing the plantation to erosion of alluvial surfaces.

2. Black cottonwood can be regenerated relatively easily and it establishes rapidly, so that sites vulnerable to erosion are rapidly stabilized, which in turn reduces siltation of fish habitat, reduces plantation erosion, and stabilizes hydrologic regimes.

3. The relatively nutrient-rich litter is important for fish food chains.

4. Foliage provides summer shade to maintain cool water temperatures. Open canopies in the winter allow higher light penetration.

Near Haney, van der Kamp (1986) detected nitrogen fixation activity in the wetwood of black cottonwood. He suggested that wetwood of black cottonwood harbours nitrogen-fixing bacteria that may contribute to the total nitrogen input of forested ecosystems.

Allelopathy: A pot study (Heilman and Stettler 1985) indicated that black cottonwood leaf and litter material had an inhibitory effect on red alder seedlings. However, red alder seedlings grew normally in field soil collected from the cottonwood plots. This finding suggests that, at most, allelopathy is probably of minor significance under field conditions.

199 Perry 1983.
RESPONSE TO DISTURBANCE AND MANAGEMENT

Forest Canopy Removal: Black cottonwood is not found as an understory species beneath mature forest canopies. Following logging, seeding-in occurs from residual or nearby trees. Trees cut during logging sprout profusely and may produce some root suckers (Roe 1958). On northern Vancouver Island, D. Harrison (pers. comm., July 1989) has observed that black cottonwood cover increased through respouting following forest canopy removal.

Fire: Black cottonwood is highly susceptible to fire and even light burns can cause considerable injury (Fowells (compiler) 1965). Cottonwood is apparently not a fire-adapted species, but there are no reports in the literature documenting its response to natural or prescribed fire.

Cutting: Young black cottonwood responds to cutting with vigorous sprouting. Repeated cutting on a 2-year cycle does not significantly affect sprouting vigour (DeBell et al. 1984). DeBell and Alford (1972) found that when 2-year-old trees were cut in February to a 30-cm stump, sprouts were abundant after two growing seasons. Most sprouts arose from dormant buds more than 15 cm above the ground level. When the same trees were cut to 15 cm in height 2 years later, they sprouted more slowly and some sprouts arose out of callus tissue. These adventitious sprouts were smaller and more susceptible to damage and decay than those arising from dormant buds. The authors speculated that if the first cutting height had been used for the second cutting, there would have been no decline in sprouting vigour. The same study found that sprouting vigour of eastern cottonwood (P. deltoides) was lowest when cutting took place early in the growing season, probably because food reserves were low after initiation of growth in spring.

Mid-summer cutting of 4-year-old black cottonwood in the CWH zone near Chilliwack resulted in effective control 2 years after treatment, as a result of the shading of cut stumps by salmonberry. On a nearby site that lacked shade, a mid-summer cutting treatment was followed by rapid respouting (B. D'Anjou, pers. comm., Nov. 1989).

Herbicides: In British Columbia, Washington, and Oregon, excellent control of black cottonwood is obtained after summer or fall broadcast applications of glyphosate (Conard and Emmingham 1984b; Boateng and Herring 1990). D'Anjou200 found that late spring broadcast applications can also be somewhat effective. When he applied glyphosate at 2.0 kg a.i./ha on various dates to a site in the CWH zone, he found that the August 12 and September 3 applications were most effective, the June 4 application was next most effective, and the July 9 application was ineffective.

Broadcast applications of hexazinone generally have caused moderate to severe injury to black cottonwood in British Columbia, while spot applications have provided severe to very severe injury (Boateng and Herring 1990). Excellent control of black cottonwood was maintained 4 years after a September application of 9–11 mL/spot of hexazinone on a mesic SBSmc site in the Prince Rupert Forest Region. The single herbicide application was anticipated to release the conifers to a free-growing condition (N. Endacott, pers. comm., July 1989). Black cottonwood suffered 80–95% defoliation and almost no respouting one season after a mid-May application of hexazinone applied at 2 and 4 mL/spot on a 1 x 2 m grid in the Nelson Forest Region.

Broadcast applications of 2,4-D amine have resulted in light to moderate injury to black cottonwood in British Columbia. In Washington and Oregon, summer or late summer applications of 2,4-D amine to cut surfaces have severely injured black cottonwood (Conard and Emmingham 1984b).

Soil Disturbance: Logging disturbance or mechanical site preparation that exposes patches of moist mineral soil can create an ideal seedbed for germination and survival of black cottonwood seedlings (Fowells (compiler) 1965). Stem or root fragments incorporated into moist mineral soil can be expected to regenerate, and damaged trees will produce new shoots.

