

Bird Diversity and Abundance in Aspen Forests in Northern B.C.

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Introduction

Aspen (*Populus tremuloides*) forests in northern British Columbia support a rich array of wildlife, particularly a number of cavity-nesting and migratory birds whose habitats elsewhere have been much reduced by forest fragmentation and removal. Some 25 species of the bird fauna in B.C. are wholly or largely confined to the Peace River and Fort Nelson districts east of the Rockies and north of latitude 54°. This is where the Province's biggest supply of aspen also occurs (Enns et al. 1993).

Until the 1980s, the B.C. forest industry looked upon aspen as a weed tree, taking up space that might otherwise grow conifers such as spruce. Aspen also interfered with conifer harvesting, and was treated as wastewood to be piled and burned or left to rot. By the 1990s, however, this perception had changed. Faced with the prospect of smaller allowable cuts in other forest types, the industry began to look upon aspen as an under-used resource. Its limitations for pulp and paper had been overcome, and its advantages for particle board, chopsticks, and other specialty products began to be realized. Aspen is now regarded as a valuable

timber resource, and an expanding sector of the B.C. forest industry is based specifically upon it. By 1990, the B.C. Forest Service had granted rights to harvest 1.4 million m³ of aspen per year in the Peace River district alone.

Over most of its range, aspen is classed ecologically as a seral species, colonizing ground deforested by wildfire, windthrow, or pest outbreak, but eventually giving way to spruce or pine. From both an ecological and a silvicultural standpoint, aspen-dominant forest is merely an interim product of site history, constantly at risk of decline by natural succession. Insofar as harvesting can restart the seral sequence, it can be seen as beneficial—even necessary—if aspen forests are to be sustained in the long-term. The question arises: how should aspen be managed so as to keep its wildlife as well as its timber value, both of which might otherwise decline or be lost simply through the passage of time?

A range of possibilities exists. At one extreme, any and all harvesting and post-harvest silvicultural regimes (including benign neglect) could conceivably perpetuate these values by simply resetting the seral process to a pioneer stage with initial characteristics that are

pioneer stage with initial characteristics that are unimportant. At the other extreme, the exact course and outcome of post-harvest succession might dictate which values of the uncut forest are restored and which are lost. Between these extremes may lie a mixture of alternatives that would affect the rate of recovery as well as its course.

In order to find the alternatives that are most acceptable, their implications for wildlife need to be known. Most of the available information is for aspen outside B.C. The nearest source is west-central Alberta, where Westworth and Telfer (1993) described differences in bird species composition and abundance in seral stands of aspen and lodgepole pine. Flack (1976) listed 55 species of breeding birds that preferred aspen-dominant forest in western North America. The aspen wildlife community consists of more than just birds of course, but birds are more diverse and easier to observe than the rest of the vertebrate fauna. They are also good barometers of management effects.

What bird species occur in B.C.'s aspen forests? Which of these species appear to depend especially on aspen, and what characteristics of aspen appear to be most important to them? What changes occur in the bird fauna when aspen is removed? Does the difference vary with the amount removed? How quickly does the fauna return to 'normal' as aspen regrows?

These are questions addressed by two recent studies in different parts of northern B.C.—one in the Bulkley Valley near Smithers, the other near Dawson Creek in the Peace River district. Both have examined the bird content of aspen at different stages of growth. At both locations, aspen is near the periphery of its range. Conifers dominate most of the forest cover, and in the Bulkley Valley especially, aspen is only locally abundant. During this century, fire suppression (succession to conifers) and clearance to pasture have reduced it further. Around Dawson Creek, aspen is more abundant and widespread, but much has been lost to clearance there too and the remainder is now sandwiched between pasture at lower elevations and conifers above.

Due to this combination of factors, fewer bird species might be expected in these aspen stands than further east or south. The early findings from these two studies are summarized here.

Birds in a Successional Aspen Forest in West-central B.C.

Pojar (1993) compared 13 stands in four growth-stages. Ten of the stands were pure aspen; three also contained some spruce and pine. The four growth stages were: recent clearcuts (three stands, 4–6 years old), shrub/pole stage (three stands, <7–23-years old), mature (five stands, 50–60 years old), and old (two stands, again 50–60 years old but also containing some veteran trees aged 85–125 years). Two of the stands with conifers were in the mature age-range; the third was old. Birds were censused 10 times per year for 2 years, by the point-count method within a fixed distance of random points on a transect through each stand. Mean numbers of species and their relative abundances were calculated for each stand.

Sixty-three species were recorded during the 2 years (Table 1). The range was from a mean of 11 per stand in the recent clearcuts, to 24 per stand in old aspen, to 29 in the mixed stands of aspen, spruce, and pine. Numbers in shrub/pole and mature aspen stands were intermediate (Figure 1). The differences amongst stages were statistically significant in both years, except between the mature and old stages in 1991.

Mean number of species per plot

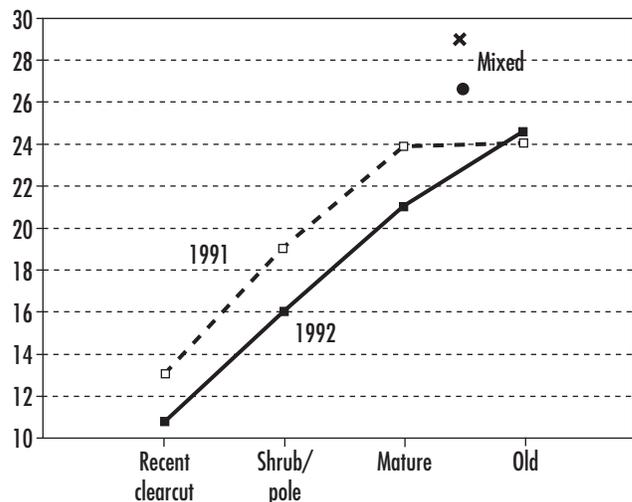


Figure 1. Number of bird species in four growth stages of aspen in the Bulkley Valley, west-central British Columbia (after Pojar 1993).

Table 1. Bird species recorded in the Bulkley Valley by Pojar (1993) and at Dawson Creek British Columbia

Species	Code ^a	Bulkley Valley ^b	Dawson Creek ^c	Species	Code ^a	Bulkley Valley ^b	Dawson Creek ^c
Alder Flycatcher	ALFL	*	*	Lincoln's Sparrow	LISP	*	*
American Crow	AMCR	*	*	Mallard	MALL	*	*
American Kestrel	AMKE	*	*	Magnolia Warbler	MAWA	*	*
American Pipit (Water Pipit)	AMPI	*	*	MacGillivray's Warbler	MGW	*	*
American Redstart	AMRE	*	*	Mountain Bluebird	MOBL	*	*
American Robin	AMRO	*	*	Mourning Warbler	MOWA	*	*
American Wigeon	AMWI	*	*	Northern Flicker	NOFL	*	*
Black and White Warbler	BAWW	*	*	Northern Goshawk	NOGO	*	*
Black-billed Magpie	BBMA	*	*	Northern Harrier	NOHA	*	*
Black-backed Woodpecker	BBWO	*	*	Northern Oriole	NOOR	*	*
Black-capped Chickadee	BCCH	*	*	Northern Waterthrush	NOWA	*	*
Brown-headed Cowbird	BHCO	*	*	Orange-crowned Warbler	OCWA	*	*
Blue Grouse	BLGR	*	*	Ovenbird	OVEN	*	*
Blue Jay	BLJA	*	*	Philadelphia Vireo	PHVI	*	*
Boreal Chickadee	BOCH	*	*	Pine Siskin	PISI	*	*
Bohemian Waxwing	BOWA	*	*	Pileated Woodpecker	PIWO	*	*
Blackpoll Warbler	BPWA	*	*	Purple Finch	PUFI	*	*
Brewer's Blackbird	BRBL	*	*	Rose-breasted Grosbeak	RBGR	*	*
Brown Creeper	BRCR	*	*	Red-breasted Nuthatch	RBNU	*	*
Black-throated Green Warbler	BTNA	*	*	Red-breasted Sapsucker	RBSA	*	*
Canada Goose	CAGO	*	*	Ruby-crowned Kinglet	RCKI	*	*
Calliope Hummingbird	CAHU	*	*	Red Crossbill	RECR	*	*
Canada Warbler	CAWA	*	*	Red-eyed Vireo	REVI	*	*
Clay-coloured Sparrow	CCSP	*	*	Red-tailed Hawk	RTHA	*	*
Cedar Waxwing	CEWA	*	*	Ruffed Grouse	RUGR	*	*
Chipping Sparrow	CHSP	*	*	Rufous Hummingbird	RUHU	*	*
Common Grackle	COGR	*	*	Red-winged Blackbird	RWBL	*	*
Common Nighthawk	CONI	*	*	Say's Phoebe	SAPH	*	*
Common Raven	CORA	*	*	Savannah Sparrow	SAVS	*	*
Common Snipe	COSN	*	*	Spotted Sandpiper	SDSA	*	*
Connecticut Warbler	COWA	*	*	Short-eared Owl	SEOW	*	*
Common Yellowthroat	COYE	*	*	Solitary Sandpiper	SOSA	*	*
Dark-eyed Junco	DEJU	*	*	Song Sparrow	SOSP	*	*
Downy Woodpecker	DOW	*	*	Solitary Vireo	SOVI	*	*
Dusky Flycatcher	DUFL	*	*	Sharp-shinned Hawk	SSHA	*	*
Eastern Kingbird	EAKI	*	*	Sharp-tailed Grouse	STGR	*	*
European Starling	EUST	*	*	Swainson's Thrush	SWTH	*	*
Evening Grosbeak	EVGR	*	*	Tennessee Warbler	TEWA	*	*
Fox Sparrow	FOSP	*	*	Townsend's Solitaire	TOSO	*	*
Golden-crowned Kinglet	GCKI	*	*	Townsend's Warbler	TOWA	*	*
Great Horned Owl	GHO	*	*	Tree Swallow	TRSW	*	*
Gray Jay	GRJA	*	*	Three-toed Woodpecker	TTWO	*	*
Hammond's Flycatcher	HAFL	*	*	Varied Thrush	VATH	*	*
Hairy Woodpecker	HAWO	*	*	Vesper Sparrow	VESP	*	*
Hermit Thrush	HETH	*	*	Warbling Vireo	WAVI	*	*
House Wren	HOWR	*	*	White-breasted Nuthatch	WBNU	*	*
Killdeer	KILL	*	*	White-crowned Sparrow	WCSP	*	*
Lapland Longspur	LALO	*	*	Western Tanager	WETA	*	*
LeConte's Sparrow	LCSP	*	*	Wilson's Warbler	WIWA	*	*
Least Flycatcher	LEFL	*	*	Winter Wren	WIWR	*	*
				White-throated Sparrow	WTSP	*	*
				White-winged Crossbill	WWCR	*	*
				Western Wood-Pewee	WWPE	*	*
				Yellow-bellied Flycatcher	YBFL	*	*
				Yellow-bellied Sapsucker	YBSA	*	*
				Yellow Warbler	YEWA	*	*
				Yellow-rumped Warbler	YRWA	*	*

^a From Campbell and Harcombe (1987).^b 1991-92.^c 1992-93.

Numbers of individuals (all species combined) showed a similar pattern, the youngest stands containing the fewest birds and old stands the most, regardless of whether the stand was pure aspen or mixed (Figure 2). These differences were statistically significant. Although species and individuals both were fewer in the second year (1992), the relative differences from stage to stage were still preserved.

Pojar attributed the differences between pure aspen stands to changes in the structural diversity of the stand as it matured. As it grew taller, the canopy gradually closed and new sub-canopy layers developed beneath it. As the number of bird species increased, the species composition also changed, but more so than the species totals alone would indicate. During the progression from stage to stage, species were lost while others were added, but more were gained than lost.

Some species merely changed in abundance rather than being gained or lost. Some were sparse in young aspen and then increased in older stands. Others did the opposite, declining into scarcity but remaining present while some eventually disappeared. This blurred the difference in species composition from stage to stage. In all, the process was a gradual change in bird content rather than a distinctly different series of species groups.

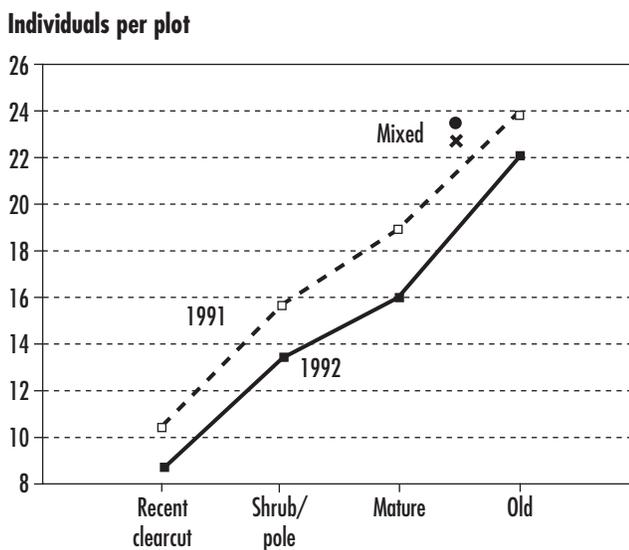


Figure 2. Numbers of individuals per plot in four growth stages of aspen in the Bulkley Valley, west-central British Columbia (after Pojar 1993).

Birds in a Successional Aspen Forest in Northeast B.C.

A study being conducted near Dawson Creek (Lance and Phinney 1992) is comparing 32 aspen-dominant stands, grouped into two size-classes: large (>25 ha) and small (<25 ha), and four growth stages: Newly Cut (1–2 years old), Shrub stage (3–10 years), Pole stage (20–38 years), and Mature (83–100 years). There are four replicates of each size and growth stage combination. Birds are censused 15 times per year from early April to mid-July by moving point-count along a sample transect through each stand. The approach and methods are similar to those of Pojar (1993), but with the added aims of (1) assessing the effect of stand or cutblock size, (2) assessing the influence of other habitats that adjoin any given stand, and (3) of tracking changes within the same stand as it develops over time.

Some 11 500 birds of 102 species have been recorded during the first 2 years (Table 1). So far, as in Pojar (1993), the average number of species per stand has differed from one stage of aspen to the next, young stages having the fewest species and mature aspen the most (Figure 3). Large stands have had more species than small stands, except in the Pole stage where the average number was the same (Figure 3).

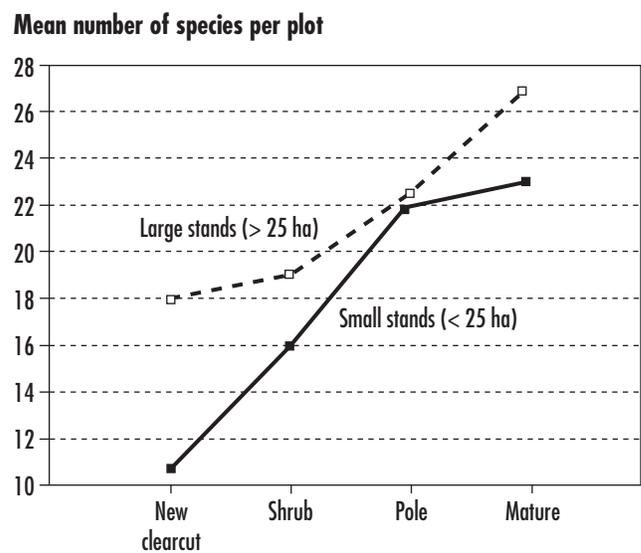
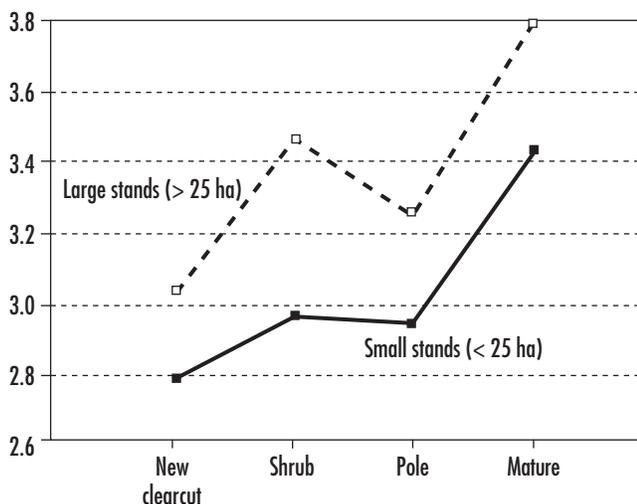


Figure 3. Numbers of bird species in four growth stages of aspen near Dawson Creek, north-eastern British Columbia (1992).

Number of individuals per stand showed much the same trend as species, except that Pole-stage stands averaged fewer individuals than the Shrub stage (Figure 4). The difference between large and small stands was more pronounced than with the number of species. So far, there has been no significant interaction between growth stage and stand size, either for the number of species or the number of individuals per stand: the difference between growth stages does not result from a greater effect of stand size in some stages than others.

How have the species distributed themselves from stage to stage? Each growth stage has had a few species showing a preference for it, but more have preferred mature aspen than have preferred younger stages; half the species recorded thus far have had one-third or more of their occurrences in Mature stands. Next most preferred was the Pole stage, and then the Newly Cut stage. Stages next to each other in the regrowth sequence have shared more species than stages further apart. The earliest and the latest stages have been the most discrete. The Newly Cut stage has resembled the Shrub stage more than the Pole and Mature stages, which in turn most closely resemble each other. By late Pole stage at about 40 years, many species typical of mature aspen could be found, though less abundantly than in the older stands.

Individuals per 10 m of transect^a



^a Transformed to square roots

Figure 4. Numbers of individuals per 10 m of transect in four growth stages of aspen near Dawson Creek, north-eastern British Columbia (1992).

Figure 5 compares the relative numbers of scarce and abundant species in each growth stage, plotted on a log scale to focus on the displacement (position) and inflection (change in shape) of each curve. All four curves have the same basic shape, with some scarce species, many moderately common ones, and some abundant ones. But they differ in their proportions of each. The Newly Cut stage has the most scarce species—birds with sparse numbers and erratic occurrence from stand to stand. From the Shrub to the Mature stage, the trend is reversed, with increasing numbers of common species and fewer erratic ones.

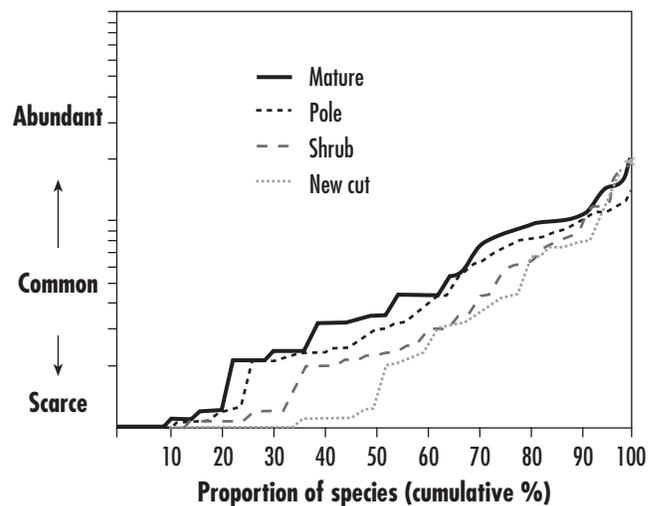


Figure 5. Relative proportions of scarce, common, and abundant species in four growth stages of aspen, Dawson Creek, British Columbia (1992).