Fertilization: Fertilization increased black cottonwood growth in a 20-year-old stand on a floodplain in British Columbia that had medium nutrient status. However, no response occurred on two nutrient-rich floodplain

200 D'Anjou 1988a.
sites supporting 10- to 15-year old black cottonwood trees. In addition, black cottonwood did not respond
to nitrogen fertilization on nutrient-rich sites on the Fraser River. Phosphorus added below the soil surface
at the time of planting had increased growth and survival of black cottonwood whips (D. McLennan, pers.

WILDLIFE

Food: Black cottonwood is a moderately important source of food to wildlife in British Columbia. It is an
important browse for Roosevelt elk in winter, a moderately important winter and spring browse for
moose (Singleton 1976), and a moderately important browse for white-tailed deer. Black cottonwood

Black cottonwood is a preferred food of beaver on Vancouver Island (Sadoway 1986) and probably
elsewhere. Squirrels feed on the flowers and leaf buds in the spring (Harestad 1983). Damage by small
mammals, especially voles or meadow mice, can be severe on young trees growing on grassy or herb-
covered sites. Rabbits and hares can clip twigs and girdle around stem bases (D. DeBell, pers. comm.,
Dec. 1984). Brewer (1980, cited by Cade and Sousa 1985) noted that ruffed grouse feed on buds and
catkins during winter in Washington.

Other Resources: Black cottonwood is important for daytime perching of bald eagles in winter. Stalmaster
and Newman (1979) found that bald eagles spent 44% of their perching time on black cottonwood. In
southern British Columbia, black cottonwood is an important cavity nesting tree for woodpeckers. Many
other birds nest in black cottonwood including owls, hummingbirds, starlings, sapsuckers, flickers,
veeries, orioles, grosbeaks, and vireos (Cannings et al. 1987).

201 Blower 1982.
202 Ibid.
203 Korol and Wallis 1983.
*Populus tremuloides*
(trembling aspen)

Distribution of *P. tremuloides* in British Columbia.
Populus tremuloides Michx.

A comprehensive review of literature pertaining to the autecology and management responses of trembling aspen is provided by Peterson et al. (1989).

DESCRIPTION

Trembling aspen is a small to medium-sized deciduous tree with a narrow dome-like crown that forms extensive clones by means of root suckering. It is commonly 6–12 m tall but can reach 25 m in height. The bark, whitish to greenish-grey with characteristic black scars, is smooth but becomes furrowed at the base with age. Twigs are slender, reddish or grey, with long, pointed buds. Leaves are nearly round with a pointed tip, rounded teeth, and a flattened stalk that causes them to tremble in the breeze. The long, drooping male and female catkins appear on separate trees. Female catkins release many tiny, cottony seeds (Viereck and Little 1972; Brayshaw 1978).

Variation: Aspen is the most widely distributed native tree in North America (Brisette and Barnes 1984). Three poorly defined local varieties are recognized in British Columbia. The variety vancouveriana is found on Vancouver Island and adjacent coastal areas; var. aurea appears in the Cariboo Region to the Rocky Mountains; and the typical var. tremuloides is widely distributed throughout the British Columbia mainland (Taylor and MacBryde 1977; Brayshaw 1978). Because the species forms extensive, genetically identical, male or female clones, marked phenological or behavioural differences between adjacent clones can be easily observed (Fowells (compiler) 1965; Steneker and Wall 1970; Brayshaw 1978).

DISTRIBUTION AND ABUNDANCE

Aspen occurs throughout British Columbia, east of the Coast Mountain Range. Variety vancouveriana is scattered throughout the Georgia Strait area, but northwards, aspen occurs only sporadically on the coast where it has migrated westward along major river valleys. It is extremely abundant in the central and northeastern parts of the province, especially in the BWBS, SBS, and IDF biogeoclimatic zones, where it forms extensive stands (Brayshaw 1978; Krajina et al. 1982).

Altitudinal Range: Trembling aspen extends from valley bottoms to approximately 1200 m in the interior and is occasionally found near sea level on the coast (Lyons 1952). In interior Alaska it is confined to elevations below 900 m (Viereck and Little 1972).

HABITAT

Climatic Relations: The broad geographic distribution of this species indicates that it is adapted to a wide variety of climates. Cold continental and boreal climates appear to be more favourable than the humid, equable coastal environment, and the species is almost absent in cool perhumid areas. Towards the southern limits of its range in the U.S., it tends to be found at higher elevations in the mountains only, and in dry climates it may be restricted to protected habitats (Fowells (compiler) 1965). In northern British Columbia and at high elevations it is most abundant on sunny, south aspects.

Site and Soil Conditions: Aspen can inhabit a wide range of sites, including shallow rocky soils, loamy sands and wet clays, but it is predominantly a species of well-drained uplands. Best growth is on moist but well-drained and porous, loamy soils; rockiness greatly limits stand development (Fowells (compiler) 1965; Steneker 1976; Burns (compiler) 1983). In British Columbia, trembling aspen occurs dominantly on Luvisol soils.

Nutrient Relations: Aspen is tolerant of poor soils and exhibits its best growth on nutrient-rich substrates, especially calcium-rich soils derived from limestone (Fowells (compiler) 1965; Krajina et al. 1982). However, studies in Wisconsin indicated that soil nutrient levels were of little importance in determining aspen site index (Fralish 1972). Aspen is regarded as a soil improver, particularly after fire (Fowells (compiler) 1965). It has high levels of potassium in its foliage, wood, bark, and litter relative to other northwestern tree species (Minore 1979), and it redistributes great quantities of nutrients (especially calcium, magnesium, and nitrogen) to the surface soil layers through its litter (Fowells (compiler) 1965;
Trembling aspen

Krajina et al. 1982). Biogenic cycling of calcium by trembling aspen is believed to maintain the Luvisolic soils of the Fort Nelson area in a relatively productive state by retarding acid leaching (Valentine et al. (editors) 1978).

Water Relations: Aspen is abundant on sites ranging from xeric to hygric in moisture status, but best growth is found on sites with abundant moisture (Krajina et al. 1982; Angove and Bancroft 1983). Fralish (1972) indicates that soil moisture is the most important factor affecting the relative growth of aspen, and water tables between 1.0 and 2.5 m in depth are preferred, especially in coarse- and medium-textured soils. Aspen can survive long periods of flooding (Krajina et al. 1982).

Light Relations: Aspen is a shade-intolerant species that requires full sunlight for growth (Lutz 1955; Krajina et al. 1982). When overtopped by larger trees, it deteriorates and eventually dies (Mueggler 1984). Strong light is needed to stimulate production of root suckers and ensure their continued, vigorous growth. Higher light intensities increase production of roots in young suckers (Fowell (compiler) 1965; Johansson and Lundh 1988). At less than 10% full sunlight, sucker density is less than 10% of that on a clearcut (Mueggler 1984).

Temperature Relations: Frost resistance in aspen is high, and the species survives easily in frozen ground having no snow cover (Krajina et al. 1982). In the taiga of Alaska it is dominant on sites where the permafrost layer comes to within 20 cm of the soil surface (Foote 1983). Foliage is susceptible to late spring frosts (Strain 1966). Soil temperature is very important in the production of root suckers. Direct heat must reach the forest floor and temperatures must be 20–30°C for maximum production of root suckers (Fowell (compiler) 1965; Steneke 1976). Root cuttings from 10-year-old aspen exposed to different temperatures (10 and 25°C) and light intensities produced the most and largest suckers at 25°C and high light intensities (Johansson and Lundh 1988).

GROWTH AND DEVELOPMENT

Aspen is characterized by rapid early growth and a relatively short life-span. Although individual trees may live as long as 200 years, stands generally reach an advanced state of decay between 55 and 90 years. The tree develops a slender, limb-free trunk and a small crown. The wide-spreading roots typically extend 1.0 to 1.5 m into the soil but can penetrate to as deep as 2.2 m and may extend as far as 14 m from the stem base. Root development can be greatly hindered in rocky soils (Lutz 1955; Fowell (compiler) 1965; Main 1972; Hosie 1973).

Aspen is most often seen in cutover or recently burned areas as small clumps of trees, each consisting of large numbers of root suckers (Schier and Campbell 1978). Sandberg (1951, cited by Schier and Campbell 1978) found that competition between the suckers usually reduces most clumps to a single stem by the fifth year and almost all to a single stem by the tenth year. Vigorous suckers may grow as much as 2 m in their first year, but subsequent height growth will average 30–60 cm annually (Steneke 1976). Seedling growth is much slower. Fowell (compiler, 1965) reports that growth in the first year averages 30 cm, while in Alaska, 3-year-old seedlings reached a maximum height of 27.5 cm (Zasada et al. 1981).