Discussion

Two years' data are not enough for firm conclusions, but the similarities in the two studies are worth discussing briefly.

At 63 species in the Bulkley Valley study and 102 at Dawson Creek, neither area can be considered species-poor. In both cases, however, these are totals from all stand types combined. So far, the most species that any one aspen growth stage has contained is 49 (Pole stage and Mature aspen at Dawson Creek). The inference is that all four growth stages are needed if these totals are to be retained, and also to ensure that the mature stage does not eventually disappear through harvesting and succession to conifers.

Both studies indicate that the bird species assemblage changes quite markedly during aspen growth, but that no stage is discretely different—not even the Mature stage. As in Westworth and Telfer's aspen-pine succession in west-central Alberta, the change in bird content has been gradual rather than abrupt, consisting more of differences in relative abundance than differences in occurrence.

The lack of distinction between growth stages seems due more to high species numbers in the younger stages—Newly Cut and Shrub stage especially—than to a shortage of species in the older ones. The 49 species recorded from Pole-stage and Mature stands at Dawson Creek is not much less than the 55 which Flack (1976) listed as aspen-preferring in western forests. Flack's study covered places as far south as Colorado, and included species that do not range as far as northeast B.C. The species richness in Table 1 is therefore noteworthy.

Why has the difference between growth stages not been more discrete? As inhabitants of a successional forest type, the birds of aspen may be inherently suited to habitat change. The context surrounding any one stand may also have an effect. The aspen stands compared above do not sit in isolation; they are adjoined by other forest stands, comprised most often of mature aspen. Each individual stand may contain some birds that have their main habitat in neighbouring forest types.

The context factor is being examined in a further study at Dawson Creek, comparing four examples of mixedwood forest containing some of the 32 aspen stands discussed above. These four forests represent a gradient from complex (with many small stands of many different forest cover-types) to simple (with large stands and few different cover-types). Their bird populations are expected to differ in parallel: the more complex the forest, the more bird species and more individual birds it should contain.

In due course, the findings from these studies can be applied to commercial aspen harvest planning at both stand and landscape level. In the meantime, attention will also be given to internal differences within stands of similar size and growth stage, as well as differences in external surroundings. As data accumulate, this can be done on a species-by-species basis. For the more common species, sample sizes are already big enough, but for management purposes scarcer species are the most relevant, since these tend to be more vulnerable to disturbances such as logging. If their habitat influences can be identified in this way, the management of aspen forests for bird diversity should be capable of a prescriptive footing.

Acknowledgements

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References

- Campbell, R.W. and A.P. Harcombe. 1985. Wildlife Habitat Handbooks for British Columbia: Standard Taxonomic List and Codes of Amphibians, Reptiles, Birds, and Mammals. B.C. Min. Environ., B.C. Min. For., Min. Prov. Secretary and Gov. Serv. Wildl. Rep. No. R-11 86 pp.
- Enns, K., E. Peterson, and D. McLennan. 1993. Impacts of hardwood management on British Columbia wildlife: problem analysis. For. Can. and B.C. Min. For., Victoria, B.C. FRDA Rep. No. 208.
- Flack, J.A.D. 1976. Bird populations in aspen forests in western North America. Ornithological Monographs 19.
- Lance, A.N. and M. Phinney. [1992]. Bird diversity and abundance following aspen clearcutting in the Boreal White and Black Spruce Biogeoclimatic Zone. B.C. Min. For., Victoria, B.C. Unpubl. Rep.
- Pojar, R.A. [1993]. The diversity of breeding bird communities in aspen forests of the Sub-Boreal Spruce (SBSdk) in the Prince Rupert Forest Region. B.C. Min. For., Victoria, B.C. Unpubl. Rep.
- Westworth, D.A. and E.S. Telfer. 1993. Summer and winter bird populations associated with five age-classes of aspen forest in Alberta. Can. J. For. Res. 23:1830–1836.

The Nature of Nutrient Limitation in Black Cottonwood Stands in South Coastal British Columbia

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Abstract

This study examined relationships between the productivity of black cottonwood (as estimated by site index) and site units of the biogeoclimatic system, and quantitative estimates of soils and foliar nutrients in 29 black cottonwood stands in south coastal British Columbia. Membership in site association explained 87% of the variation in black cottonwood site index. Soil nutrient regime explained 88% of the variance in site index when stratified within site association, which can be used as a surrogate for soil moisture regime class. It was demonstrated in the study that soil nutrient regime was principally a gradient of increasing N availability, and that the availability of other important nutrients, such as P and K, did not increase along the same gradient in the stands studied.

All methods of analysis revealed consistent relationships between measures of site nutrient status and site index. Sample stands with high pH, high levels of exchangeable Ca and Mg, and low levels of soil N, P, and K, had foliar concentrations of N, P, and K diagnosed as limiting to black cottonwood growth, and had the lowest site index. High site index was recorded in stands with opposite soil and foliar nutrient properties.

Site index was seen to decrease in site units with increasing flood frequency and duration on alluvial floodplains. The decrease was attributed to the negative influence of flooding on the rate of organic matter mineralization, on nutrient uptake, and to the negative effects of high levels of soil Ca and high soil pH on the availability of soil P. On upland sites, soil gleying and prolonged rooting zone flooding during the growing season was correlated with low site index.

Optimal foliar levels for 13 foliar nutrients (based on mean foliar concentrations from the high site index class) were used as a field standard (Leech and Kim 1981) for DRIS interpretations of black cottonwood nutrient status. Using DRIS norms from the fastest-growing, fertilized trees in another experiment (McLennan 1993), it was concluded that black cottonwood stands in the high site index class are limited by K and then P.

Introduction

Black cottonwood (*Populus balsamifera* L. ssp. *trichocarpa* (Torrey and Gray) Brayshaw) is the largest, and most rapidly growing broadleaf tree in western north America (Roe 1958; Debell 1990). When provided with abundant

soil moisture and abundant soil nutrients, the species is capable of very rapid height growth (Smith 1980) and biomass accumulation (Heilman et al. 1972; Heilman and Peabody 1981; Heilman and Stettler 1983 1985b). This study examined the productivity of black cottonwood, as measured by site index, in a number of unmanaged stands that span the site index gradient for the species. Utilizing measures of nutrient status, the study attempted to understand the nature of nutrient limitation in unmanaged black cottonwood stands in south coastal British Columbia.

Although many studies have examined ecological aspects of the growth of coniferous species in western North America (Eis 1962; Monserud 1984; Kabzems and Klinka 1987b; Green et al. 1989; Klinka et al. 1989; Carter and Klinka 1990; Kayahara 1991; Wang, 1992), there have been fewer studies on broadleaved species such as red alder (Harrington 1986; Courtin 1992), and none on black cottonwood, except for a brief overview by Smith (1957). There have also been a number of evaluations of soil and foliar nutrient status and diagnosis of conifers (Klinka et al. 1984; Ballard and Carter 1986; Kabzems and Klinka 1987b; Courtin et al. 1988), but none have been conducted in broadleaved ecosystems, with predominantly Mull humus forms and rich soils. Many of the studies cited have shown that site index of the species studied is strongly correlated with soil moisture, soil nutrient, and regional climatic classes of the biogeoclimatic classification, but this work has not been done for black cottonwood.

Although no studies examining the ecological factors that determine the site index of black cottonwood have been carried out, work of this nature has been done on the eastern cottonwood (*P. deltoides*) by Broadfoot (1960), and Baker and Broadfoot (1976, 1979). The approach taken by Baker and Broadfoot (1976, 1979) combines both subjective and objective approaches by using quantitative measures of site properties to define the characteristics of four subjectively derived factors important for cottonwood growth on all sites soil physical condition, moisture availability, nutrient availability, and soil aeration. Harrington (1986) used a similar approach employing stepwise linear regression to identify major environmental factors affecting site index of red alder in western Washington and Oregon.

In the present study, correlations of black cottonwood site index with subzone, soil nutrient regime, and site association are used as a starting point for assessing the factors that determine black cottonwood productivity. Qualitative

estimates of soil nutrient regime describe nutrient availability for a site in general terms, but cannot account for the fact that the availability of soil nutrients for a particular species will differ from other species because of different physiological adaptations and nutrient requirements (Chapin et al. 1986). By establishing relationships between black cottonwood site index, quantities of soil-available nutrients (soil nutrient contents), and measures of nutrients taken up by the target trees (foliar nutrient concentrations), the particular nutrient or nutrients that are potentially limiting can be identified (White and Carter 1970a,b; Attiwil 1986; Chapin et al. 1986). Relationships within groups, such as soil nutrient interactions, and between soil and foliar nutrient levels, can also aid in the interpretation of the measurements as they may affect the productivity of black cottonwood. The determination of foliar nutrient status also permits the application of analytical methods such as critical nutrient levels (Lavender 1970; Ballard and Carter 1986; Weetman and Wells 1990) and assessments of nutrient balance through the determination of DRIS indices (Beaufils 1973; Leech and Kim 1979,1981; Schutz and de Villiers 1986), which are based on foliar nutrient concentrations. By summarizing soil and foliar nutrient measures over black cottonwood site index classes, the optimal amounts of nutrients can be assessed, and these can be compared to nutrient measures in each of the site associations. This will provide quantitative information for interpreting the nature of black cottonwood nutrient limitation within the site associations, and will express the results of the analysis in a format that has operational application.

The rate of height growth of black cottonwood at the 29 sites used for the study shows a greater than three-fold increase from 8.5 m/15 yrs in a low bench alluvial site to 30.8 m/15 yrs on an upland loess soil with seepage. This range in site index implies that there is a range of ecological conditions that parallels the increase in height growth. The general objective of this study was to begin to understand the changes in nutrient availability that occur as ecological factors change along this range of black cottonwood height growth in coastal British Columbia. The specific objectives of the study were:

1. to correlate black cottonwood site index with taxa of the biogeoclimatic ecosystem classification (Pojar et al. 1987—especially site associations, subzones, and soil nutrient regimes);

2. to characterize black cottonwood site index classes, and site association in terms of soil and foliar nutrient quantities;
3. to establish relationships among foliar nutrients, soil nutrients, and black cottonwood site index so that limiting nutrients and optimal foliar ratios can be established; and
4. to use foliar nutrient levels, DRIS indices, and soil contents to interpret the potential cause of nutrient limitation or sufficiency in the different site units.

Methods

Stand Selection

Twenty-nine stands were selected to represent the range of sites on which black cottonwood commonly grows in south coastal British Columbia (Table 1). The majority of sites were situated on alluvial floodplains, although upland landforms such as glaciomarine, glaciofluvial, and loess over till landforms were also sampled (Table 1). Alluvial floodplain sites were dominated by different subgroups of Regosol soils, while soils on upland landforms are Gleyed, Sombric, or Orthic Humo-ferric Podzols and Orthic Humic Gleysols. Soils were mostly coarse fragment-free, although a few sites had a significant amount of coarse fragments. Soil textures ranged from clay to sand, but generally soils had predominantly loamy (silt loam to sandy loam) soil textures. Most sites had Mull humus forms although some Moder humus forms were described.

Most of the sites selected for sampling supported well-stocked (500–900 stems/ha) deciduous stands dominated by black cottonwood (Table 1). However, to sample across the edatopic range of sites on which black cottonwood occurs, it was necessary to include a number of stands where black cottonwood was not the dominant species. At several sites, black cottonwoods sampled were scattered among well-stocked plantations of *Populus robusta* (Table 1), and these were considered to be ecologically very similar to pure black cottonwood stands. On upland sites, natural stands of black cottonwood do not occur, and black cottonwood is common as scattered individuals in a mixture of other deciduous and coniferous species. Stands of this nature were also sampled.

Ecosystem Description and Site Classification

Site, soil, and vegetation characteristics of 29 sample stands were described following methods described in Luttmerding et al. (1990). Site variables assessed included slope, aspect, mesoslope position, elevation, and landform. Classification of humus form (Klinka et al. 1981), and assessments of soil depth and texture, percentage of coarse fragments, rooting depth, root impeding horizons, seepage, water table depths, mottling, gleying, and genetic horizons were made in a soil pit excavated to a depth of 1 m (or to a root-impeding horizon). The soil pit used for the ecosystem classification was selected randomly from the soil pits excavated for soil chemical analysis. Qualitative estimates of the percent coverage of all plant species in a 20 × 20 m plot surrounding the soil pit were made in eight vegetation strata. Taken together, these observations permitted the determination of soil moisture and soil nutrient regime, and the identification of site association (Table 1), following keys provided in Banner et al. (1990).

Soil Sampling

Field Methods for Soil Sampling

Soil sampling for chemical and physical properties was carried out at two levels of intensity. The most intensive sampling, carried out at nine sites, was used in McLennan (1993) to evaluate within-site variability of soil nutrient concentrations and contents, and some other soil physical parameters. Soil nutrient concentration is an estimate of the amount of a nutrient, expressed as a percentage, or as parts per million, of the dry mass of the soil fine fraction (<2 mm diameter). Soil nutrient content attempts to estimate the total amount of a nutrient, and is expressed as kg/ha for a given soil depth.

Each of the nine intensively sampled black cottonwood stands was divided into 15 approximately even-area plots, and a random process was used to select a soil pit location within each. For soil chemical analysis a 5 × 5 cm column of soil was excavated from the side of a pit, starting at the top of the mineral soil to a depth of 1 m. Estimates of main rooting depth, absolute rooting depth, depth of the Ah horizon, and changes in the texture of the soil horizons were made concurrently. Main rooting depth was defined as that depth of soil that is more or less completely occupied by roots. Absolute rooting depth was defined as that level beyond which no additional roots could be found.

Table 1. Ecological and stand characteristics of 29 sample stands used in the study. Sample stands are listed in order of increasing black cottonwood site index and are divided into three black cottonwood site index classes, low, medium and high. Sites denoted by an asterisk were included in the reduced data set.

Sample stand	CWH subzone/ variant ^a	aSMR ^b	SNR ^c	Site association ^d	Elevation (masl)	Landform	Soil subgroup ^e	Site index (m/15 yrs)	Stand age (years) ^f	Relative % tree cover in main canopy ^g
1. Herring*	dm	lbF	M	Ac-Willow	30	floodplain/lb	CU.R	8.5	18	Ac (100)
2. Polygon 19*	dm	lbSD	M	Ac-Willow	30	floodplain/lb	CU.R	10.3	22	Ac (100)
3. Murphy 2*	dm	mbM	R	Ac-Red-osier dogwood	30	floodplain/mb	O.HR	11.5	27	Ac (72)/Dr (28)
4. Straw 1*	dm	lbM	R	Ac-Willow	20	floodplain/lb	CU.R	11.8	23	Ac (100)
5. Oyster*	xm1	fM	R	Cw-Salmonberry	200	glaciomarine	GL.HFP	12.2	49	Dr (60)/Ac (30)/Ar (10)
6. Polygon 20	dm	mbM	R	Ac-Red-osier dogwood	30	floodplain/mb	CU.R	13.0	43	Ac (87)/Dr (13)
7. Chilliwack	dm	M	R	Cw-Foamflower	250	glaciofluvial	GL.HFP	13.6	47	Fd (53)-Dr (27)/Ac (20)
8. Murphy1*	dm	lb/VM	R	Ac-Willow	30	floodplain/lb	O.R	13.9	19	Ac (85)/Dr (15)
9. Elk 3	xm1	fVM	R	Cw-Black twinberry	200	glaciomarine	O.HG	14.5	49	Ac (75)/Dr (25)
10. Elk 1*	xm1	fM	VR	Cw-Salmonberry	200	glaciomarine	GL.HFP	15.0	49	Dr (82)/Ac (9)/Mb (9)
11. Chipmunk	dm	SD	M	Cw-Swordfern	250	glaciofluvial	O.HFP	16.3	44	Fd (50)/Mb (25)/Ac (13)/Bg (12)
12. Elk 2	xm1	fVM	VR	Cw-Black twinberry	200	glaciomarine	O.HG	17.2	49	Dr (62)/Ac (38)
13. Straw 2*	dm	mbM	R	Ac-Red osier dogwood	25	floodplain/mb	O.R	18.5	25	Ac (83)/Dr (17)
14. Pierce*	dm	M	R	Cw-Foamflower	250	glaciofluvial	GL.HFP	20.4	46	Ac (40)/Dr (25)/Cw (20)/Hw (15)
15. Island 12*	dm	mbF	R	Ac-Red-osier dogwood	30	floodplain/mb	O.R	20.9	31	Ac (62)/A rob (30)/Dr (8)
16. Squam 38*	ds1	M	R	Cw-Foamflower	150	alluvial fan	O.R	21.1	22	Arob (69)/Ac (31)
17. Mercer*	dm	mbM	R	Ac-Red-osier dogwood	30	floodplain/mb	O.HR	21.2	38	Arob (65)/Ac (25)/Dr (5)/Mb (5)
18. Carey*	dm	mbM	VR	Ac-Red-osier dogwood	25	floodplain/mb	O.HR	21.9	25	Arob (80)/Ac (18)/Dr (2)
19. Salmon*	xm1	hbM	VR	Ss-Salmonberry	50	floodplain/hb	O.HR	23.0	27	Ac (85)/Dr (15)
20. Soowahlie*	dm	hbF	VR	Ss-Salmonberry	90	floodplain/hb	O.HR	23.0	12	Ac (90)/Mb (8)/Dr (2)
21. Squam 23*	ds1	hbM	VR	Ss-Salmonberry	75	floodplain/hb	O.HR	24.4	14	Ac (85)/Dr (10)/Mb (5)
22. Borden*	dm	hbF	R	Ss-Salmonberry	100	floodplain/hb	O.R	24.6	25	Ac (37)/Dr (60)/Cw (3)
23. Tam Fan*	dm	M	VR	Cw-Foamflower	100	alluvial fan	O.R	25.2	18	Ac (100)
24. Chester*	dm	mbM	VR	Ac-Red-osier dogwood	15	floodplain/mb	O.HR	25.7	28	Arob (80)/Ac (15)/Dr (3)/Mb (2)
25. Tam C ¹ *	xm1	hbM	VR	Ss-Salmonberry	100	floodplain/mb	O.HR	26.2	15	Ac (83)/Mb (12)/Dr (5)
26. Sumas*	dm	M	VR	Cw-Foamflower	150	loess/til	SM.HFP	27.1	30	Arob (75)/Ac (15)/(Dr (10)/Mb (5)/Cw (5)
27. Squam 29*	ds1	hbM	R	Ss-Salmonberry	45	floodplain/hb	CU.HR	28.1	19	Ac (53)/Dr (35)/Arob (6)/Cw (6)
28. Ashlu *	dm	hbM	R	Ss-Salmonberry	30	floodplain/hb	CU.HR	28.4	21	Ac (60)/Dr (40)
29. Ryder*	dm	M	VR	Cw-Foamflower	150	loess/til	SM.HFP	30.8	25	Arob (75)/Ac (15)/Ep (8)/Dr (2)

^a CWH subzones and variants identified from Nuszdoerfer et al. (1990); dm=dry maritime, xm=very dry maritime, and ds = dry submaritime
^b Actual soil moisture regime (aSMR) classes are; SD=slightly dry; F=fresh; M=moist, and Mb=very moist and were identified using Banner et al. (1990) and Green et al. (1984). For alluvial sites SMRs refer to the moisture conditions when the site is not flooded, and hb, mb, and lb denote flooding regimes for the high, middle, and low bench sites respectively. Sites with poorly drained, fine-textured soils in depressions with winter-summer fluctuating water tables are denoted with an 'f', and the SMR noted is that during the growing season.
^c Soil nutrient regime (SNR) classes are M=nutrient medium; R=nutrient rich, and VR=nutrient very rich, and were determined from field observations using Banner et al. (1990) and Green et al. (1984)
^d Site associations were determined from Banner et al. (1990)
^e O.HFP=Orthic Humo-Ferric podzol; SM.HFP=Sombic Humo-Ferric Podzol; O.HG=Orthic Humic-Gleysol.
^f Refers to total age of the stand in 1989 based on the mean total age of site index trees
^g Codes for species are; Ac = black cottonwood; Arob = 'Robusta' hybrid; Dr = red alder; Mb = bigleaf maple; Ep = trembling aspen; Fd = Douglas-fir; Bg = grand fir; Cw = western redcedar; Hw = western hemlock

The accurate determination of absolute rooting depth was impractical, given the depth of many of the soils studied. In many cases, absolute rooting depth was described simply as greater than the maximum depth of the soil pit excavated. Surface organic horizons (L, F, or H layers) were either absent or too thin to be included in the soil chemical sampling in all of the intensively sampled sites.

In the 20 less intensively sampled study sites, each black cottonwood stand was divided into four equal areas, and a random procedure used to select a soil sampling location within each. In each quadrat a soil pit was excavated to a depth of at least 1 m (or to a restricting layer), and soil samples were removed from each of the four walls, using the same procedure described above for the intensively sampled plots. These four samples were then placed in one sample bag to make up a composite soil chemical sample. In some cases the less-intensively sampled ecosystems had forest floors, and, in these cases, separate mineral soil and forest floor samples were collected in the following manner. At each of the four pits, four forest floor samples were cut with a knife so that the undisturbed dimensions of the rectangular section of forest floor removed could be measured and the volume calculated. Each forest floor sample was bagged separately for laboratory analysis, and later composited to get one sample for each of the four pits sampled.

As for soil chemical sampling, mineral soil bulk densities were measured differently in the intensively, and the less intensively, sampled sites. In the intensively sampled sites, a cylindrical hole was excavated to 30-cm soil depth and all material placed into a plastic bag and labelled. The volume of the hole was measured by inserting a thin, plastic bag into the hole, filling the bag with water to the soil surface, and then measuring the volume of water within the plastic bag in a graduated cylinder. At the less intensive sites, a coring device was used to excavate a 7 cm long cylinder of known volume, after which the soil was removed and placed into a plastic bag. To coincide with the soil chemical sampling, this procedure was repeated until bulk density measures were made over the same soil depths as the soil chemical samples.

Coarse fragment content within the pits was evaluated by separating and weighing, in the field, all mineral fragments larger than 2.5 cm diameter, and by carefully excavating the soil pit to a known dimension so that the volume of the soil pit could be calculated. Using an average solid particle density conversion factor of 2.65, the total mass

of coarse fragments >2.5 cm for the pit was converted to volume and expressed as a percentage of the soil volume. All mineral fragments greater than 2 mm diameter were removed by sieving soils in the laboratory, converted to a volume measure using the average solid particle density factor, and then added to the >2.5 cm coarse fragment fraction to get a total coarse fragment percentage.

Laboratory Analysis of Soil Samples

Mineral soil samples were transported in plastic bags to the laboratory, where they were thoroughly mixed, air dried, passed through a 2 mm sieve to remove coarse fragments, and then subsampled for analysis. Forest floor soil chemical samples were air dried to constant mass, ground in a Wiley mill, and then composited for analysis. Mineral soil pH was measured with a pH meter using a 1:2 soil:0.01 M CaCl₂ suspension, as described by Peech (1965). Forest floor pH was measured with a pH meter using a 1:5 suspension in distilled water. Total carbon was determined using a Leco Induction Furnace (Bremner and Tabatabai 1971). Total nitrogen was determined by semi-microKjeldahl digestion (Bremner and Mulvaney 1982), followed by colorimetric analysis of ammonium using a Technicon Autoanalyzer (Anonymous 1966). Mineralizable nitrogen was determined from incubated samples for 14 days at 30°C using the anaerobic incubation method of Wareing and Bremner (1964), as modified by Powers (1980), using a Technicon Autoanalyzer to measure released ammonium. The Mehlich extraction method (Mehlich 1978) was used to measure extractable P, as suggested by Curran (1984). Available sulphate-sulphur was determined by ammonium acetate extraction (Bardsley and Lancaster 1965), reduction to sulphide, followed by colorimetric determination of the reduced sulfide (Kowalenko and Lowe 1972). Extractable K, Ca, and Mg were determined by extraction with Morgan's solution of sodium acetate with a pH of 4.8 (Grewelling and Peech 1960), as recommended by Klinka et al. (1980). All soil nutrient measurements were expressed as percent or parts per million of soil dry mass.

Subsamples of the soil chemical samples were used to determine the percentage of clay, silt, and sand in the samples using the pipette method (Council for Soil Testing and Plant Analysis 1974). Measurements of soil texture were carried out on samples composited over the entire depth used for the soil chemical sampling.

Coarse fragment free bulk densities were determined by measuring the mass of samples of known volume after oven-drying at 105°C to constant mass, and passing the samples through a 2 mm sieve to remove the coarse fragments. Mass of soil <2 mm in diameter was then divided by the volume of soil <2 mm diameter (corrected for coarse fragments >2 mm using the average solid particle density factor) to arrive at coarse fragment-free bulk density.

Soil nutrient measurements were expressed as concentrations (% or ppm) of soil dry mass based on the analytical procedures. Using soil nutrient concentration, coarse fragment-free bulk density, and a measure of soil volume (coarse fragment corrections and main rooting depth/root restricting layer measurements), soil nutrients were expressed on a mass per unit area (kg/ha) basis.

Foliar Sampling

Field Methods for Foliar Sampling

The closest healthy, dominant or codominant black cottonwood to each of the 15 randomly selected soil pits was selected for foliar sampling. In stands with only four soil pits, 11 additional trees that met the sampling criteria were randomly selected for foliar sampling. Foliage samples were collected between August 15 and 30 in 1987 and 1988 by a variety of methods (clipping with a pole pruner, tree felling, and shooting) depending on stand height and canopy characteristics, and followed the recommendations of Mitchell (1936). Black cottonwood is characterized by heterophyllous foliage so that two types of leaves (preformed, early leaves and late leaves) are found within the same branch (Critchfield 1960). In this study, black cottonwood late leaves were easily distinguishable from early leaves by their larger size and darker green colour. Only the most recently matured late leaves were sampled and this meant avoiding both the early leaves and the newly formed, apical late leaves. Using these sample selection criteria, 30 g fresh weight foliage samples were collected from lateral branches within the upper one-third of the canopy at all locations.

All foliage samples were placed in paper bags and air-dried briefly until they could be oven-dried at 70°C for 24 hours, and then ground to pass a 20-mesh screen.

Laboratory Analysis of Foliar Samples

Foliar concentrations of N, P, K, S, SO₄-S, Ca, Mg, Cu, Zn, Fe, active-Fe, Mn, and B were determined using the following procedures. One-gram samples were wet ashed following Parkinson and Allen (1975), followed by colorimetric analysis for N (phenol-hypochlorite method) and P (unreduced vanadomolybdate complex), and atomic absorption spectrophotometry for K, Ca, Fe, Mg, Mn, Zn and Al. Copper was determined by digestion in nitric acid and hydrogen peroxide followed by atomic absorption spectrophotometry. Boron was determined by dry ashing followed by colorimetric analysis by the azomethine H method (Gaines and Mitchell 1979). Active-Fe was extracted by a modification of the method of Oserkowsky (1933) using 1 M HCl and analyzed using atomic absorption spectrophotometry. Sulphur was analyzed using a Fisher Sulphur Analyzer, as described by Guthrie and Lowe (1984). The method of Johnson and Nishita (1952) was used to assess concentrations of SO₄-S. Macronutrients were expressed as percentage concentration and micronutrients as parts per million (ppm) of oven-dry mass.

Stem Analysis and Site Index Determination

Black cottonwood trees selected for stem analysis were canopy dominants or codominants, without physical damage or evidence of disease or suppression. Stem analysis trees were felled at 0.30 m, after which total height of the tree was measured. Based on the difference between total height and breast height (1.3 m), disks were removed at breast height and at 10 equal-length segments to the top of the tree. Height of the section above the ground surface was noted for all disks removed. Stumps were cut off flush with the ground to get an estimate of total age. This involves some error on alluvial sites because trees may be buried by sedimentation, so that the germination point can occur somewhere below ground level. Given the rapid juvenile growth of black cottonwood, this error was considered to be small.

All disks were taken from the field for counting of the annual rings because of the difficulty in obtaining reliable age estimates from the diffuse porous wood of black cottonwood. All disks were dried in a lumber kiln, sanded with a belt sander, and moistened before counting under a 10× power binocular stereoscope. All disks were counted until the same age was arrived at on two separate counts, by two different observers.

Height at an index age of 15 years (breast height age) was estimated by first correcting estimated heights to true heights (Carmean 1972; Dyer and Bailey 1987), and then using an interpolation program to calculate total height by 1 year increments. Except for the Sites 4, 10, 20, and 21, all curves are based on the means of three site trees. At Site 10, only two trees were sampled, and at Sites 4 and 21 means are based on the 15 (10 at Site 20) control trees used in fertilizer experiments conducted at those sites. Since a sample size of 15 trees was used at Sites 4 and 21, they can be used to estimate the accuracy and precision of black cottonwood site index estimates where only three trees were collected. The mean CV for Sites 4 and 21 was 8.3%. Using an alpha of 0.90, site index means at the sample sites with three trees per plot (assuming that the variances do not differ significantly among sites) are estimated at $\pm 15\%$ error.

Breast height age of the stands were distributed fairly evenly between 12 and 49 years (Table 1). Site index of black cottonwood showed an almost four-fold increase from 8.5 to 30.8 m in 15 years. Estimates of site index for the two stands younger than the index age (Sites 20 and 21) were based on extrapolation of the distinctly linear height-age curves that characterize juvenile height growth of black cottonwood. By dividing the population of study sites by approximately 3, study sites were assigned to low, medium, and high site index classes. These groups are used to analyze relationships between black cottonwood site index and ecological variables.

Statistical Methods

A single-factor, one-way ANOVA model was used to test the hypothesis of no significant difference in black cottonwood site index among subzones, site associations, and soil nutrient regimes. In all cases the data met the criteria of being normally distributed variables from a random sample, as determined by visual inspections of plots of the measured values against those expected from a normally distributed population (Wilkinson 1990). Homogeneity of variance was achieved through logarithmic transformations of those samples that did not satisfy the Bartlett test. Since the treatment effect was random and quantitative, and the objective was to compare site index among groups, Duncan's multiple range test was used to compare means (Mize and Schultz 1985).

Multiple linear regressions were carried out using the approach that ANOVA and linear regression are both

components of the general linear model (Cohen 1968; Wilkinson 1990), and model assumptions for the linear regression were tested in the same manner as for the ANOVAs, as described above. Ecological variables such as foliar nutrients or soil nutrient contents, used here to predict black cottonwood site index, are not independent, and thus violate a major assumption of linear regression (Chatterjee and Price 1977). For this reason a series of univariate regressions was used to demonstrate relationships between dependent and independent variables, and these were combined into complete multivariate models only for independent variables where intercorrelations were not significant. The major diagnostic tool used to evaluate the multiple regression models was the coefficient of determination.

For brevity, correlations of site index with quantitative measures of soil and foliar nutrients reported in this paper are based on a reduced data set (Table 1), and include only sample stands dominated by hardwoods. Comparisons with results for the full data set are included in the discussion of results. Models using all 29 sites, as well as principal components analysis, site index vegetation correlations, ANOVAs of all groups, and univariate regression models are reported in McLennan (1993).

Results

Correlations of Site Index with CWH Subzones, Site Associations, and Soil Nutrient Regimes

The relatively low influence of location within the three different CWH subzones on black cottonwood site index is shown by the ANOVA comparing means for the three groups (Table 2). The ANOVA was not significant ($p=0.593$) and suggests that differences in the limited range of climates in which study sites were located did not outweigh variation in site index within subzones.

The ANOVA on site associations (sa's) was highly significant ($p<0.001$) and explained 87% of the variance in black cottonwood site index (Table 2). Black cottonwood site index fell into two main groups - a group with significantly lower site index which includes study stands within the Ac-Willow, "Gleyed" (Cw-Salmonberry/Cw-Black twinberry), and a second group, with significantly higher site index, which includes the Ac-Red-osier dogwood, Ss-Salmonberry, and Cw-Foamflower site

associations. The one site included in the Cw-Swordfern site association falls into the lower site index group. Because of the small number in each class and similar black cottonwood site index, study sites within the Cw-Salmonberry/Cw-Black twinberry site associations were considered together as the “Gleyed” sa’s in this study.

Table 2. Means and results of ANOVAs for black cottonwood site index (m/15 yrs) in 3 subzones, 3 soil nutrient regime groups, and 5 site associations. Values with the same letter are not significantly different at $p < 0.05$.

Group/subgroup	n	Black Cottonwood site index (m/15 yrs)
Subzone		
CWHdm	17	19.3a
CWHds	6	21.8a
CWHxm	6	18.1a
Significance ^a		NS
Soil nutrient regime		
Medium	3	11.7 a
Rich	15	18.3 a
Very rich	11	23.6 b
Significance ^a		**
Site association		
Ac-Willow	6	11.5 a
“Gleyed”	4	14.7 a
Ac-Red-osier dogwood	5	21.6 b
Ss-Salmonberry	7	25.4 b
Cw-Foamflower	6	23.5 b
Significance ^a		***

^a statistical significance of the ANOVA; NS = $p > 0.05$; * = $0.05 > p > 0.01$; ** = $0.01 > p > 0.001$; *** = $p < 0.001$

The results of the ANOVAs on soil nutrient regime show that average black cottonwood site index between the medium and rich SNR groups was not statistically different, but they were significantly lower than black cottonwood site index in the very rich SNR group. As for site associations, the ANOVA on SNR groups was highly significant ($p = 0.003$), but the SNR ANOVA explained only 36% of the variance in black cottonwood site index.

The ANOVAs of black cottonwood site index within site association or soil nutrient regime did not isolate the effect of soil moisture or soil nutrients because the site association groupings included medium to rich soil nutrient regimes, and the soil nutrient classes encompass the range of

flooding regimes and soil moisture conditions. The ANOVA of black cottonwood site index within site associations stratified by soil nutrient regime explained 88% of the variance within the rich class, and 74% of the variance within the very rich class. Because of the small numbers in each group it was not possible to assess the effect of nutrient regime within site association.

Linear Regressions of Soil Nutrient Contents on Black Cottonwood Site Index

Parameters and summary statistics for univariate regressions of soil nutrient contents (kg/ha) on black cottonwood site index for the reduced data set are shown in Table 3. Models are listed in order of increasing R^2 . Only significant ($p > 0.05$) regressions are shown, and, if significant, only the most significant of either log-transformed or non-log-transformed variables are included. Log total N (ltotN), total C (totC), log mineralizable N (lminN), and log available P (lavP) all had significant positive relationships. Coefficients for exchangeable Ca (exCa) and log exchangeable Mg (exMg) were significant but negative.

Table 3. Probability (p), coefficients of determination (R^2), and standard error of the estimate (SEE) for univariate regressions of soil nutrient contents on black cottonwood site index in the reduced data set. Only soil nutrients with significant ($p < 0.05$) regressions are shown.

Model	p	R^2	SEE (m)
(1) $SI_{Ac} = 11.58 + 0.001 (totN)$	0.000	0.52	4.64
(2) $SI_{Ac} = -93.19 + 9.810 (ltotC)$	0.000	0.57	4.45
(3) $SI_{Ac} = -8.14 + 6.16 (lminN)$	0.000	0.62	4.12
(4) $SI_{Ac} = 6.12 + 4.198 (lavP)$	0.009	0.31	5.68
(5) $SI_{Ac} = 26.62 - 0.003 (exCa)$	0.013	0.30	5.76
(6) $SI_{Ac} = 24.88 - 0.001 (lexMg)$	0.030	0.22	5.99

Univariate regressions of soil nutrient contents on black cottonwood site index for the reduced data set were similar to those shown for the full data set, except that exchangeable K was not significant, and exchangeable Ca and Mg demonstrated significant and negative linear relationships. For all nutrients except exchangeable K, the variance explained by the linear models based on the reduced data

set was about twice as high as that based on the complete data set. The stronger relationships demonstrated for soil nutrients in the reduced data set were due primarily to the reduction in humus form variability, and in the deletion of upland sites where soil drainage was impeded, so that uptake of nutrients present within the soil was impaired.

Multiple regression models of soil nutrients with significant univariate regressions on black cottonwood site index explained about 80% of the variance in black cottonwood site index for the reduced data set (Models 1–5, Table 4). Complete models with regression coefficients are not given because of significant correlations among the explanatory variables with significant univariate probabilities (Table 5). Correlation matrices for both the log-transformed and the non-log-transformed values of soil nutrients significantly correlated with site index (Table 5) show that total N, total C, and mineralizable N formed a significantly, positively correlated group, as did exchangeable Ca and Mg. Available P had a significant negative correlation with both exchangeable Ca and Mg. In the multiple regressions, total C and N were not entered and mineralizable N was used to represent them. Given the high positive correlation of exchangeable Ca and Mg, a new variable was created (ex Ca+Mg) that sums the two values. This variable did not increase the explanatory power of the models (Model 2, Table 4). Dropping exchangeable Mg from the model did not reduce the percentage of variance explained (Model 3, Table 4), although, when exchangeable Ca was omitted, the percentage of variance explained dropped to 69% (Model 4, Table 4). The model using the log-transformed values explained about the same percentage of variance as the non-log-transformed soil nutrient values (Model 5, Table 4).

Table 4. Probability (p), coefficients of determination (R^2), and standard error of the estimate (SEE) for multiple regressions of soil nutrients on black cottonwood site index, using variables with significant univariate regressions on black cottonwood site index in the reduced data set (n=22)

Model	p	R^2	SEE (m)
(1) minN, avP, exCa, exMg	.000	.79	3.59
(2) minN, avP, ex (Ca+Mg)	.000	.79	3.38
(3) minN, avP, ex Ca	.000	.80	3.34
(4) minN, avP, ex Mg	.000	.69	4.08
(5) lminN, lavP, lex(Ca+Mg)	.000	.80	3.46

Table 5. Correlation matrices for soil nutrient variables with significant univariate linear regressions on black cottonwood site index for the reduced data set. Bolding indicates significant ($p < 0.05$) correlations.

	totN	totC	minN	avP	exCa
totC	0.870				
minN	0.662	0.728			
avP	0.070	-0.070	0.350		
exCa	-0.407	-0.396	-0.471	-0.600	
exMg	-0.118	-0.174	-0.278	-0.527	0.745
	ltotN	ltotC	lminN	lavP	lexCa
ltotC	0.920				
lminN	0.850	0.865			
lavP	0.226	0.057	0.407		
lexCa	-0.294	-0.279	-0.389	-0.473	
lexMg	0.046	0.009	-0.119	-0.416	0.881

Interaction of Soil Available-P, Soil Exchangeable Ca, and Soil pH

The solubility and availability of soil P is determined to a large extent by soil pH and the concentrations of Ca available to fix P as calcium phosphate concretions (Boishot et al. 1950; Cole et al. 1953; Griffin and Jurinak

1973; Russell 1974). The significant ($p < 0.05$) negative relationship between available P and exchangeable Ca (Table 5) suggests that this effect may be responsible for the low amounts of available P in study site soils with high exchangeable Ca contents. This relationship is well demonstrated for the 22 sites in the reduced data set (Figure 1). In Figure 1, available P is much lower when soil pH is in excess of 6.5, and when exchangeable Ca contents increase over about 15,000 kg/ha. Data labels in Figure 1 refer to high (H), medium (M), and low (L) site index classes, and the trend is for high site index class sites to have high amounts of available P, relatively low amounts of exchangeable Ca, and relatively low pH. Although an indication of total P in these soils is required to confirm it, one explanation for this relationship is that soil contents of available P are fixed and thus made unavailable in black cottonwood stands with high pH and exchangeable Ca contents.