Phenology: Flowering takes place before the leaves appear in early spring (usually April or May). All trees within a clone develop their flowers simultaneously, although separate clones flower at different times. Male clones flower before females clones. The fruits mature as the leaves expand and are normally ripe during May or June, about 4–6 weeks after flowering. Seed dispersal takes place shortly after ripening is complete, typically in the first few weeks of June. Within ecotypic zones, flowering period and time of seed maturity appear to be quite regular and differences in flowering time apparently depend on current temperatures (Fowell (compiler) 1965; Steneke and Wall 1970; Vierreck and Little 1972; USDA 1974; Brayshaw 1978). Leaf phenology is also identical for all trees within the same clone. Earliest and latest flushing clones within a given area may be 1–3 weeks apart in their phenological development, giving a patchwork appearance to an aspen stand, and making delineation of individual clones easy. There may also be several weeks difference in the timing of leaf fall among different clones (Steneke and Wall 1970).

In a provenance study located in Michigan (Brissette and Barnes 1984), clones from western North America initiated shoot growth earlier in spring than clones from Michigan, indicating that, under native conditions, the western families are adapted to initiate growth at lower accumulated degree-days. Clones
from northern latitudes or high elevations also ceased growth much earlier than the Michigan clones because they are genetically adapted to the photoperiods and growing season temperatures of their native habitats.

REPRODUCTION

*Seed Production and Dispersal:* Aspen begins to flower between 10 and 20 years of age. Flowers are typically unisexual, with male and female trees occurring in separate clones, but a small percentage of both male and female trees bear perfect flowers. The ratio of male to female trees is approximately 3 to 1 in natural populations in the eastern U.S. Pollen is wind-dispersed between clones. Female trees produce an adequate seed crop annually, with good seed crops every 4–5 years. The tiny cottony seeds can be carried several kilometers by wind (Fowells (compiler) 1965; Maini 1972).

*Seed Viability and Germination:* The viability of fresh fertile seed is high (Fowells (compiler) 1965), but seeds remain viable for only 2–3 weeks after maturity (Strothman and Zasada 1957). Reproduction does occur from seed (Maini 1972) but is rare, primarily because the short period of viability rarely coincides with environmental conditions that are sufficiently moist to allow seedling establishment (Barnes 1966). Peterson et al. (1989) indicate, however, that seedling establishment may be more important in relatively cold northern soils than is generally believed. Germination rates of 90–100% are possible if conditions are suitable (Mueggerli 1984). Seed germination and seedling survival are best on moist mineral or humus seedbeds with moderate temperatures, good drainage, and little competition from other vegetation (Stenecker 1976; McDonough 1979; Mueggerli 1984). Germination is optimum between 10 and 21°C and temperatures in excess of 27°C are detrimental (Mueggerli 1984). Regeneration from seedlings is of minor significance as a means of reproduction in western North America (Fowells (compiler) 1965; Stenecker and Wall 1970).

*Vegetative Reproduction:* The dominant form of regeneration in aspen is through suckers or adventitious shoots that develop from the extensive lateral root system (Stenecker 1976; Schier 1981; Schier et al. 1985). Meristems that begin in the cork cambium during secondary growth either develop into buds and then elongate into shoots or, more frequently, stop growing after the bud forms (Schier et al. 1985). Suppressed buds do not sprout as vigorously and may remain inhibited, while newly initiated meristems develop into suckers. Sprouts from the root collar or stump are uncommon but do occasionally occur (Maini 1972) in saplings and younger stems (Mueggerli 1984). Root suckers in Alaska appeared up to 25 m away from a fire-killed mature aspen, with the majority of the suckers occurring within 10 m of the stem base (Lutz 1955). However, Schier (1981) provides evidence that suckering from lateral roots does not appear to depend on distance from the parent plant tree or root age. Suckers normally originate from roots in the upper 10 cm of soil but can appear on roots as deep as 28 cm (Kemperman 1978; Schier and Campbell 1978).

Sucker development on aspen roots appears to be suppressed by auxin transported from the aerial parts of the tree (i.e., apical dominance). When movement of auxins into roots is halted or reduced by cutting, burning, girdling, or defoliation of trees, auxin levels in the roots decline. In addition, cytokinins can no longer move out of the roots, resulting in an increase in the ratio of cytokinins to auxins, which promotes suckering (Mueggerli 1984; Schier et al. 1985).

Suckers are dependent on the parent root carbohydrate reserves until they emerge from the soil surface and can photosynthesize. Low levels of carbohydrate reserves in the parent root can limit the density of suckers. This is particularly true of deep-rooted clones, because the suckers require more energy to push up to the soil surface. Carbohydrate reserves can be exhausted and sucker production drastically reduced by repeated destruction of new suckers by browsing, cutting, burning, or herbicide spraying (Mueggerli 1984; Schier et al. 1985).

A few suckers will arise every year, even in undisturbed stands, but strong light and heat must reach the forest floor to stimulate vigorous suckering (Fowells (compiler) 1965). High temperatures increase cytokinin production in the roots and may also lower auxin concentrations in roots by speeding its degradation. Thus, high temperatures increase the cytokinin to auxin ratio and stimulate suckering (Mueggerli 1984; Schier et al. 1985). The temperature range for suckering is 18–35°C, with 24° being
TREMBLING ASPEN

optimum (Peterson et al. 1989). Light is not essential for sucker initiation, although increased light intensity increases sucker density and growth.

Suckering produces extensive clones of genetically identical trees. Clones as large as 81 ha in size have been identified in western North America (Kemperman and Barnes 1976), but most clones are much smaller. Trees of different clones vary significantly in their suckering ability, phenology, growth rates, form, and disease susceptibility (Steneker and Wall 1970; Maini 1972; Mueggler 1984).

Age does not seem to affect suckering capacity, provided that the stand is not breaking up as a result of decay and old age (Steneker 1976). In deteriorating stands, sprouting is inhibited because the shrinking root system results in a low cytokinin:auxin ratio. If root density has declined appreciably, regeneration following cutting or burning will be sparse or patchy (Mueggler 1984). Barring (1988) provides some evidence, however, that the roots of the closely related European aspen (Populus tremula) may remain alive for a long time after the disappearance of parent trees, enabling the species to form suckers continuously.

PESTS

Aspen is highly susceptible to various forms of decay and periodically suffers from major insect infestations. Young suckers without at least one injury due to insects or pathogens are rare (Peterson et al. 1989). Principal disease and insect pests are outlined by Fowell (compiler, 1965).

Galls, lesions, and shoot dieback are very common in young aspen stands and increase with decreasing site quality (Peralta 1984). However, most injuries heal within a few years and do not contribute to suppression or mortality. Hypoxylon mammatum is a prevalent and lethal canker disease of young aspen. Peak infections occur at about 7 years of age and stem infections kill saplings within 2 or 3 years. White trunk rot (Phellinus tremulae) is the most important cause of decay in aspen stands older than 20 years (Peralta 1984). Armillaria mellea infections of aspen stump roots have increased with succeeding short-rotations of aspen stands in Ontario (Stell and Berry 1986). The high incidence of Armillaria probably contributed to the observed decrease in the number and size of aspen suckers, and similar Armillaria infections may reduce the productivity of short-rotation stands.

EFFECTS ON CROP TREES

Competition: Aspen is considered to be a serious competitor with coniferous trees throughout most of the interior of British Columbia, especially in the BWBS zone, where it is particularly well established. However, aspen rarely exceeds 10% cover within 15 years of site disturbance in the wetter 1CH subzones in the Kamloops and Nelson Forest Regions. It is not considered to be a hindrance to establishment, survival, or growth of conifers in these productive subzones.\(^\text{204}\) It rarely seeds-in to clearcuts, thus competition results from the suckers of trees already established prior to harvesting. The numbers of young suckers produced can be immense: a single tree in Alaska reportedly produced 36 230 suckers within 3 years (Lutz 1955). Aspen density and the rapid growth of young suckers provide young conifers with severe competition for root and crown space (Lees 1966). Suckers have the advantage of an established root system and always grow more rapidly than coniferous seedlings when open-grown (Jones 1974).

Conifers growing beneath an understory of aspen are also subject to significant mechanical damage (Kittredge and Gevorkantz 1929). “Whipping” damage is particularly severe at approximately 55–75 years when understory trees begin to pass through the increasingly decadent aspen overstory (Lees 1966).

Beneficial Effects: Aspen is considered to be a site improver where burning or other forms of disturbance have reduced soil nutrient levels, because it returns large quantities of nutrients to surficial layers through its litter (Fowell (compiler) 1965; Krajina et al. 1982).

Aspen stands of present or potential value occur on many NSR and non-commercial brush areas in the province. Some of these stands may be best managed for pure hardwood or mixed wood production.

\(^{204}\) Mather 1988.
Nutrient losses due to harvesting will be minimized if rotations are greater than 60 years and if whole-tree harvesting occurs during the leafless season, so that the foliage component of the nutrient pool is not removed from the site (Peterson et al. 1989).