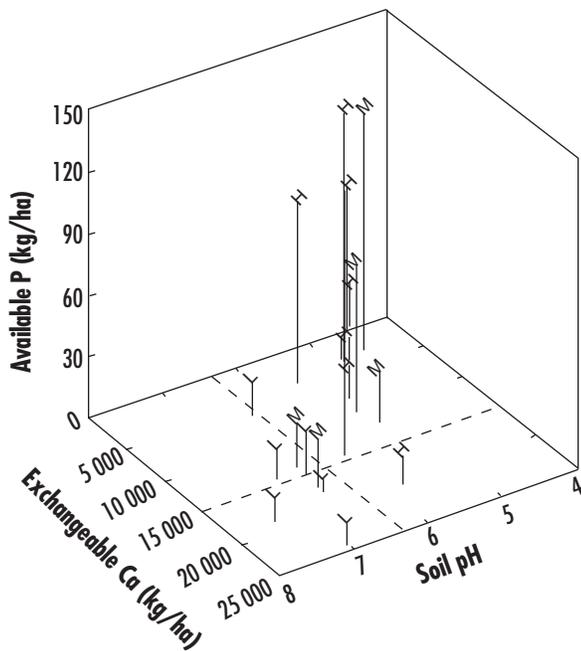


Figure 1. Three-dimensional scattergram showing the effect of increasing soil pH and content of soil exchangeable Ca on content of soil available P for the reduced data set ($n=22$). Study sites are labeled by their black cottonwood site index class (L=low; M=medium; H=high).

Linear Regressions of Foliar Nutrient Concentrations on Site Index

Table 6 presents model parameters for foliar nutrients with significant regressions on site index for the reduced data set. Foliar N (folN) alone accounted for about 70% of the variation in black cottonwood site index, followed by foliar K (folK), Cu (folCu), P (folP), and S (folS), in decreasing order of variance explained. The list of significantly correlated foliar nutrients in the reduced data set (Table 6) was essentially the same as for the complete data set, except that the regression with foliar P was significant, and that for foliar SO_4 was not. In general, the percentage of variance explained was higher for the reduced data set, and the standard errors of the estimate about the same.

Table 6. Probabilities (p), coefficients of determination (R^2), and standard errors of the estimate (SEE) for univariate regressions of foliar nutrients on black cottonwood site index. Only foliar nutrients with significant ($p < 0.05$) regressions are shown.

Model	p	R^2	SEE (m)
(1) $SI_{Ac} = -7.937 + 12.767$ (folN)	0.000	0.701	3.36
(2) $SI_{Ac} = 2.772 + 11.506$ (folK)	0.001	0.458	4.66
(3) $SI_{Ac} = 274.66 + 446.19$ (folCu)	0.004	0.381	4.98
(4) $SI_{Ac} = 2.550 + 80.442$ (folP)	0.010	0.315	4.76
(5) $SI_{Ac} = 4.903 + 61.107$ (folS)	0.010	0.315	5.24

The multiple regression model that included all foliar nutrient variables with significant univariate regressions on black cottonwood site index (Model 1, Table 7) had the highest explanatory power with an R^2 of about 80%. As for soil nutrient contents, the correlation matrix presented in Table 8 shows a high degree of intercorrelation among foliar nutrients that have significant regressions on site index. Model 2 (Table 7), which excluded S, had a slightly lower R^2 , as did Model 3 (Table 7), which included only foliar N, P, and K. Forward stepwise regression that began with all foliar variables with significant univariate regressions identified foliar N and P as the most important nutrients determining site index in the reduced data set (Table 7, Model 4). This model explained 78% of the variation in black cottonwood site index, and had a standard error of the estimate of 3.07m.

Table 7. Probabilities (p), coefficients of determination (R^2), and standard errors of the estimate (SEE) for multiple regressions of foliar nutrients on black cottonwood site index in the reduced data set

Foliar nutrients	p	R^2	SEE (m)
(1) N,P,K,S,Cu	0.001	0.795	3.28
(2) N,P,K,Cu	0.000	0.788	3.20
(3) N,P,K	0.000	0.779	3.24
(4) Forward stepwise (N,P,K,S,Cu) - N,P	0.000	0.775	3.07

Table 8. Correlation matrix for foliar nutrient variables with significant univariate linear regressions on black cottonwood site index. Bolding indicates significant ($p < 0.05$) correlations.

	N	P	K	S
P	0.573			
K	0.817	0.687		
S	0.824	0.272	0.648	
Cu	0.823	0.287	0.650	0.804

Relationships between Foliar and Soil Nutrients

Univariate regressions (Table 9) show that concentrations of P, N, K, and Mg in black cottonwood foliage were well correlated with measures of soil contents (kg/ha) for the same nutrients. Scattergrams for all nutrients listed in Table 9 are shown in Figure 2, where best-fit lines are shown. Measures of soil available P, as measured by the new Mehlich method, accounted for 83% of the variation in foliage concentration of black cottonwood trees on those sites, and had a standard error of the estimate of 0.018% dry mass. Increases in foliar P were also associated with increasing black cottonwood site index, as shown by the site index class labels for the sites shown in Figure 2. Although the percentage of variance explained is not as high (Table 9), similar relationships exist for foliar N and foliar K concentrations (Figure 2). The increasing concentrations of foliar Mg were significantly correlated

with measures of soil exchangeable Mg contents, but the increase was not associated with increases in black cottonwood site index (Figure 2). Most sites in the high site index class had relatively low foliar Mg concentrations and soil Mg contents. Regressions for foliar S and Ca on measures of soil SO_4 and Ca contents were not significant, and suggested that soil contents of these nutrients were sufficient and did not limit their uptake in the sites studied.

The results of the regressions shown in Table 9 and illustrated in Figure 2 support a trend that is evident from analysis of both the soil and foliar nutrient data for the stands studied. The availability of N, P, and K in soils within the study sites were the principal nutrient factors that determined black cottonwood site index. Foliar S was associated with increases in black cottonwood site index, but was not considered to be causative. This conclusion is supported by the regressions shown in Figure 2, where increases in foliar S are unrelated to the availability of SO_4 in study area soils. As suggested by several authors (Dijkshoorn and van Wijk 1967; Kelly and Lambert 1972; Turner and Lambert 1977), S is taken up in proportion to the uptake of N, and in a ratio required for the synthesis of plant proteins.

Table 9. Univariate models, probabilities (p), coefficients of determination (R^2), and standard errors of the estimate (SEE) for regressions of foliar nutrients on soil nutrient content of the same nutrient

Model	p	R^2	SEE (%)
(1) Foliar P = $0.175 + 0.001$ (soil available P)	0.000	0.831	0.02
(2) Foliar N = $1.642 + 0.004$ (soil mineralizable N)	0.001	0.497	0.28
(3) Foliar Mg = $0.190 + 0.00002$ (soil exchangeable Mg)	0.011	0.323	0.04
(4) Foliar K = $1.042 + 0.004$ (soil exchangeable K)	0.018	0.272	0.32
(5) Foliar S = $0.210 + 0.0005$ (soil available SO_4)	0.365	0.051	0.04
(6) Foliar Ca = $-1.197 + 0.0004$ (soil exchangeable Ca)	0.922	0.001	0.29

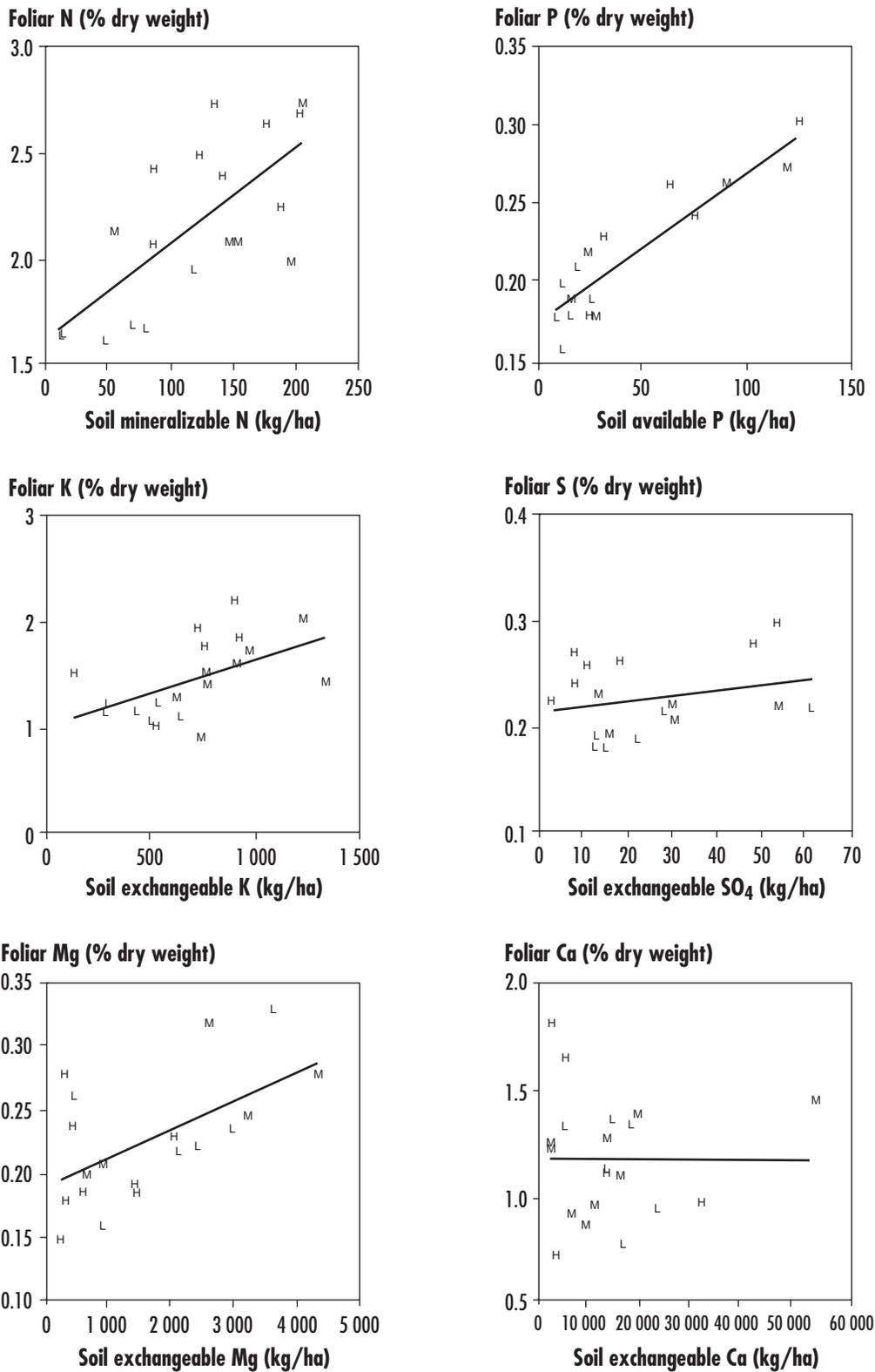


Figure 2. Regressions of foliar nutrient concentrations on their soil nutrient contents. Study sites are labeled by their black cottonwood site index class (L=low; M=medium; H=high). Linear best-fit lines are shown to demonstrate trends of the different regressions.

Identification of Optimal Nutrient Levels for Black Cottonwood

Scattergrams relating foliar concentrations of N, P, K, and Cu to site index are shown in Figure 3. Mean values for foliar nutrient concentrations in the high site index class are shown as vertical dashed lines in Figure 3, and are included for reference. A distance-weighted least squares smoothing algorithm (McLain 1974) has been used to fit a second-order polynomial line through the data points to show the general trend of the data. For foliar N, P, and Cu the trend is for black cottonwood site index to increase through the low and medium black cottonwood site index classes, as the concentrations of the foliar nutrients increase, and then to taper off in the high site index class as foliar concentrations increase. These trends can be interpreted as a “deficiency to sufficiency,” or critical levels curves (Leyton 1958; Lavender 1970; Ballard and Carter 1986; Chapin et al. 1986; Weetman and Wells, 1990). The trend for foliar K differs from the other three nutrients in that no leveling of the curve is apparent, and the relationship is more or less linear. This suggests that, given the concentrations of the other nutrients, the K sufficiency level has not been reached, and thus higher levels of foliar K will result in higher black cottonwood site index. Although foliar Cu concentrations follow an almost identical trend to foliar N and P, it is difficult to attach a critical level to it, since requirements for Cu are normally very low (Ballard and Carter 1986).

The increase in foliar Cu concentration may reflect higher uptake of the element, as more rapid growth occurs in cottonwoods on sites well supplied with other limiting nutrients such as P, N, and K.

Table 10 presents published critical foliar nutrient concentrations for black cottonwood and other *Populus* species. Mean foliar concentrations for the high black cottonwood site index class are included in the table to compare foliar levels in this study. Compared to a study of similar-aged *P. deltoides* in natural stands in Mississippi (Study 1, White and Carter, 1970a), foliar concentrations in the fastest-growing trees in this study are higher for all nutrients except Ca and Mg. Foliage concentrations of N and P in young hybrid poplars grown in greenhouse culture are much higher than those for older, native trees in this study. The value of 2.5% for foliar N, as reported by Heilman (1985) is for a 6-year-old plantation of black cottonwood and was very close to the value of 2.45% measured in this study. For all five nutrients considered,

foliage concentrations measured for the high site index class in this study were most similar to those reported by Leech and Kim (1981) for plantations of hybrid poplars in Ontario. No critical values have been published for the other macro- and micro-nutrients measured in this study. Given the paucity of other data for black cottonwood, and the relatively good correlations with the data for other *Populus* species and hybrids that are available, the mean foliar concentrations measured in the 11 stands in the high site index class (site index >22m/15 years), were considered to be optimal foliage levels for the species, and were used in the calculation of DRIS ratios for comparing the nutrient status of the different site associations.

Table 10. Published foliar nutrient critical levels (% dry mass) for *Populus* spp. and hybrids

Foliar nutrient	1	2	3	4	5	6	This study
N	2.00	2.20	3.00	2.50	3.78	2.45	2.45
P	0.17	–	0.30	–	0.57	0.24	0.24
K	1.30	1.40	1.20	–	2.64	1.40	1.76
Ca	2.30	–	–	–	1.21	0.68	1.21
Mg	0.18	0.20	–	–	0.26	0.15	0.21

¹ White and Carter (1970a) for *P. deltoides*

² White and Carter (1970a) for *Populus* spp.

³ Bonner and Broadfoot (1967) for *P. deltoides* in greenhouse culture

⁴ Heilman (1985) for *P. trichocarpa*

⁵ Leech and Kim (1981) for *P. deltoides* clone D38 in greenhouse culture

⁶ Leech and Kim (1981) for *P. deltoides* clone D38 in field plantation

Diagnosis of Nutrient Limitations in the Site Associations

DRIS (Beaufils 1973; Leech and Kim, 1981) ratios for the six site associations sampled in this study are presented in Table 11, and utilized foliar nutrient concentrations in the high site index class as norms for comparison among the site associations. The DRIS process assumes that not only are the concentrations of foliar nutrients optimal for natural stands (nutrient intensity—Shear et al. 1946), but also that the relative concentrations among species in the high site index class represent a condition of nutrient balance (Shear et al. 1948).

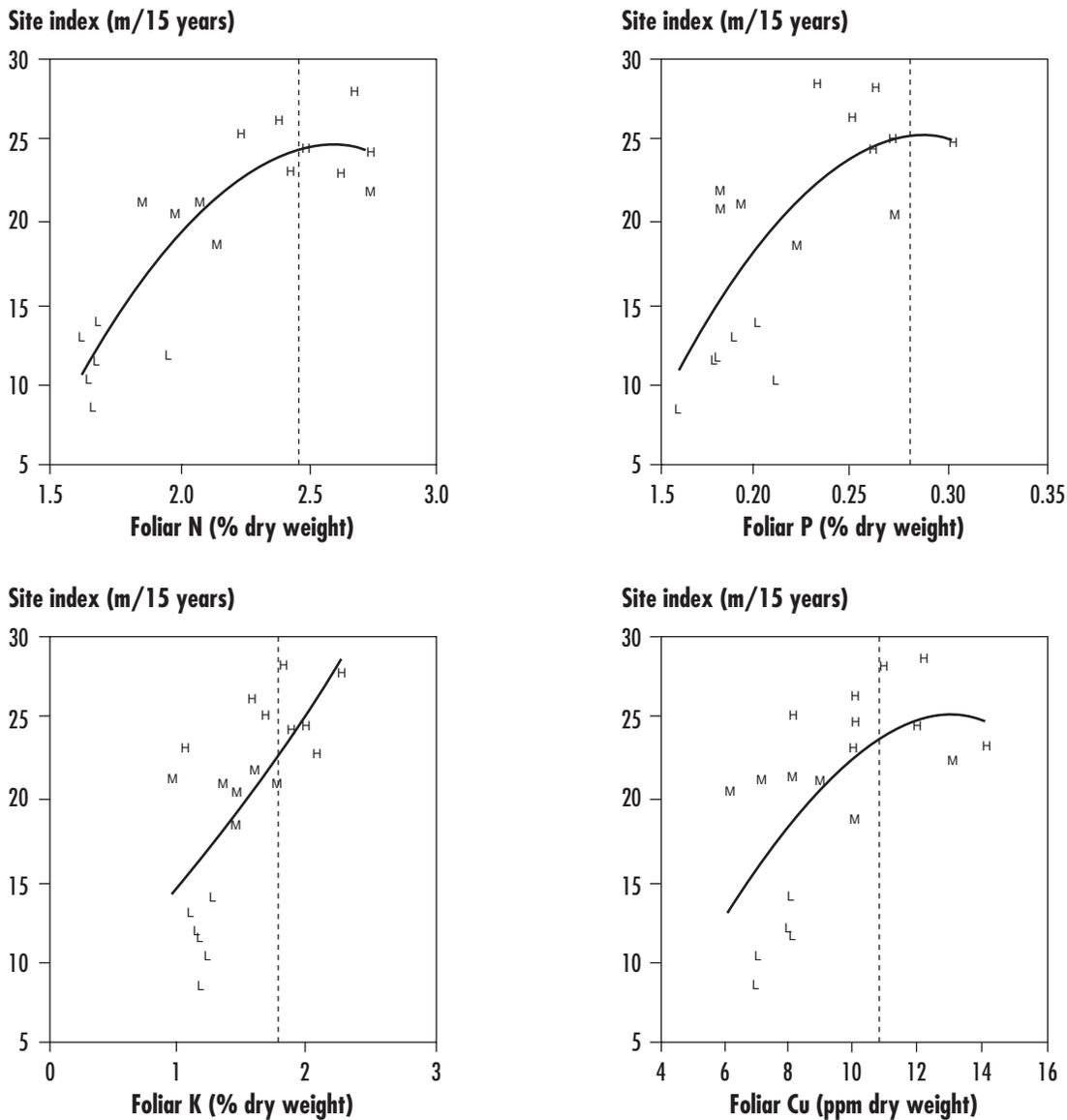


Figure 3. Scattergrams of black cottonwood site index and selected foliar nutrients. Study sites are labeled by their black cottonwood site index class (L=low; M=medium; H=high). Best fit second order polynomial lines have been drawn using a distance-weighted least squares smoothing algorithm (MacLain 1974).