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: Trembling aspen rapidly increase following overstory removal. However, it has been observed (J. Wright, pers. comm., July 1989) that much fewer suckers are produced in the drier ICH subzones than in cooler zones such as the MS and SBS (J. Wright, pers. comm., July 1989). Even where there are only a few scattered aspen residuals in a conifer stand, aspen root suckers will generally dominate regeneration after logging as long as aspen root density is adequate (Schier et al. 1985). Trees cut or damaged during logging will produce prolific suckers. Even trees that remain undamaged after logging will produce suckers because the root system is stimulated by the increased light and heat on the forest floor (Fowells (compiler) 1985). Suckers can grow up to 2 m in height during the first growing season following overstory removal (Steneker 1976). In the Penticton Forest District, 1-year-old suckers average 40 cm in height on moisture-deficient sites and 95 cm in height on sites with moisture available all year. Sucker densities in the first year after harvest can reach 225 000 stems per hectare, but regardless of the first-year density, stands self-thin and usually stabilize in the range of 20 000–25 000 stems per hectare (Peterson et al. 1989).

Fire: Trembling aspen is adapted to an environment with recurring fires. High severity fires kill aspen, promote prolific sprouting, and maintain the seral aspen stage (Brown 1985b; Jones and DeBye 1985). Almost all even-aged aspen stands in the western U.S. appear to be the result of severe fire (Jones and DeBye 1985). Low severity fires thin aspen stands; aspen suckers and fire-tolerant conifer species (e.g., Douglas-fir and ponderosa pine) fill in canopy gaps.

Most suckers arise in the first year following a burn (Bailey and Anderson 1979; Zieroth 1984). The rapidly growing aspen suckers dominate burned sites before shrubs or trees that regenerate from seed are able to compete successfully. Brown (1985b) found that within about 4 years of burning, sucker density decreases and stabilizes as a result of competition-induced mortality. Burned areas typically produce more suckers than unburned areas because burning increases light intensity reaching the forest floor, and high soil temperatures in the rooting zone stimulate suckering (Horton and Hopkins 1965; Rouse 1986). A temperature threshold of 16°C for sucker initiation may exist (Hungerford 1988). The release of nutrients associated with burning may stimulate the growth rate of suckering during the first year after a fire (Fowells (compiler) 1985). High cytokinin:auxin ratios promote aspen suckering. These high ratios result when fire kills phloem tissue and leaves, thus preventing the downward flow of auxins and the upward flow of cytokinins (Brown 1985b).

Aspen suckering is common on burned sites in the SBS zone and is particularly prolific on dry sites that have abundant aspen prior to harvest (Hamilton 1988; Hamilton and Yearsley 1988). Root suckers can reach over 2 m in height within a few years and attain 10–20% cover in 16 years following burning of submesic and mesic sites.

Repeated burning is thought to promote suckering and result in denser stands (Fowells (compiler) 1965), but the regenerative capacity of aspen roots is not unlimited. A study by Buckman and Blankenship (1965) found that repeated spring burns eventually caused a significant reduction in sucker density. Jones and DeBye (1985) suggest that frequent fires may adversely affect site quality for aspen.

Cutting and Grazing: Cutting at any time of the year results in rapid regrowth of root suckers. In the ICH/mw subzone in the Salmon Arm District, suckers average 0.5–1 m in height after one growing season (J. Wright, pers. comm., July 1989). Many suckers were 1 m tall 2 years after cutting with chainsaws and brush saws in the SBS/mk subzone near MacKenzie (D. Greenley, pers. comm., July 1989). Suckers appear immediately after cutting treatments carried out during the growing season, or early in spring after a dormant season cutting (Fowells (compiler) 1965; Steneker 1976; Mueggler 1984). Factors that may influence sucker production include light availability, temperature, site quality, stump height, and cutting season (Johansson 1985b).

Cutting during the active season tends to minimize the number of suckers (Fowells (compiler) 1965; Sutton 1984), but Stenecker (1976) found that the effect of cutting season was negligible 2 or 3 seasons after treatment. Similarly, Bella (1986) found that initial differences in stand density on summer and winter cut areas diminished significantly within 5 years of treatment. Although winter cutting usually results in more suckering than summer cutting, Bella (1986) found the opposite effect after cutting 70- to 80-year-old aspen stands in east central Saskatchewan. This apparent discrepancy is explained by the fact that the winter-logged area had more slash than the summer-logged area, hence soil warming was inhibited on the winter-logged area.