The Ss-Salmonberry site association came closest to representing optimal nutrient intensity and balance for black cottonwood growth, as shown by very low DRIS indices (Table 11). This is to be expected because it was principally Ss-Salmonberry sites that made up the high site index class (see Table 1) and thus they were used to calculate the norms. DRIS norms generated from the 25 fastest-growing, fertilized trees in a parallel, black cottonwood fertilization experiment at Site 21 can be used

to assess nutrient limitation in the high site index class. Trees used to develop the norms were fertilized with a balanced fertilizer, which included all macro- and micro-nutrients. Using DRIS, nutrient deficiencies for trees in the high site index class were identified as B (-24) > K (-18) > P (-13) > S (-6). The role of B in limiting growth of black cottonwood growth is difficult to assess (Carter and Brockley 1990), and the foliar concentrations of trees in the high site index class were well above that required for

Table 11. Comparisons of DRIS ratios in 6 site associations sampled in the study. Norms for the establishment of the ratios are based on mean foliar concentrations from stands in the high site index class.

Site association	n	N (%)	P (%)	K (%)	Ca (%)	Mg (%)	Cu (ppm)	Zn (ppm)	Fe (ppm)	Mn (ppm)	B (ppm)	S (%)
Ss-Salmonberry	7	1	3	3	-3	0	0	0	-4	3	-3	0
Ac-Red-osier dogwood	5	-8	-10	-10	-1	17	-4	-2	4	12	17	-11
Ac-Willow	6	-11	-5	-5	3	10	-13	2	8	13	13	-8
Cw-Foamflower	6	-8	6	-7	6	0	-22	-1	5	34	-5	-1
"Gleyed"	4	-4	-3	-41	24	49	-21	-10	8	45	-35	-10
Cw-Swordfern	1	-2	5	-1	18	-7	-23	-8	-20	9	34	-8

conifers (Ballard and Carter 1986). Also, B deficiency should be expressed in apical areas of the trees (Carter and Brockley 1990), and there was no indication of B deficiency symptoms in the fast-growing population of cottonwood studied. It was apparent from regressions of foliar S on soil S that sufficient soil S was available, but was not taken up by the trees. For this reason it is assumed that S is not limiting to black cottonwood in the stands studied. The regression of foliar K on soil K was the only relationship that was more or less linear, and it was suggested that increasing the uptake of K may result in a growth increase for rapidly growing black cottonwood stands. The high negative K index from the DRIS analysis supports this conclusion. Based on the DRIS analysis, and the data presented in this study, it is concluded that, in unmanaged stands, the fastest-growing black cottonwoods are limited by the uptake of K and then P.

Sites in the Ac-Red-osier dogwood site association were diagnosed as deficient in the order $S > P = K > N > Cu > Zn$. It was concluded from the regression of foliar S on soil S that S was not limiting, but was likely taken up in proportion to N (See Section 5.3.9). DRIS indices for Cu and Zn were very low and thus not considered critical. From this analysis, site index in Ac-Red-osier dogwood sites appears to be limited principally by P and K, and to a lesser degree N.

According to the DRIS indices given in Table 11, Ac-Willow sites are limited in the order $Cu > N > P = K$. Foliar Cu concentrations were never below 6.8 ppm in any of the site associations, and Ballard and Carter (1986) suggest that, in conifers, Cu deficiencies do not occur until at least 4 ppm. Thus, for Ac-Willow sites, it is assumed

that N is the most limiting nutrient, followed by P and K, which are about equally deficient.

DRIS indices for the Cw-Foamflower site association indicate deficiency in the order $Cu > N > K$. Using the same reasoning for Cu deficiency level, it can be argued that N, and then K, limit black cottonwood growth in this site association.

Gleyed site associations demonstrated a more complex pattern of nutrient deficiency, and are diagnosed as nutrient-limited in the order $K > B > Cu > Zn = S > N > P$. The very high K DRIS index is considered to be very important in limiting black cottonwood growth on these site associations. The mean foliar concentration of 0.82% for the gleyed site associations is well below all critical levels for this nutrient. The mean B concentration for the gleyed group of site associations is 13 ppm, which is diagnosed as "possibly deficient" by Ballard and Carter (1986) based on observations of conifers. It is possible, therefore, that black cottonwood on sites within the gleyed group are also limited by low B levels. As discussed above for Cu, Zn concentrations are well above deficient levels proposed by Ballard and Carter (1986) for conifers, and are not considered to be limiting. Thus, black cottonwood growth on the gleyed sites is considered to be limited principally by K and B, and only slightly by P and N.

The Cw-Swordfern site association was represented by only one study site, which was diagnosed as limited in the order $Cu > Fe > S > Mg > N > K$. As discussed above, Cu and S at the foliar concentrations measured are not considered to be limiting. Fe and active-Fe concentrations were 53 and 38, ppm respectively, neither of which was

considered limiting in conifers by Ballard and Carter (1986). The foliar concentration of Mg was 0.16%, which was considerably lower than those of the other site associations, and was below the critical level proposed by White and Carter (1970a) for hybrid poplars, and for *P. deltoides* (see Table 10). Based on this reasoning, this site is interpreted as having a moderate Mg deficiency, and a slight N and P deficiency.

Discussion

Nutrient Availability and Site Index – General Trends

In this study, sample sites with low soil organic matter (total N, total C, and mineralizable N), high pH, and high soil contents of exchangeable Ca and Mg had low site index, were contrasted with sites with high soil organic matter, lower pH, relatively high contents of available P and exchangeable K, and overall higher site index. In the linear regressions of soil and foliar nutrients on black cottonwood site index, measures of soil and foliar N, P, and K were consistently associated with increasing black cottonwood site index, while pH, and foliar soil measures of Ca and Mg, had negative relationships.

The high concentration of Ca, high pH, and low P contents found in this study have been reported by Peterson and Rolfe (1982 and 1985) in alluvial sites subjected to periodic annual flooding. They observed a decrease in soil P concentrations and an increase in pH and Ca content following flooding in 2 years of measurements, and attributed the increase in Ca concentration and pH to soil reducing conditions (Ponnamperuma 1984). In that study, the pH increased above 6.5, after which solubility of P decreased rapidly, and a higher concentration of Ca resulted in the precipitation of P as insoluble calcium phosphates (Peterson and Rolfe 1982). In this study it has been demonstrated that high pH and high soil Ca content were negatively correlated with soil P content, and with site index. If soils on the frequently flooded sites sampled in this study do become anaerobic, then the mechanism suggested by Peterson and Rolfe (1982) may be responsible.

Analysis of soil nutrient-foliar regressions, and of black cottonwood site index class, provided the opportunity to identify levels of foliar nutrients considered optimal for black cottonwood growing in unmanaged stands in coastal

British Columbia. The levels are similar to critical levels published by other workers for *Populus* spp. growing in plantations or natural stands. The mean foliar concentrations were used as DRIS norms for comparing nutrient deficiencies among the different site associations. Interpretations of black cottonwood site index in the context of the ecological processes operative within the various site associations are described below.

Interpretations of Black Cottonwood Growth and Nutrient Limitation in the Site Associations

Alluvial Site Associations

Stands dominated by black cottonwood occur mainly as primary or secondary successional series on alluvial floodplain landforms in south coastal British Columbia. The frequency, duration, and physical influence (aggradation, erosion) of the flooding that characterizes these sites is highly variable, and has important effects on the productivity and composition of plant communities on alluvial floodplains. Banner et al. (1990) recognized three “benches” that divided the flooding gradient into three strata. The term “bench” is not used in a strict geomorphological sense, but rather to stratify the small elevational differences that influence the effects of flooding regimes on alluvial plant communities.

Ac-Willow Site Association (low bench)

The Ac-Willow site association represents sites located on the lowest elevations of alluvial floodplains, and thus they are the most frequently flooded. These site units are flooded more or less annually for 2 to 3 weeks, above the surface during the growing season (McLennan 1993). Ac-Willow sites had considerably lower soil contents of total C, total N, mineralizable N, and available P, and higher exchangeable Ca, than all ecosystems studied. Only the gleyed site associations had lower levels of soil exchangeable K. Comparisons of foliar concentrations from black cottonwoods on these sites with those in the high site index class suggested serious limitation by the availability of N, P, and K, in that order.

It appears that growth of black cottonwood on sites representing the Ac-Willow site association is limited by low availability of soil nutrients, and possible impedance of uptake of those nutrients that are available, due to

frequent and prolonged inundation during the growing season. Frequent inundation erodes surfaces, disrupts decomposer communities, and reduces mineralization of soil organic matter. Nitrogen will be leached from the soil if flooding is prolonged enough to create reducing conditions. Soil P may be less available because of flooding-related interactions with high soil pH and content of soil Ca. Low soil K may be the result of leaching where soils have high Ca concentrations, so that K is displaced from the exchange complex. All of these factors can reduce nutrient availability and uptake and severely limit black cottonwood growth on Ac-Willow sites.

Ac-Red-osier Dogwood Site Association (middle bench)

Sites classified within the Ac-Red-osier dogwood site association occur in the middle of the flooding gradient on active alluvial floodplain surfaces, and are inundated above the surface during the growing season about once every 5 years, for a period of about 2 weeks (McLennan 1993) Soil contents on Ac-Red-osier dogwood sites reflect the intermediate flooding position in that, compared to Ac-Willow sites, they have much higher levels of organic matter (total C, total N, and mineralizable N) and exchangeable K, but have comparable soil contents of exchangeable Ca and Mg. Available P is almost double that of Ac-Willow sites, but is half that of Ss-Salmonberry sites, located on the highest areas of alluvial floodplains. According to the DRIS analysis, Middle Bench ecosystems were limited mainly by P and K, and to a lesser extent N.

Black cottonwood site index on sites of the Ac-Red-osier dogwood site association is mostly in the upper half of the medium site index class. This significant increase in productivity over Ac-Willow sites is attributed primarily to the reduced flooding frequency and reduced physical and soil chemical effects of flooding. The reduced flooding effect permits more active decomposition, and thus promotes nutrient cycling and the availability of N, and other important nutrients that have been correlated with black cottonwood growth in this study. The infrequent flooding that does occur has a relatively long duration (about 2 weeks), which may impede the uptake of nutrients during the warmest part of the growing season. The flooding may also limit the development of humus layers, and, given the high soil Ca and Mg contents and relatively low available P, may also limit the availability of P and K, as discussed above for Ac-Willow sites.

Ss-Salmonberry Site Association (high bench)

Sites located within the Ss-Salmonberry site association are inundated less frequently, and for a shorter duration, than all other site units on alluvial floodplains. It is estimated that these sites are flooded about as frequently as sites of the Ac-Red-osier dogwood site association, but for a much shorter duration. Whereas Ac-Red-osier dogwood sites can be expected to flood for 2–3 weeks, Ss-Salmonberry sites are inundated above the surface, during the growing season, for several days at the most (McLennan 1993). Compared to the Ac-Red-osier dogwood site association, Ss-Salmonberry sites have approximately equal amounts of total C, total N, mineralizable N, and exchangeable K, much lower contents of soil Ca and Mg, and about twice the available P. Based on the DRIS analysis, the nutrient status of this site association is optimal, and, relative to stands growing on sites representing other site associations, no nutrients are limiting growth. Compared to nutrient concentrations in the fastest-growing trees provided with all nutrients in a fertilizer experiment, K and then P limit black cottonwood growth on the very best sites.

The mean site index for the Ss-Salmonberry sites was 25.4 m/15 yrs, and was higher than for all other site units. All study stands for this site association fell within the high site index class. The high productivity of these sites is attributed to reduced negative flooding effects, especially flooding duration in the rooting zone during the growing season, which permits the development of a deep Mull humus that is a dynamic centre for cycling of nutrients within the ecosystem. Because flooding is of short duration, the main effect is to recharge soil water and provide optimal conditions for nutrient uptake and black cottonwood growth. Higher availability of soil P may be related to lower levels of soil Ca. Although soil K is higher in Ac-Red-osier dogwood sites, foliar K is considerably higher in Ss-Salmonberry sites, and this may also be a result of shorter duration of flooding.

Upland Site Associations

In upland areas in coastal British Columbia, black cottonwood is more or less restricted to sites without a growing season water deficit. In this study, only one site was sampled that has the potential for temporary soil drought during the growing season. On other upland sites sampled, soil moisture is available, or excessive, throughout the growing season.

Gleyed Site Associations

The four sites considered together as the gleyed group are comprised of two sites belonging to the Cw-Black twinberry site association, and two sites classified within the Cw-Salmonberry site association. All four sites were located in poorly drained landscape depressions, where relatively well drained marine sands overlay compact, gleyed marine silt and clay at various depths. The depth to the underlying compact layer is the basis for site differentiation, so that sites classified within the Cw-Salmonberry site association, had at least 35 cm above the gleyed horizon, and the Cw-Black twinberry site association, between 15 and 35 cm (Banner et al. 1990). A third site association, the Cw-Slough sedge, is defined where the gleyed layer is less than 15 cm from the soil surface, and the Elk 2 site is transitional to this unit. Soil moisture in these ecosystems fluctuates seasonally, so that in the winter there may be standing water to various depths (wet and very wet SMRs soil moisture regimes), while in the summer, the most elevated site unit (Cw-Salmonberry site association) may achieve a fresh SMR, which implies that there is no soil moisture in excess of that required for uptake (Pojar et al. 1987). Soil contents of total C, total N, mineralizable N, and available P were comparable, but contents of exchangeable Ca, Mg, and K were lower than at all other sites. The Gleyed site associations were diagnosed as having serious B and K deficiencies, with slight deficiencies of P and N.

Black cottonwood site index in the gleyed group of site associations was in the low, or low half of the middle, site index class, and ranged from 12.2 m/15 years at the Oyster site to 17.2 m/15 years at Elk 2. This poor growth is interpreted to be a function of reduced volume above compact, gleyed horizons, and to nutrient deficiencies particular to the marine soils on which the sites were located. The reduced rooting depth decreased the volume of soil available for supplying nutrients and probably impedes uptake where soils are anaerobic. The deficiencies of K can be related to very low soil K contents, and may be a result of the type of mineral present for weathering in the marine soils in which all of the sites occur. Although no data on soil B were collected, B deficiencies have been diagnosed in coastal British Columbia on sorted sandy soils (Carter and Brockley 1990), such as those that occur over the compact deposits in the soils sampled.

Cw-Foamflower Site Association

Sites in the Cw-Foamflower site association had a moist to very moist soil moisture regime, which means that available soil moisture ranges from soil water being in excess of that which can be utilized, to soils where a water table is present at greater than 30 cm depth (Pojar et al. 1987). As a result, soil moisture is available for nutrient uptake over the entire growing season. For black cottonwood, an important differentiation of sites with very moist SMRs is whether subsurface water is freely flowing and oxygenated, as in the case of seepage sites, or whether water is slow moving and anaerobic conditions develop, as evidenced by gleyed soil horizons. In this study, seepage sites were sampled on alluvial fans (Tam Fan, Squam 38) and where deep loess blankets overlie impermeable basal till (Ryder, Sumas). Gleyed sites were sampled in level terrain, where fine-textured glaciofluvial materials have been deposited over compact layers at depth (Chilliwack, Pierce) so that soil drainage is impeded. Soils sampled in the Cw-Foamflower site association had the highest total N, total C, mineralizable N, and available P contents of all of the site associations sampled. Levels of exchangeable Ca, Mg, and Ca were comparable to sites of the Ss-Salmonberry site association. As a group, sites within this site association were diagnosed as deficient in N and then K, using DRIS analysis.

Productivity of black cottonwood in the Cw-Foamflower site association must be broken down into the seepage and gleyed types described above to assess the range of site index that this site unit encompasses. Black cottonwood site index on one of the two seepage sites sampled for this study is the highest for all study sites (Ryder, 30.8 m/15 years) and the other is the fourth highest (Sumas, 27.1 m/15 years). Both of these sites had Ah horizons in excess of 10 cm, silty loess soils, and permanent seepage, all of which are features interpreted as providing optimal growth conditions for black cottonwood. The Tam Fan (25.2 m/15 years) and Squamish 38 (21.1 m/15 years) sites were located on alluvial fan landforms where seepage is present throughout the year, but soils were considerably coarser, and Ah horizons thinner. Under these conditions, mineralization processes were probably somewhat reduced (although foliar N was high at both sites) and the surface area for cation exchange and nutrient retention was considerably lower. Given the coarse soil textures and thin

humus layers, the high productivity of alluvial fan sites is somewhat anomalous, and requires further investigation. Two of the six sites in the Cw-Foamflower site association were gleyed within 60 cm of the surface, and thus the sites experience anaerobic conditions within the rooting zone. The Pierce site (20.4 m/15 years) had a permanent water table at a depth of about 1 m, with gleyed horizons beginning at a depth of 55 cm. The Chilliwack site (13.6 m/15 years) had a compact silty soil with pronounced mottles and gleying that start at 10 cm and increase with depth. The negative influence of soil gleying on black cottonwood site index is demonstrated by this comparison, and by the low site index of the gleyed group of site associations described above.

Cw-Swordfern Site Association

Only one study site was sampled in the Cw-Swordfern site association thus few general conclusions can be drawn about the productivity of black cottonwood within the unit. On the site sampled, black cottonwood had a site index of 16.3 m/15 years, and was located on relatively coarse glaciofluvial materials, with a Moder humus form. The site was diagnosed as having a moderate Mg deficiency, and slight N and P deficiencies. The medium productivity of the species is attributed to a relatively short moisture deficit, relatively slower mineralization rate, and soil mineralogy that is somewhat deficient in content of soil Mg.

Conclusions

Site index differed insignificantly among the three subzones sampled, and it was concluded that the limited climatic range of study sites was insufficient to significantly affect growth of black cottonwood. Membership in site association and soil nutrient regime classes explained 87% and 36% of the variation in black cottonwood site index, respectively. This showed that black cottonwood site index was highly predictable if the site association was known, and much less predictable based on soil nutrient regime alone. Much of the poor predictive capability of soil moisture regime can be attributed to the fact that the three soil moisture regime classes incorporated a range of soil moisture regime classes and flooding regimes. Soil nutrient regime explained 88% of the variance in site index when stratified within site association, which can be used as a surrogate for soil moisture regime class. Also, it was

demonstrated in the study that soil nutrient regime was principally a gradient of increasing N availability, and that the availability of other important nutrients, such as P and K, did not increase along this same gradient in the stands studied. P and K were diagnosed as limiting nutrients on some sites, especially in the high site index class, and this may also help explain the poorer predictive power of soil nutrient regime.