When suckers are extremely numerous after clearcutting, the number of suckers rapidly declines over time due to self-thinning and other damaging factors including insects, browsing, and snowpress (Schier et al. 1985).

In a study examining the effect of repeated harvesting (cutting) at rotations ranging from 1 to 20 years, Stiell and Berry (1986) found that the shortest rotation at which sucker production can be physiologically maintained is about 10 years. Reduced growth in short rotations may be due to depletion of root stores by the frequent removal of photosynthesizing tops.

Cut trees can produce more than twice as many suckers as girdled trees, and sucker growth from cut trees is superior (Schier 1978). Bancroft indicates that complete girdling is recommended to kill aspen effectively and that mortality may occur in 1–3 years. He recommends girdling in the spring to obstruct the full growing season's supply of carbohydrates to the roots.

Moderate browsing causes vigorous sprouting of aspen, but intense browsing can severely damage or kill aspen sprouts. Although sheep are more destructive than cattle, aspen sprouts are out of reach of sheep sooner than of cattle (Brown 1985a). Trembling aspen showed severe signs of lost vigour 1 year after spring and early summer sheep grazing near Clearwater (G. Ellen, pers. comm., Aug. 1989).

**Herbicides:** Broadcast applications of 2–3 kg a.i./ha glyphosate have provided good to excellent control of trembling aspen (Sutton 1984; P. Wadey, pers. comm., June 1989; J. Wright, pers. comm., June 1989). Both Sutton (1984) and Mihajlovich and Switzer found that fall applications were generally much less effective than summer applications. Length of control following aerial applications of glyphosate is variable. One year after a late August broadcast spray of 3.0 kg a.i./ha near Dawson Creek, the treated area had 400 aspen (and balsam poplar) shoots per hectare compared to 22 300 aspen (and balsam poplar) shoots per hectare on an untreated control.

Hack and squirt treatments with glyphosate are highly effective. Hack-and-squirt may be most effective on stems smaller than 40 cm dbh. A mid-July hack-and-squirt treatment in the SBSmk subzone with a 50% solution of glyphosate and water 1 year prior to harvest eliminated 90% of aspen root suckering. This treatment was considerably more effective in reducing suckering than a post-harvest cut stump application. Near Penticton, hack-and-squirt was effective at one hack per 3 cm dbh with 1 ml of 50% glyphosate injected. Another study found that undiluted glyphosate applied by hack-and-squirt in August at 1 mL per 3–5 cm dbh resulted in complete aspen top-kill. Fall applications of 1.6 kg ai/ha glyphosate with brush saws equipped with herbicide applicators has been severely damaging to aspen in a dry IDF subzone in the Cariboo. Bancroft suggests that tree injections of glyphosate be applied in late summer or fall to ensure movement of the chemical to the roots. He recommends a 3-year period between tree injection treatments and harvest of the coniferous component of the stand to control aspen suckering.

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207 Mihajlovich and Switzer 1984.
208 Herring 1984a.
212 Bancroft 1989.
213 George 1989.
Broadcast or spot applications of hexazinone control aspen providing organic soil layers are not deep. Excellent control of aspen was maintained 4 years after September applications of 9–11 mL per spot hexazinone on a mesic SBSMc site in the Prince Rupert Forest District (N. Endacott, pers. comm., July 1989). Hexazinone applied in four spots within 30 cm of tree bases at 1 mL per 10 cm dbh resulted in 70% kill after 1 year.\textsuperscript{215} Liquid hexazinone applied around stem bases at 0.24–0.48 g per 1 cm of dbh controlled aspen seed trees in the Prince Rupert Forest Region.\textsuperscript{216} Spot gun applied hexazinone caused 90–100% defoliation of aspen within 2 years of treatment on a variety of sites in British Columbia.\textsuperscript{217}

Air or ground application of 2,4-D at 2.2 kg a.i./ha will kill all above-ground tree parts, but it will not prevent suckering (Bowes 1981; Harliss and Bartos 1985). However, 2,4-D applied at 4.4 kg a.i./ha kills aspen and results in minimal suckering. Basham (1982) found that after being sprayed with 1.4 kg a.i./ha of 2,4-D, surviving aspen had reduced height and diameter growth, but within 6 years they had resumed normal growth rates. To stimulate aspen regeneration, Harliss and Bartos (1985) recommend herbicide application soon after aspen leaves are fully expanded. For conifer release, they recommend herbicide application 1–3 weeks before aspen leaf fall.