All methods of analysis revealed consistent relationships between measures of site nutrient status and site index. Sample stands with high pH, high levels of exchangeable Ca and Mg, and low levels of soil N, P, and K had foliar concentrations of N, P, and K diagnosed as limiting to black cottonwood growth, and had the lowest site index. High site index was recorded in stands with more or less opposite soil and foliar properties.

Site index was seen to decrease in site units with increasing flooding frequency and duration on alluvial floodplains. The decrease was attributed to the negative impact of flooding on the rate of organic matter mineralization, on nutrient uptake, and on the negative effect of high levels of soil Ca and high soil pH on the availability of soil P. On upland sites, soil gleying and prolonged rooting zone flooding during the growing season was correlated with low site index.

Optimal foliar levels for 13 foliar nutrients based on mean foliar concentrations from the high site index class were used as a 'field standard' (Leech and Kim 1981) for DRIS interpretations of black cottonwood nutrient status. Using DRIS norms from the fastest-growing, fertilized trees in another experiment (McLennan 1993), it was concluded that black cottonwood stands in the high site index class are limited by K and then P.

The interpretations of nutrient limitation in black cottonwood ecosystems discussed in his paper cannot provide conclusive evidence for the role of the nutrients identified as potentially limiting to black cottonwood growth. The validity of the nutrient-limiting interpretations can be tested by fertilizing stands and measuring pre- and post-treatment growth rates. The results of fertilization experiments that test the hypotheses of nutrient limitation from this paper are presented in McLennan (1993).

References

- Agriculture Canada Expert Committee on Soil Survey. 1987. The Canadian system of soil classification. 2nd ed. Agric. Canada Public. 1646. Supply and Services Canada, Ottawa, Ont. 164 p.
- Anonymous. 1966. Technicon Autoanalyzer II. Methodology: individual/simultaneous determination of nitrogen and/or phosphorus in BD acid digests. Industrial Method No. 329-74W/A.
- Attiwill, P.M. 1986. Interactions between carbon and nutrients in the forest ecosystem. *Tree Physiol.* 2: 389-399.
- Baker, J.B. and W.M. Broadfoot. 1976. Soil requirements for site selection for *Aigeiros* poplar plantations. In Proceedings of a Conference on Eastern Cottonwood and Related Species. B. A. Thielges and S.B. Lambs (editors), Louisiana State University, Baton Rouge, La. pp. 225-238.
- _____. 1979. A practical field method of site evaluation for commercially important southern hardwoods. Gen. Tech. Rep. SO-26. USDA For. Serv., South. For. Res. Stn., New Orleans, La. 51 p.
- Ballard, T.M. and R. E. Carter. 1986. Evaluating forest stand nutrient status. B.C. Min. For. and Lands., Victoria, B.C. Land Manage. Rep. No. 20. 60 p.
- Banner, A., R.N. Green, K. Klinka, D.S. McLennan, D.V. Meidinger, F.C. Nuszdorfer, and J. Pojar. 1990. Site classification for coastal British Columbia: a first approximation. B.C. Min. For., Victoria, B.C. 2 p. (coloured pamphlet).
- Bardsley, C.E. and J.D. Lancaster. 1965. Sulfur. In *Methods of Soil Analysis*. C.A. Black, D.D. Evans, J. L. White, L.E. Ensminger, and F.E. Clark (editors.). *Agronomy No. 9*, Amer. Soc. Agron., Madison, Wis. pp. 1102-1116.
- Beaufils, E.R. 1973. Diagnosis and recommendation integrated system (DRIS). *Soil Sci. Bull.* No. 1, Dept. of Soil Sci. and Agro-Meteorology. Univ. Natal, Pietermaritzburg, S. Afr. 132 p.
- Boishot, P.M. Coppenet, and J. Hebert. 1950. The fixation of phosphoric acid on calcium carbonate in soils. *Plant and Soil* 2:311-322.
- Bonner, F.T. and W.M. Broadfoot. 1967. Growth response of eastern cottonwood to nutrients in sand culture. USDA South. For. Exp. Stn., New Orleans, La. Res. Note SO-65.
- Bremner, J. and C.S. Mulvaney. 1982. Use of automated combustion techniques for total carbon, total nitrogen, and total sulfur analysis of soils. Pgs. 1-16 in L.M. Walsh (ed.). *Instrumental methods for analysis of soils and plant tissue*. Soil Sci. Soc. Amer., Madison, Wis.
- Bremner, J. and M.A. Tabatabai. 1971. Nitrogen - Total. Pgs. 595-624 in A. L. Page. (ed.). *Methods of soil analysis*. *Agronomy No. 9, Part 2*. A. Soc. Agron. and Soil Sci. Soc. Amer., Madison, Wis.
- Broadfoot, W.M. 1960. Field guide for evaluating cottonwood sites. USDA For. Ser., South. For. Res. Stn., New Orleans, La. Occas. Pap. No. 178. 6 p.
- Carmean, W.H. 1972. Site index curves for upland oaks in the Central States. *For. Sci.* 18:102-120.
- Carter, R.E. and R.P. Brockley. 1990. Boron deficiencies in British Columbia: Diagnosis and treatment evaluation. *For. Ecol. and Manage.* 37:83-94.
- Carter, R.E. and K. Klinka. 1990. Relationships between growing-season soil water deficit, mineralizable soil nitrogen, and site index of coastal Douglas-fir. *For. Ecol. Manage.* 30:301-311.
- Chapin, F.S. III, K. van Cleve, and P. Vitousek. 1986. The nature of nutrient limitation in plant communities. *Am. Nat.* 27:148-158.
- Chatterjee, S. and B. Price. 1977. *Regression Analysis by Example*. John Wiley and Sons, New York, N.Y. 228 p.
- Cohen, J. 1968. Multiple regression as a general data-analytical system. *Psychological Bulletin* 70 (6): 426-443.
- Cole, C.V., S.R. Olsen, and C.O. Scott. 1953. The nature of phosphate sorption by calcium carbonate. *Soil Sci. Soc. Amer. Proc.* 17:352-356.
- Council for Soil Testing and Plant Analysis. 1974. *Handbook on reference methods for soil testing*. Athens, Ga. 101 p.

- Courtin, P.J. 1992. The relationship between ecological site quality and site index and stem form of red alder in south-western British Columbia. M.S.For. Thesis, Dep. For. Sci., Fac. For., Univ. B.C., Vancouver, B.C. 87 p.
- Courtin, P.J., M.C. Feller, and J.P. Demaerchalk. 1988. An approach to quantitative classification of nutrient regimes of forest soils. *Can. J. Bot.* 66:2640–653.
- Critchfield, W.B. 1960. Leaf dimorphism in *Populus trichocarpa*. *Amer. J. Bot.* 47:699–711.
- Curran, P.M. 1984. Soil testing for phosphorus availability to some conifers in British Columbia. M. Sc. Thesis, Dep. Soil Sci., Fac. For., Univ. B.C., Vancouver, B.C. 130 p.
- DeBell, D. 1990. *Populus trichocarpa* Torr. and Gray – Black Cottonwood. Pp. 570–576 in R.M. Burns, and B.H. Honkala. (eds). *Silvics of North America*. USDA For. Serv. Agric. Handbook. No. 654. 877 p.
- Dijkshoorn, W. and A.L. van Wijk. 1967. The sulphur requirements of plants as evidenced by the sulphur-nitrogen ratio in organic matter—A review of the published data. *Plant and Soil* 26:129–157.
- Dyer, M.E. and R. L. Bailey. 1987. A test of six methods for estimating true heights from stem analysis data. *For. Sci.* 33:3–13.
- Eis, S. 1962. Statistical analysis of several methods for estimation of forest habitats and tree growth near Vancouver, B.C. *Fac. For., For. Bull. No. 4*. Univ. B.C., Vancouver, B.C.
- Gaines, T.P. and G.A. Mitchell. 1979. Boron determination in plant tissues by azomethine H method. *Comm. Soil Sci. Plant Anal.* 10:1099–1108.
- Green, R. N., P. J. Courtin, K. Klinka, R. J. Slaco, and C.A. Ray. 1984. Site diagnosis, tree species selection, and slashburning guidelines for the Vancouver Forest Region. *B.C. Min. For., Victoria, B.C. Land Manage. Handb. No. 8*. 54 p.
- Green, R. N., P. L. Marshall, and K. Klinka. 1989. Estimating site index of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) from ecological variables in southwestern British Columbia. *For. Sci.* 35:50–63.
- Grewelling, T. and M. Peech. 1960. Chemical soil tests. *Cornell Agric. Exp. Stn. Bull.* 960.
- Griffin, R. A. and J. J. Jurinak. 1973. The interaction of phosphate with calcite. *Soil Sci. Soc. Amer. Proc.* 37:847–850.
- Guthrie, T.F. and L.E. Lowe. 1984. A comparison of methods for total sulphur analysis of tree foliage. *Can. J. For. Res.* 14:470–473.
- Harrington, C. 1986. A method of site evaluation for red alder. *USDA For. Serv., Pac. NW Res. Sta., Portland, Oreg. Gen. Tech. Rep. PNW-192*. 22 p.
- Heilman, P.E. 1985. Sampling and genetic variation of foliar nitrogen in black cottonwood and its hybrids in short rotation. *Can. J. For. Res.* 15:1137–1141.
- Heilman, P.E., D.V. Peabody Jr., D.S. DeBell, and R.F. Strand. 1972. A test of close-spaced, short rotation culture of black cottonwood. *Can. J. For. Res.* 2:456–459.
- Heilman, P.E. and D.V. Peabody Jr. 1981. Effect of harvest cycle and spacing on productivity of black cottonwood in intensive culture. *Can. J. For. Res.* 11:118–123.
- Heilman, P. and R.F. Stettler. 1983. Phytomass production in young mixed plantations of *Alnus rubra* (Bong.) and cottonwood in western Washington. *Can. J. Microbiol.* 29:1007–1013.
- . 1985. Genetic variation and productivity of *Populus trichocarpa* and its hybrids. II. Biomass production in a 4 year plantation. *Can. J. For. Res.* 15:384–388.
- Johnson, C.M. and H. Nishita. 1952. Microestimation of sulphur in plant materials, soils, and irrigation waters. *Anal. Chem.* 24:736–742.
- Kabzems, R.D. and K. Klinka. 1987. Initial quantitative characterization of soil nutrient regimes. II. Relationships among soils, vegetation, and site index. *Can. J. For. Res.* 17:1565–1571.

- Kayahara, G.J. 1991. An investigation of relationships between western hemlock ecosystems, ecological site quality, and productivity in the Coastal Western Hemlock Zone of British Columbia. M. Sc. Thesis, Dep. For. Sci., Fac. For., Univ. of B.C., Vancouver, B.C. 157 p.
- Kelly, J. and M.J. Lambert. 1972. The relationship between sulphur and nitrogen in the foliage of *P. radiata*. *Plant and Soil* 37:395–408.
- Klinka, K., M.C. Feller, L.M. Lavkulich, and A. Kozak. 1980. Evaluation of methods of extracting soil cations for forest productivity studies in southwestern British Columbia. *Can. J. Soil Sci.* 60:697–705.
- Klinka, K., R.N. Green, R.L. Trowbridge, and L.E. Lowe. 1981. Taxonomic classification of humus forms in ecosystems of British Columbia. B.C. Min. For., Victoria, B.C. Land Manage. Rep. No. 8. 54 p.
- Klinka, K., P.J. Courtin, and R.N. Green. 1984. An approach to quantitative classification of hygrotopes and trophotopes of forest soils. IUFRO Workshop on Quantitative Assessment of Forest Sites, with Special Reference to Soils. Swiss Federal Institute of Forestry Research, CH-8903 Birmensdorf, Switzerland. September 10–15, 1984. 40 p.
- Klinka, K., R.E. Carter, M.C. Feller, and Q. Wang. 1989. Relations between site index, salal, plant communities, and sites in coastal British Columbia. *For. Sci.* 36:815–830.
- Kowalenko, G.F. and L.E. Lowe. 1972. Observations on the bismuth sulfide colorimetric procedure for sulfate analysis in soil. *Commun. Soil Sci. Plant Anal.* 3:79–86.
- Lavender, D.P. 1970. Foliar analysis and how it is used - A review. Research Note No. 52, School of Forestry, For. Res. Lab., Oreg. State Univ., Corvallis, Oreg. Res. Note 52. 8 p.
- Leech, W.S. and Y.T. Kim. 1979. Assessment of nutrient requirements of poplars. Proc. North American Poplar Council Meeting, Ont. Min. of Nat. Res., Info. Paper No.102. 16 p.
- _____. 1981. Foliar diagnosis and DRIS as a guide to fertilizer amendments in poplar plantations. *For. Chron.* 57(1): 17–21.
- Leyton, L. 1958. The relationship between the growth and mineral nutrition of conifers. *In The Physiology of Trees*. K.V. Thimann (editor). Ronald Press, New York, N.Y. pp. 323–345.
- Luttmerding, H.A., D.A. Demarchi, E.C. Lea, D. V. Meidinger, and T. Vold (editors). 1990. Describing ecosystems in the field. 2nd ed. B.C. Min. For., Victoria, B.C. 213 p.
- McLain, D.H. 1974. Drawing contours from arbitrary data points. *The Computer Journal* 17:318–324.
- McLennan, D.S. 1993. Growth and nutrient relations in black cottonwood in south coastal British Columbia. Ph. D. Thesis, Dep. For. Sci., Fac. For., Univ. of B.C., Vancouver, B.C. 198 p.
- Mehlich, A. 1978. New extractant for soil test evaluation of phosphorus, magnesium, calcium, sodium, manganese, and zinc. *Comm. Soil Sci. Plant Anal.* 9:477–492.
- Mitchell, H.L. 1936. Trends in nitrogen, phosphorus, potassium, and calcium content of leaves of some forest trees during the growing season. *Black Rock Forest Paper* 1:29–44.
- Mize, C.W. and R.C. Schultz. 1985. Comparing treatment means correctly and appropriately. *Can. J. For. Res.* 15:1142–1148.
- Monserud, R.A. 1984. Height growth and site index curves for inland Douglas-fir based on stem analysis data and forest habitat type. *For. Sci.* 30(4):943–965.
- Nuszdorfer, F.N., K.L. Kassay, and A.M. Scagel. 1990. Biogeoclimatic units of coastal British Columbia. 1:500,000 Colour Map. Res. Br., B.C. Min. For., Victoria, B.C.
- Oserkowsky, J. 1933. Quantitative relation between chlorophyll and iron in green and chlorotic pear leaves. *Plant Physiol.* 8:449–468.
- Parkinson, J.A. and S.E. Allen. 1975. A wet oxidation procedure for the determination of nitrogen and mineral nutrients in biological material. *Comm. Soil. Sci. Plant. Anal.* 6:1–11.

- Peterson, D.L. and G.L. Rolfe. 1982. Seasonal variation in nutrients of floodplain and upland forest soils of central Illinois. *Soil Sci. Soc. Amer. J.* 46:1310–1315.
- _____. 1985. Temporal variation in nutrient status of a floodplain forest soil. *For. Ecol. Manag.* 12:73–82.
- Pojar, J., K. Klinka, and D.V. Meidinger. 1987. Biogeoclimatic ecosystem classification in British Columbia. *For. Ecol. Manage.* 22:119–154.
- Ponnamperuma, F.N. 1984. Effects of flooding on soils. Pp. 9–45 *in*, T.T. Koslowski (ed.). *Flooding and Plant Growth*. Academic Press Inc., Orlando, Fla.
- Roe, A.L. 1958. *Silvics of Black Cottonwood*. Misc. Pub. 17. USDA For. Serv., Intermountain For. and Range Exp. Stn., Moscow, Idaho
- Russell, E.W. 1974. *Soil Conditions and Plant Growth*. Longman, London, U.K.
- Schutz, C.J. and J.M. de Villiers. 1986. Foliar diagnosis and fertilizer prescription in forestry—The DRIS system and its potential. *Proceedings: 18th IUFRO World Congress, Ljubljana, Slovenia*. 16 p.
- Shear, C.B., H.L. Crane, and A.T. Myers. 1946. Nutrient element balance: a fundamental concept in plant nutrition. *Proc. Amer. Soc. Hort. Sci.* 51:319–326.
- _____. 1948. Nutrient element balance: application of the concept to the interpretation of foliar analysis. *Proc. Amer. Soc. Hort. Sci.* 51:319–326.
- Smith, J.H.G. 1957. Some factors indicative of site quality for black cottonwood. *J. For.* 55:578–580.
- Smith, J.H.G. 1980. Growth and yield of poplar in British Columbia. Paper presented at 1980 Meeting, Poplar Council of Canada. *Fac. For., Univ. B.C., Vancouver, B.C.*
- Turner, J., M.J. Lambert, and S.P. Gessel. 1977. Use of foliage sulphate concentrations to predict response to urea application by Douglas-fir. *Can. J. For. Res.* 7:476–480.
- Wang, Q. 1992. Ecological and height growth analysis of some sub-boreal, immature lodgepole pine stands in central British Columbia. Ph.D. Thesis, *Fac. For., Univ. B.C., Vancouver, B.C.* 183 p.
- Wareing, S.A. and J.M. Bremner. 1964. Ammonium production in soil under waterlogged conditions as an index of soil nitrogen availability. *Nature*. 201:951–952.
- Weetman, G.F. and C.G. Wells. 1990. Plant analyses as an aid in fertilizing forests. Chapter 25 *In Soil Sci. Soc. Amer., Soil Testing and Plant Analysis*, 3rd ed. *Soil Sci. Soc. Amer. Book Series No. 3.*, Madison, Wis.
- White, E.H. and M.C. Carter. 1970a Relationships between foliage, nutrient levels, and growth of young natural stands of *Populus deltoides* Bartr. *In Tree growth and forest soils. Proc. 3rd North Am. For. Soils Conf.* C.T. Youngberg and C.B. Davey (editors). pp. 283–294.
- _____. 1970b. Properties of alluvial soils supporting young stands of eastern cottonwood in Alabama. *USDA For. Serv., South. For. Res. Stn., New Orleans La. Res. Note SO-111*. 4 p.
- Wilkinson, L. 1990. *SYSTAT: The System for Statistics*. Evanston, Ill. 677 p.

Evaluation and Testing of Hybrid Poplars in British Columbia

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Abstract

Until recently, B.C.'s considerable hardwood resources have received little attention from the forestry community. Utilization of aspen and balsam poplar in the northeast and alder and cottonwood on the coast, coupled with recognition of the importance of the hardwood tree species in many integrated resource management issues, has spawned new efforts in management and research throughout the province.

Collection, propagation, and experimentation with inter-specific hybrid poplar clones and native cottonwoods by the B.C. Forest Service began in 1984 at the Kalamalka Forestry Centre in Vernon. Since then several demonstration plantations as well as growth and adaptedness screening trials have been planted. In addition to the short-rotation intensive-culture plantations near Vernon using treated municipal wastewater, three series of wild site screening trials were planted in 1988, 1989, and 1993 at several coastal and interior locations. The objective of these trials has been to measure the stem growth potentials and general

adaptedness of several hybrid clones in comparison to native black cottonwoods and balsam poplars.

The 1988 trial consisted of 50 hybrid clones and native controls planted at three northern locations—Prince George, Dawson Creek, and Fort Nelson. After three growing seasons it was apparent that none of the hybrids tested was capable of tolerating the hard early fall frosts and/or severe winter cold (desiccation) events typical of these northern environments.

The 1989 test series consisted of 90 hybrid clones and native controls planted at two southern interior and four coastal locations. After one growing season, the *P. trichocarpa* × *P. deltoides* hybrids as a group are the superior stemwood volume producers with certain clones exceeding native cottonwood controls by 3x. Most of the hybrids tested have been quite tolerant of cold events in the low-elevation southern interior and coastal environments with little damage observed to date. We are just beginning to evaluate these materials for susceptibility to both local and recently imported *Melampsora* leaf rusts as well as to stem-boring insects.

Management and Culture of Poplars by Scott Paper Limited

Peter McAuliffe

Scott Paper Ltd.

Scott Paper has managed and utilized poplars in B.C. for over 40 years in the production of household paper products. Scott Paper grows about half of its annual requirement of 100 000 m³ of poplar fiber on 5000 ha of alluvial valley-bottom lands along the coast of B.C. These lands are very productive but not well-suited to other tree species because of frequent flooding and high brush hazard.

Since being awarded Tree Farm License #43 (B.C.'s first TFL) in 1985, Scott Paper has continued to replace mixed second-growth stands with more productive stands containing a high proportion of poplar.

Nowadays, non-timber resources (such as wildlife, fish, and water) on alluvial sites are being assigned progressively higher values by society, making the primary objective of growing pulpwood on these dispersed and fragmented ecosystems very challenging. As an alternative, Scott Paper is moving towards the short-rotation (12–15 years) intensive culture of poplars on good quality farmland to meet fibre needs. Poplars managed under an agricultural system for the first 3 years will grow at an impressive rate of over 30 m³ha⁻¹yr⁻¹. Scott Paper currently practices intensive silviculture on about half of currently harvested lands and we are encouraging private landowners in the Fraser Valley to grow poplar pulpwood too.

We have tested more than 400 different clones of poplar and are currently planting about 20 of these operationally. Our clones were bred in other regions (USA, Ontario, Europe, Japan). The recent spread of an exotic European leaf rust into B.C. has threatened a number of our operational clones, forcing us to shift to resistant hybrids. This disease has underscored the need to constantly test and improve planting stocks. B.C. needs a tree improvement program for poplars right now!

The culture of poplars has great potential in B.C. and is only now beginning to be recognized. Poplars can supplement a dwindling fibre supply, offset the regional shortages predicted for the next three decades, provide environmental diversity in coniferous stands, and afford environmental protection in special management zones. Poplar make tremendous tissue, perfect papers, super strand board, and dependable dimension lumber.

By concentrating our forest management efforts on our most productive and operable sites, we can reduce the pressure on the balance of our provincial forest to provide the full range of resources demanded by the public.

Management and Culture of Poplars by MacMillan Bloedel Limited

Cees van Oosten

MacMillan Bloedel

Three main economic objectives of poplar plantation management by MacMillan Bloedel Limited:

1. To improve utilization of privately held high-site bottomland, within short haul distances from processing facilities.
2. To produce a competitively priced, incremental chip supply in the shortest possible time.
3. To lower pulp and paper manufacturing costs and to enable production of higher paper grades.

Site rehabilitation of high-site land is expensive; cost-effective use of herbicides remains controversial and does not always yield the desired results.

The combination of good clonal selection, hybrid poplar's growth potential, thorough site preparation, and several years of weed control can produce a free-growing stand in less than 2 years. We can do all of this virtually without using herbicides.

We have been developing our technology since 1987 with assistance from the University of Washington/

Washington State University's Poplar Research Team, Peter McAuliffe of Scott Paper Canada Ltd., and Mike Carlson of the B.C. Ministry of Forests.

Our research includes testing 376 different hybrid poplar crosses in several field trials, of which we selected 29 that combine good growth with disease resistance. These trials continue to date and new trials will be established on an ongoing basis.

In 1988 we established the first growth and yield plantation plots with a few selected hybrid poplars (of which we know virtually nothing) to verify yields reported elsewhere in the Pacific Northwest and Europe. The early growth results show that we are on the right track.

During 1990 and 1993 we investigated and identified MacMillan Bloedel private lands suitable for poplar plantation management. Since poplar thrives under conditions of high summertime temperatures and moist soils, we restricted ourselves to the best soils on east Vancouver Island (including the Alberni Valley) and the mainland (Powell River).

Ecology of Red Alder (*Alnus rubra* Bong.)¹

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Abstract

This paper provides an overview of the ecology of red alder (*Alnus rubra*), with emphasis on aspects important in forest management. Published and unpublished sources are summarized; where appropriate the author indicates topic areas where “common knowledge” or generalizations included in past reports are not supported by quantitative information. Autecological characteristics, such as site requirements, seed production, growth rates, and damaging agents, are highlighted. Where information is available, the functional roles of red alder in forested ecosystems are also discussed.

Introduction

Red alder (*Alnus rubra*), also called Oregon alder, western alder, and Pacific coast alder, is the most common hardwood in the Pacific Northwest. It is a relatively short-lived, shade-intolerant pioneer with rapid juvenile growth and the capability to fix atmospheric nitrogen. Regeneration of the species is favoured by soil disturbance and often occurs after harvesting and burning. Because the commercial value of alder has traditionally been lower

than that of its associated conifers, many forest managers have tried to eliminate the species from conifer stands. On the other hand, red alder is the major commercial hardwood tree species in the region; its wood is used for furniture, cabinets, and pallets, and to make paper (Harrington 1984b). Its value has increased substantially in recent years and interest in the management of the species has increased accordingly. However, as management attention increases, so does the need for detailed information on the biology of the species. This paper summarizes information on the ecology of red alder and points out subject areas where common assumptions or beliefs about red alder are not supported by specific data.

Taxonomy

Red alder is in the Betulaceae family. Other common western North American genera in this family are the birches (*Betula*) and hazelnuts (*Corylus*). The most conspicuous feature these 3 genera have in common is the presence of male catkins (compact aggregates of staminate flowers) (Brayshaw 1976). The seed-bearing catkins in alder and birch are similar when immature. However, the birch catkin disintegrates as seeds are dispersed, while those of alder remain intact and attached to the plant during seed dispersal and for a time after dispersal is completed.

¹ Portions of this manuscript were taken from Harrington et al. (1994).

Genetic Variation

Geographic variation in growth rates, sensitivity to frost, and other characteristics has been reported (DeBell and Wilson 1978; Lester and DeBell 1989; Ager and Stettler 1994). In one study, provenances from areas with cold winters (i.e., Alaska, Idaho, high elevations in Washington and Oregon) had the poorest growth but the greatest resistance to frost damage. Specific gravity did not differ significantly among provenances, nor was it correlated with growth rate (Harrington and DeBell 1980). In another study, which compared families from coastal sources, it was possible to identify families with high growth rates and low sensitivity to spring frosts (Peeler and DeBell 1987; DeBell et al. 1990). A 24-family progeny trial in western Washington also demonstrated family variation in height-growth response to water-table depth (Hook et al. 1987).

As forest managers plant red alder on increasing acreage, additional information will be needed on genetic variation in the species. Preliminary recommendations are available on seed zones for red alder (Hibbs and Ager 1989; Ager et al. 1994). However, information is lacking on the variation within the species in its tolerance of low nutrient or low soil moisture conditions and on the possible interactions among silvicultural practices, genotype, and wood quality characteristics.

Habitat

Native Range

Red alder occurs most commonly as a lowland species along the northern Pacific coast. Its range extends from southern California (lat. 34° N) to southeastern Alaska (60° N). Red alder is generally found within 200 km of the ocean and at elevations below 750 m. Tree development is best at elevations below 450 m in northern Oregon, Washington, and British Columbia. In Alaska, red alder generally occurs close to sea level. Farther south, scattered trees are found as high as 1100 m, but most stands are at elevations below 750 m. Red alder seldom grows east of the Cascade Range in Oregon and Washington or the Sierra Nevada in California, although several isolated populations exist in northern Idaho (Johnson 1968a, b).

Climate

Red alder grows in climates varying from humid to super-humid. Annual precipitation ranges from 400 to 5600 mm; most of the precipitation is rain in winter. Summers are generally warm and dry in the southern part of the range and are cooler and wetter in the northern portion. Temperature extremes range from -30°C in Alaska and Idaho to 46°C in California. Low winter temperatures and lack of precipitation during the growing season appear to be the main limits to the range of red alder. For good development of trees, either annual precipitation should exceed 630 mm or tree roots should have access to ground water (Harrington 1986).

Soils and Topography

Red alder is found on many types of soils. In Washington and Oregon it grows primarily on soils of the orders Inceptisols and Entisols, but is also found on some Andisols, Alfisols, Ultisols, Spodosols, and Histosols (Harrington and Courtin 1994). In British Columbia, alder occurs on Brunisols, Gleysols, Organics, Podzols, and Regosols (Harrington and Courtin 1994). The most productive stands are found on deep alluvial soils in river and stream floodplains; however, some excellent stands are also found on upland sites on residual or colluvial soils derived from volcanic materials. A field guide to predict site index based on soil and site characteristics is available (Harrington 1986). The field guide was developed based on plots in northwestern Oregon and western California; it may need to be modified to improve its performance outside that range (Harrington and Courtin 1994).

Red alder stands occur on a relatively wide range of soil drainage classes (Harrington and Courtin 1994). Although productivity may be reduced, alder can tolerate very poorly drained soil conditions and some flooding during the dormant and growing seasons (Minore 1968; Harrington 1987). Because some of its common tree associates do not tolerate very wet soils (Minore 1979), pure alder stands can occur along stream bottoms or in swamps or marshes. However, it does not commonly occur on droughty soils and in areas of low precipitation, it seldom grows on steep south- or southwest-facing slopes. Alder stands of above-average productivity are found on some well or excessively drained soils if they occur in floodplains or river terraces where trees have access to ground water. In Idaho and

California, stands are usually limited to borders of streams or lakes.

Nutrient requirements of red alder are not well defined. Phosphorus appears to be the element most likely to be limiting to growth (Radwan and DeBell 1994) with both P concentrations and soil rooting depth influencing the amount of available soil P (Harrington and Courtin 1994). In a recent analysis of approximately 200 alder stands in Oregon, Washington, and British Columbia (Harrington and Courtin 1994), pH in surface soil ranged from 4.0 to 6.5; the most productive stands were on soils with pH above 4.5.

Associated Forest Cover

Red alder grows in both pure and mixed stands. Pure stands are typically confined to stream bottoms and lower slopes. Red alder is, however, much more widely distributed as a component of mixed stands. It is a major component of the Red Alder cover type (Society of American Foresters Type 221) and occurs as a minor component in most of the other North Pacific cover types (Eyre 1980).

Common tree associates are Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*), grand fir (*Abies grandis*), Sitka spruce (*Picea sitchensis*), black cottonwood (*Populus trichocarpa*), bigleaf maple (*Acer macrophyllum*), and willow (*Salix* spp.). Occasional tree associates include cascara buckthorn (*Rhamnus purshiana*), Pacific dogwood (*Cornus nuttallii*), and Oregon ash (*Fraxinus latifolia*). Western paper birch (*Betula papyrifera* var. *commutata*) is an occasional associate in the northern portion of the range of alder, and redwood (*Sequoia sempervirens*) in the southern portion.

Common shrub associates include vine maple (*Acer circinatum*), red and blue elder (*Sambucus callicarpa*, *S. cerulea*), Indian plum (*Osmaronia cerasiformis*), salmonberry (*Rubus spectabilis*), western thimbleberry (*R. parviflorus*), devil's club (*Oplopanax horridum*), Oregon grape (*Berberis nervosa*), and salal (*Gaultheria shallon*).

Herbaceous associates include stinging nettle (*Urtica dioica*), skunk cabbage (*Lysichitum americanum*), blackberry (*Rubus laciniatus*, *R. leucodermis*), California dewberry (*R. ursinus*), swordfern (*Polystichum munitum*), lady fern (*Athyrium filix-femina*), Pacific water parsley (*Oenanthe sarmentosa*), youth-on-age (*Tolmiea menziesii*), Oregon oxalis (*Oxalis oregana*), and western springbeauty (*Montia sibirica*).

Other Ecological Associations

General associations or interactions between red alder and wildlife species have been recently summarized (McComb 1994). He reported that: 1) red alder stands are used by 136 species of vertebrates for reproduction and by 178 species for feeding; 2) several species of insectivorous birds, mammals, and amphibians are more abundant in red alder than in conifer stands; and 3) the number of bird species in unmanaged conifer stands is positively correlated with basal area of live deciduous trees (including red alder). Functional relationships between wildlife species and red alder trees or stands, however, have not been studied. Interactions between red alder and animals or insects that can result in tree damage are discussed later in this chapter.

Red alder is a key component of many riparian ecosystems within its range. The specific effects of alder on the streams associated with these riparian stands have not been much studied. Primary productivity in third-order and larger streams in western Oregon is nitrogen-limited (Gregory 1979). Alder could increase potential stream productivity by adding nitrogen via direct litter deposition or soil leaching (root or nodule exudates or decomposition of high-nitrogen materials).

For a fourth-order stream in the Oregon Cascades, Wondzell (1994) reported that alder on gravel bars supplied 2.5 times more N per unit area to the stream than the general floodplain (in Douglas-fir and western hemlock forest). However, due to the small number of gravel bars in the total floodplain area, the majority of the N supplied to the stream came from the conifer-dominated floodplain. Most nitrogen input from the alder-occupied gravel bars occurred at the beginning of the rainy season when high rainfall appeared to flush nitrogen stored within the soil into the aquifer. The levels of nitrogen inputs were lower than expected. Additional work is needed to quantify nitrogen cycling under other biogeoclimatic conditions.

Forest Succession

Red alder is a pioneer species favoured by high light levels and exposed mineral soil. Its ability to fix atmospheric nitrogen permits establishment on geologically young or disturbed sites with low levels of soil nitrogen. It can form pure stands on alluvium, avalanche paths, and other disturbed sites. Alder has been favoured by harvesting and burning; pollen records indicate that alder stands are more extensive in the 20th century than they were for several

centuries before that time (Heusser 1964; Davis 1973). Red alder pollen was also abundant between 9000 and 4800 BC; this has been interpreted as indicating a somewhat warmer climate accompanied by an increase in fire frequency (Cwynar 1987).

Observations of mature forests in the Pacific Northwest suggest that alder stands are ultimately replaced by longer-lived, more tolerant conifers having sustained growth rates at older ages than does alder. This is undoubtedly true in most cases (see discussion below for exceptions), but the time required for this to occur in unmanaged forests is not well documented. Rapid alder growth and high alder stem densities in younger stands make it difficult for conifers (especially shade-intolerant species) to regenerate and grow if they do not become established at the same time or shortly before alder invades a disturbed area. Douglas-fir can be easily eliminated in dense young alder stands while more tolerant species (western hemlock, redcedar, and Sitka spruce) can survive and, over time, grow into the alder canopy and ultimately dominate the site.

Many alder stands in western Oregon have few associated conifers and some researchers have concluded that those alder stands will be replaced by shrubs and that without disturbance a shrub-dominated community may persist for an extended period of time (Newton et al. 1968; Carlton 1988; Tappeiner et al. 1991; O'Dea 1992). Clonal shrubs, particularly salmonberry, but also thimbleberry and vine maple, often form a dense shrub canopy, which makes it difficult for conifers to invade and become established from seed. These shrub species can expand rapidly by vegetative reproduction as space becomes available due to death of the alder overstory (Tappeiner et al. 1991; O'Dea 1992; Zasada et al. 1992).

Experience suggests that alder replacement by conifers will have a high degree of spatial and temporal variation if the process is left to proceed naturally. The presence and abundance of shade-tolerant tree species are obviously important in influencing which successional trajectory will be followed; however, the specific ecological factors that determine the successional sequences in alder stands are not known.

Life History

Reproduction and Early Growth

Flowering and Fruiting

Red alder reaches sexual maturity at age 3–4 years for individual trees and age 6–8 for most dominant trees in a stand (Stettler 1978). It is generally monoecious, with separate male and female catkins developing on the previous year's twigs (Hitchcock et al. 1964). Staminate catkins occur in pendulous groups and are usually in a terminal position on a short shoot. In late winter they elongate, changing from green to reddish brown and from 2–3 cm long to about 7–8 cm. Pollen grains are small (20–23 μm in diameter, Owens and Simpson undated), lightweight, and produced in abundance. Several pistillate catkins are borne per floral bud and are commonly located on a bud proximal to the staminate catkins. They are 5–8 mm long and reddish green when receptive. Both male and female catkins usually occur in groups of 3–6. Flowering occurs in late winter or early spring; peak shedding of pollen generally precedes peak receptivity by a few days but synchrony in pollen shed and receptivity have been observed in some trees (Brown 1985). Pistillate catkins are upright at the time of flowering but become pendulous as they mature. Most alder seed is probably the result of outcrossing, but some self-pollination does occur (Stettler 1978).

Seed Production and Dispersal

Seeds are small, winged nutlets borne in pairs on the bracts of woody, cone-like strobili (Schopmeyer 1974). The seeds are without endosperm and contain only small cotyledons (Brown 1986). The strobili are 11–32 mm long, and 8–15 mm wide.

Red alder is believed to be a prolific and consistent producer of seed. However, there do not seem to be any long-term records of red alder seed production that would provide a quantitative assessment of annual variation in seed quantity and quality, timing of dispersal, and distance of dispersal. Seed production in red alder varies substantially among trees; Brown (1985) reported production rates for 45 mature trees of similar size to vary from 0 to 5.4 million seeds per tree. She reported within-stand variation to be much greater than variation among stands. Based

on a 2-year study of seedfall on two sites in British Columbia, McGee (1988) reported substantial variation between sites and years. Maximum total production was 1550 seeds/m². In the more productive year, one site produced 1.8 times more seed than the other, while in the less productive year seedfall was similar at both sites. Seed crop quality (percent viable seeds) was similar between sites with 40–50% of the seeds viable in the good year and less than 10% in the poorer year. Worthington (1957) concluded that moderate seed crops are produced almost annually and bumper crops occur every 3–5 years; however no specific studies were cited. Complete failure of a seed crop is rare, but after a severe freeze in 1955, almost no seed was produced in 1956 (Worthington 1957).

The most closely related species for which long-term seed production records are available is black alder (*A. glutinosa*, a European species occurring in the same section of the genus as *A. rubra*) in Finland (Koski and Tallquist 1978). Maximum seed production over a 13-year period did not exceed 350 seeds/m²; this level of production is substantially less than the highest total production reported for red alder (Lewis 1985; McGee 1988), but seeds of black alder are about two times larger than those of red alder. Maximum seed production in various birch species with seeds of equal or smaller size than those of red alder are 10–15 times greater than those reported for black alder (Brinkman 1974; Koski and Tallquist 1978, Zasada et al. 1991). McGee (1988) reported that red alder and paper birch seed production followed similar patterns of annual variation and had similar levels of seedfall over a 2-year period on one site where the species occurred together. The large differences in seed crop quality reported for alder (Brown 1985; Lewis 1985; McGee 1988; Ager et al. 1994) are also characteristic of seed production in birch (Safford et al. 1990; Zasada et al. 1991).