Bancroft reports that one study found that pure 2,4-D amine applied by hack-and-squirt in August at 1 mL per 3–5 cm dbh resulted in complete aspen top-kill.\textsuperscript{218} He suggests that tree injections of 2,4-D be applied in late summer or fall to ensure movement of the chemical to the roots.

**Soil Disturbance:** Site preparation methods that expose areas of mineral soil, such as scarification and disking, will increase suckering by increasing soil temperatures and light penetration in the rooting zone (Fowell, compiler 1965; Jones 1974). Rows of suckers often appear along plowing furrows prepared for conifer regeneration (Fowell, compiler 1965). A high level of cultivation that eliminates the aspen root system is needed for effective control. Deep plowing techniques that tear up the tree roots will reduce suckering. For example, 30 cm deep cultivation significantly reduced suckering of aspen in the BWBSMw subzone in the Fort St. John Forest District (P. Wadey, pers. comm., June 1989). Soil compaction as a result of silvicultural or harvest operations may reduce suckering because root buds, from which suckers are formed, are near the soil surface where compaction is greatest.

To retard aspen growth for the benefit of conifers, scarification should be carried out after the suckers have completed at least one season’s growth (Basham 1988). In contrast, to attain sucker density and stocking for the development of a mature aspen stand, scarification should be carried out within 1 year of harvest. Basham (1982) found that scarified 3-year-old aspen suckers had significantly lower stem volumes after treatment than unscarified suckers, primarily due to damage to root systems. Scarification wounds on root systems were responsible for significantly more internal decay and stain on scarified than unscarified suckers. Susceptibility to windthrow and breakage due to decay is expected to be higher in scarified than unscarified aspen.

Hamilton and Yearsley (1988) observed no differences in the abundance of aspen after mechanical site preparation compared to burning in the SBS zone.

**Fertilization:** Nitrogen fertilization significantly increases aspen foliar biomass and leaf area (Coyne and van Cleve 1977). Aspen volume increased by 6–11% five years after application of various combinations of nitrogen, phosphorus, and potassium in Saskatchewan (Weitman et al. 1987). Safford and Czapowskyi (1986) found that nitrogen fertilization increased both growth and mortality of aspen 10 years after application, possibly by increasing competition and self-thinning. However, lime decreased mortality of nitrogen-fertilized aspen, possibly by reducing the activity of *Armillaria mellea*.

**WILDLIFE**

**Food:** Trembling aspen is important for ungulates, small mammals, and birds in British Columbia. It is a common winter and summer food for moose, mule deer, and white-tailed deer, and a year-round food source.
source for Rocky Mountain elk (Banfield 1974; Singleton 1976; Rue 1978; Harvey 1981). Mule deer feed on the bark (Fowells (compiler) 1965; McLean 1979; Zieroth 1984; Sampson 1989). Aspen leaves are a preferred summer food of porcupines (Banfield 1974) and these animals also eat the buds and catkins (Chapman and Feldhamer (editors) 1983). Aspen is preferred by beaver (Denney 1952, cited by Allen 1982; Banfield 1974), although Jenkins (1961, cited by Allen 1982) indicates that the apparent preference may be a reflection of higher availability of aspen over other tree species. Trembling aspen is important to snowshoe hares, particularly in winter (Hansen and Flinders 1969; Banfield 1974; Wolff 1978). It is important winter food throughout the range of ruffed grouse, and Cade and Sousa (1985) report that in Minnesota, one mature male trembling aspen provides 8 or 9 days of food for one grouse. Aspen buds and twigs provided 55% of the winter diet of ruffed grouse in Alaska (McGowan 1973, cited by Cade and Sousa 1985) and 35% in Alberta (Doerr et al. 1974, cited by Cade and Sousa 1985).

Other Resources: Aspen clones provide cover and edge habitat for big game (Zieroth 1984) and aspen stands with dense understories are important habitat for snowshoe hares. Aspen provides habitat and nesting sites for many game and song birds. Ruffed grouse are associated primarily with forests in which trembling aspen is the dominant species (Gullion and Svoboda 1972, cited by Cade and Sousa 1985; Cannings et al. 1987), and breeding blue grouse have a preference for aspen clones (Aldrich 1963, cited by Schroeder 1982). Trembling aspen is an important nesting tree for many birds in British Columbia, including woodpeckers, owls, herons, sapsuckers, flickers, flycatchers, nuthatches, orioles, and finches (Keisker 1986; Cannings et al. 1987; Sadoway 1988).

219 Blower 1982.
220 Korol and Wallis 1983.