The annual pattern of red alder seed dispersal and how it varies over its range is not well documented. In general it is believed to begin in the middle of September in the centre of its range and slightly earlier or later to the north and south, respectively. McGee (1988), working in British Columbia, found that small amounts of seed were dispersed in September, but that the major dispersal events occurred from November to February. Lewis (1985) reported that most seedfall of red alder in Washington occurred during winter and spring, but some seedfall was observed all months of the year. Major dispersal events occurred in consecutive months as well as being separated

by several months of low dispersal, a pattern similar to that in other Betulaceae (McGee 1988; Zasada et al. 1991).

The nature of the catkin suggests that the timing of seed dispersal is regulated by factors similar to those regulating the release of seeds from the cones of conifers. That is, once catkins are mature, dispersal is determined by the occurrence of weather that dries them, thus opening the scales and allowing the seeds to be released. In general, wet weather keeps catkins closed and wet weather following dry weather closes catkins, thus terminating a dispersal event. However, heavy seedfall can occur during wet weather under certain catkin conditions (Lewis 1985) and dispersal will not occur if ice freezes the seed in the catkin (Lewis 1985; Brown 1986). The quantity of seed dispersed during a dispersal event is dependent on the length of the period during which suitable weather occurs, condition of the catkins that retain seeds, and the amount of catkin movement caused by wind and other agents that shake seeds loose. The dispersal patterns reported for red alder (Lewis 1985; McGee 1988) are consistent with the hypothesized mechanisms, but more frequent observations of seed dispersal in relation to weather and catkin condition need to be made. In coastal Alaska, drying trends brought by high-pressure weather systems are important to seed dispersal of Sitka spruce and western hemlock (Harris 1969), two common associates of alder. In addition, generally similar patterns of seed dispersal have been observed for alder and hemlock growing together in the same stand in western British Columbia (McGee 1988).

Red alder seeds are very light, numbering 800–3000/g, and wind dissemination can be effective over long distances. Lewis (1985) documented dispersal distance and some factors affecting dispersal of red alder seeds for a 2-year period. He found amount of seed, seed weight, percentage of filled seed, and viability all to be inversely correlated with distance from the seed source. Amount of seedfall 100 m from the edge of an alder stand was 2–3% of the seedfall density inside the stand. Additional information on distance of seed dispersal in the Betulaceae is available for paper birch (*Betula papyrifera*) from New England and Alaska (c.f., Bjorkbom 1971; Zasada 1986). Those studies report that birch seed as a percent of age within-stand production ranges from 5–20% at 55 m from the seed source and drops to about 1% at 100 m.

Although seeds are primarily wind dispersed, some dispersal may occur by water (Brown 1986), and birds or other animals may also play a role. Birds are commonly seen

around catkins, and alder seeds have been shown to be an important source of food for some species (White and West 1977). The role that birds play in dispersal is both passive and active. Passive dispersal would occur simply by movement of the catkins as birds work in the crown of alders. A more active role in dispersal would occur as birds actually extract seeds from the catkins while feeding.

Germination, Seedling Survival, and Development

Seed germination, seed predation, and first-year seedling survival were the subject of a detailed 2-year study in the central Oregon Coast Range by Haeussler (1987). The following briefly summarizes the main findings from this work; the reader is referred to the publications describing this research (Haeussler 1987; Haeussler and Tappeiner 1993) for the details. The study was conducted on north and south aspects in forested and clearcut environments located near the coast (west side, relatively wet micro-environment) and on the east side of the Coast Range (relatively dry). Seeds were sown on protected and unprotected microsites that were disturbed (exposed mineral soil) or undisturbed.

Seed germination in clearcut environments began in late February and early March and was completed by mid-April. There were some differences among north and south aspects but these were small compared to the forested environments where the onset of germination was delayed, relative to that in clearcuts, for a month and continued into June. On average, the number of germinants emerging was higher on disturbed than on undisturbed seedbeds. There was no clear difference in germinant appearance between forested and clearcut environments for either seedbed type. A positive relationship between spring soil moisture conditions and germinant appearance was stronger in the clearcut environment than in the modified light and temperatures prevailing under forested conditions (Haeussler 1987).

Seedling establishment—in terms of the number of seeds required to produce a one-growing-season-old seedling—differed dramatically between the west side and east side Coast Range environments. Under the drier conditions on the east side of the Coast Range, no seedlings survived through the growing season in either of the years of study. On the north aspect on the west side coast site there was an average of one seedling per 32 seeds sown; on an adjacent south aspect one seedling was produced per 181 seeds (Haeussler 1987). In another study on a south-

west-facing coastal site, sowings in each of 2 years on newly created mineral soil seedbeds at a rate of 1000–1500 seeds/m² failed to produce any surviving seedlings at the end of one growing season (J. Zasada, unpublished data). In a third study, sowing of alder seed on dry Coast Range sites similar to those studied by Haeussler (1987) resulted in germinants but no surviving seedlings after one growing season (J. Tappeiner and J. Zasada, unpublished data). The results of Haeussler's detailed study (1987) and the two smaller studies mentioned above suggest that alder establishment is not assured even when provided with large quantities of seeds on what are believed to be desirable seedbeds. This seems contrary to operational experience, where it seems that alder occurs everywhere that it is not wanted, but as Michael Newton (Oregon State University) has observed, it is difficult to predict where natural alder regeneration will be successful, and alder often fails to appear where it would seem most likely to occur.

There are a number of environmental factors that result in high mortality of seeds and seedlings between the time seeds arrive on the seedbeds and the end of the first growing season (Haeussler 1987), and these certainly contribute to the temporal and spatial variation in alder regeneration. In unprotected microsites, seedling emergence was 75% on disturbed seedbeds and 38% on undisturbed seedbeds on protected microsites. Loss of seeds to soil biota was greater under forest conditions than in clearcuts. On undisturbed and mineral soil microsites, 60 and 20%, respectively, of the seed population was destroyed by soil organisms. Causes of seedling mortality included drought and heat injury, pathogens, animals, erosion, frost, and smothering by organic debris. Drought and heat-related mortality were the major causes of mortality in clearcuts, whereas damping-off fungi and other pathogens were most important under forest conditions (Haeussler 1987).

Alder seeds are most commonly described as having little or no dormancy. This is based on studies that have shown that germination of stored seeds under optimum germination temperatures is not improved by stratification (Radwan and DeBell 1981; Berry and Torrey 1985); however, one provenance from British Columbia was reported as having a physiological dormancy that was released by stratification (Elliott and Taylor 1981a). Germination under sub-optimum temperatures, such as may prevail at the time of germination under field conditions, is enhanced by stratification (Tanaka et al. 1991). Studies with other Betulaceae species and with

common associates (e.g., bigleaf maple; J. Zasada, pers. comm.) have also shown that germination rates at lower temperatures are higher for stratified seed.

Bormann (1983) and Haeussler (1987) both demonstrated that alder seeds do not germinate in the dark and that the phytochrome system is very sensitive (i.e., germination is inhibited by exposure to far-red light). In a field study, Haeussler (1987) showed that seed germination under optimum moisture conditions created in sealed germination chambers was greater than 90% in a clearcut and under a Douglas-fir stand but less than 50% under an alder canopy. Furthermore, under all overstory conditions, germination was reduced in varying degrees by the presence of understory vegetation. Thus, this study strongly suggests that alder germination is controlled by light quality and that a type of light-enforced dormancy may prevent seeds from germinating when other conditions appear optimal. This would suggest that a persistent alder seedbank may be present under some conditions. However, because of the high seed mortality rate caused by soil organisms, Haeussler and Tappeiner (1993) concluded that alder seed was unlikely to persist in a stand's seedbank for more than 1-2 years. Although long-term storage of viable alder seed is probably unlikely under most conditions, it is important to note that seeds of some *Betula* species remain viable in the soil for much longer than would be expected based on seed coat structure and general seed germination characteristics (Granstrom 1982; Perala and Alm 1989).

Assuming that site conditions are suitable, red alder will regenerate where light levels are adequate, mineral soil is exposed, and viable seeds are present. The species is an aggressive pioneer on avalanche paths, road cuts, log landings, skid trails, or other areas where mineral soil has been freshly exposed to seed fall. For example, shortly after a heavy thinning (removal of 50% of the basal area) in a 62-year-old Douglas-fir stand, an alder understory became established and grew rapidly (Berg and Doerksen 1975). Clearcutting and large-group selection are feasible regeneration systems. During harvesting or in a subsequent site preparation treatment, the site must be disturbed sufficiently to expose mineral soil if alder regeneration is desired. Fire can probably substitute for mechanical disturbance on most sites. To exclude red alder from the next rotation stand, some forest managers try to reduce the supply of alder seed by cutting possible alder seed trees in the vicinity before or at the time of final harvest, and also to avoid creating favourable seedbed conditions by disturbing the site as little as possible during logging and,

if feasible, by not burning the logging slash (Lousier and Bancroft 1990).

Artificial regeneration can be accomplished with either bare-root or containerized seedlings and guidelines for producing planting stock are available (Berry and Torrey 1985; Radwan et al. 1992; Ahrens 1994). Survival and growth of planted seedlings are usually excellent (Radwan et al. 1992), but can vary significantly with slope, slope position, and aspect within a given clearcut. For example, when different sites within a clearcut in the Oregon Coast Range were planted with alder, there was nearly 100% survival on steep north aspects over a 3-year period while immediately adjacent south-facing and stream-bottom sites (with higher soil moisture stress and a higher probability of early season frosts, respectively) suffered as much as 60% mortality (J. Zasada, pers. comm.).

Height growth of red alder seedlings is generally rapid. On favourable sites, seedlings can grow 1 m or more the first year and, on all but the poorest sites, seedlings surpass breast height (1.3 m) the second year (Smith 1968; Harrington and Curtis 1986). Even on some frost-prone sites in western Oregon, seedlings affected by frost shortly after outplanting attained breast height in 2 years (J. Zasada, pers. comm.). Mitchell and Polsson (1988) indicated that on most sites in British Columbia, however, alder seedlings take 3 years to pass 1.3 m. Maximum annual height growth of more than 3 m/year can be achieved by 2-5-year-old seedlings (Harrington and Curtis 1986).

Seasonal growth of red alder is under strong climatic control and consequently is quite variable. The timing of radial growth is similar for red alder and its common associate Douglas-fir; in the Puget Sound area of Washington State, growth begins about mid-April and continues until mid-September (Reukema 1965). Height growth begins slightly later in the season than radial growth. Red alder has indeterminate height growth; thus, height growth continues through the growing season until soil moisture, temperature, or light conditions become unfavourable (c.f., DeBell and Giordano 1994). The specific environmental conditions that control root and shoot growth have not been determined.

Vegetative Reproduction

Red alder sprouts vigorously from the stump when young. It can be repeatedly coppiced on short cycles but rootstock mortality increases with each harvest (Harrington and

DeBell 1984). Age, time of year, and cutting height influence the likelihood of obtaining stump sprouts and the vigour of the sprouts (Harrington 1984a). Stumps will sprout best when trees are cut in the winter and when stump height exceeds 10 cm. Stumps of older trees rarely sprout and coppice regeneration cannot be expected after pole-size or sawlog-size material is harvested (Harrington 1984a). Because of reduced vigour of sprouting, manual cutting of alder as a means of competition control in conifer plantations can be an effective vegetation management practice (DeBell and Turpin 1989); however, results from cuts at different times during the summer can be variable (Pendl and D'Anjou 1990).

Red alder can also be propagated by rooting greenwood cuttings from young trees (Monaco et al. 1980), rooting succulent new spring growth from young trees or epicormic sprouts on older trees (Radwan et al. 1989), or by mound layering (rooting of stump sprouts). Alder does not root well from dormant season woody tissues, thus, "sticking" of unrooted cuttings in the field (as can be done for *Populus* or *Salix*) is not recommended.

Sapling and Pole Stages to Maturity

Growth and Yield

Alder growth form is strongly excurrent during the period of rapid height growth. Crown form becomes moderately to strongly deliquescent as the trees mature. Growth of vegetative shoots is primarily monopodial (e.g., branching with the apical bud a persistent leader and new branches arising laterally below the apex; Swartz 1971); however, shoots producing flowers exhibit sympodial growth (e.g., the terminal bud withers and the main axis of branching is made up of a series of lateral branches; Swartz 1971). Young, rapidly growing trees often exhibit sylleptic branching as current-year buds produce branches. The physiological factors that determine the amount of apical control on branch growth and angle have not been studied for alder.

Alder trees can exhibit substantial amounts of lean when grown in irregularly spaced stands or when located along roads, streams, stand boundaries, or other areas with unequal light distribution on all sides of the tree. Other changes in stem form may occur as the result of heavy snow or if gravity causes all or part of the tree to shift abruptly (e.g., as a result of soil slumping or high winds

when soils are saturated). However, if juvenile red alder is grown at wide and fairly even spacing, lean and sweep will be minimized (Bormann 1985; DeBell and Giordano 1994).

Red alder has rapid juvenile growth; of its associates, only black cottonwood grows as much or more during the juvenile phase. On good sites, trees may be 9 m at age 5, 16 m at age 10, and 24 m at age 20. One tree was 9.8 m tall and 16.3 cm dbh 5 years from seed (Smith 1968).

Growth slows after the juvenile stage, the decrease beginning much sooner on poor sites. Site index as determined at base age 20 years ranges from 10–25 m (Harrington and Curtis 1986); at base age 50, it ranges from 15–40 m (Worthington et al. 1960; Mitchell and Polsson 1988). Associated conifers have much slower juvenile growth, but they sustain height growth years longer than alder. On an average upland site, both Douglas-fir and red alder can attain the same height at about age 45 (Williamson 1968). Beyond that age, Douglas-fir surpasses red alder in height. Red alder and Douglas-fir also have different site tolerances; thus their relative performances will be site- as well as age-specific (Harrington and Courtin 1994). On better sites Douglas-fir may surpass alder in height at a younger age (c.f., Berntsen 1961).

Red alder is a relatively short-lived species, maturing at about 60–70 years; maximum age is usually about 100 years (Worthington et al. 1962). Maximum age is probably less on poor sites and those in the northern portion of the species range, and somewhat greater on the good sites, especially those in south central portion of its range (D. Hibbs, pers. comm., and pers. obs. by author). On favourable sites, trees can be 30–40 m tall and 55–75 cm in diameter. A record-size tree measured 198 cm dbh but trees over 90 cm in diameter are rare. Maximum cubic volume is attained at age 50–70 (500 m³/ha [Worthington et al. 1960; DeBell et al. 1978; Chambers 1983]). Most of the existing alder volume is in naturally regenerated mixed-species stands where growth and yield are variable.

Rooting Habit

Red alder forms extensive, fibrous root systems. Root system distribution is primarily controlled by soil drainage, soil structure, and compaction (unpublished data on file, Olympia Forestry Sciences Laboratory). In poorly drained soils, most rooting is surface-oriented, and rooting is often

prolific in the boundary between the lower organic layer and the uppermost mineral horizon. In wet soils, the uppermost mineral horizon is usually heavily rooted, as is the lower organic horizon if it is thick enough. On better-drained soils, rooting is more extensive and can penetrate quite deeply. On well-drained sites, root distribution is strongly influenced by water availability; increased rooting is common at horizon boundaries when changes in soil texture slow downward water movement through the profile. I have also observed rooting of alder to follow the path of least resistance; rooting is often enhanced in old root channels or, especially if the soil is compacted and soil structure well developed, between units of soil structure (peds). Root system extent is a function of soil characteristics and tree size. Smith (1964) showed tree diameter and average root length to be significantly correlated; larger trees also tended to have deeper roots than smaller trees. Root growth of seedlings is rapid; 2-year-old nursery-grown seedlings have been planted using a shovel because of their wide-spreading, large, woody roots.

Red alder, especially when young, will form adventitious roots when flooded. In two greenhouse studies, alder seedlings previously growing under well-drained conditions produced adventitious roots when the soil was flooded (Minore 1968) or saturated (Harrington 1987). Although it has not been documented, formation of adventitious roots could be an important adaptive trait on floodplain sites.

The sensitivity of red alder root growth to environmental conditions is not well known, but recent studies provide some information. Under soil moisture stress, red alder saplings shifted carbon allocation from leaf and stem biomass to root biomass (Chan 1990). In a companion study, root biomass decreased with increasing density of alder stems (Shainsky et al. 1992). Root:shoot ratios were significantly affected by density; however, most of the variation in root biomass was directly attributable to variation in shoot biomass. When grown in pots in a growth chamber, root:shoot ratios were decreased by fertilization and were lower in sandy soil than in loam or sandy loam (Elliott and Taylor 1981b).

Red alder roots are commonly ectomycorrhizal. Only a few species of fungi, however, are capable of forming ectomycorrhizal associations with alder. Fungal symbionts include alder-specific fungi and fungi capable of mycorrhizal associations with other hosts (Molina 1979; Molina et al. 1994).

Red alder also has root nodules that fix atmospheric nitrogen. The nodules are a symbiotic association between the tree and an actinomycete (*Frankia* spp.). Rates of nitrogen-fixation and the effects of these nitrogen additions on soil chemistry have been recently summarized (Binkley et al. 1994; Bormann et al. 1994). In natural stands, nodulation occurs soon after seed germination; root systems of seedlings a few months old commonly have dozens of visible nodules, ranging from the size of a pinhead up to 25 mm in diameter. Mature trees have nodules on both the large woody roots and the smaller new roots. Nodules found on large trees can be 80 or 90 mm in diameter. Epicormic branches with nodulated adventitious roots have been also observed to occur naturally in situations where moss and litter accumulated at the base of clumps of epicormics on older trees (M. Paschke, pers. comm.).

Reaction to Competition

Red alder requires more light than any of its tree associates except black cottonwood and is classed as intolerant of shade (Minore 1979). Light quality has been shown to be important in germination (Bormann 1983; Haeussler 1987); its role in seedling development has not been documented. Young seedlings and saplings can withstand partial shade but will grow very little and will not survive long when light levels are low. Self-thinning or mortality caused by competition is rapid in red alder stands; densities in natural stands may be as high as 124 000 seedlings/ha at age 5 (DeBell 1972) and fully stocked stands at age 20 averaged 1665 seedlings/ha (Worthington et al. 1960).

Red alder also self-prunes extremely well when grown in dense stands. Shaded lower branches rapidly die and fall off, resulting in clear and slightly tapered boles. Live crown ratios in crowded, pure stands are very low, and narrow, dome-like crowns are characteristic. However, as would be expected for a shade-intolerant species, branch retention and crown shape are strongly related to light levels in the canopy. Young alder with good growth rates will quickly occlude wounds associated with artificial pruning; however, stem breakage has been observed at the base of the live crown when heavy pruning was applied to young, very slender trees growing in exposed (windy) areas.

Epicormic sprouts are not uncommon on older trees, especially if they have been damaged or stressed or had increased light on their boles due to mortality or removal of adjacent trees. If epicormic sprouting occurs after thinning, it is most common on the south or west side of

stressed trees (personal observations); however, trees of any age that have experienced a drastic increase in light levels (e.g., via construction activities) may have epicormic branches on any or all sides. Epicormic branches appearing after early thinning or pruning are probably ephemeral, but this has not been documented.

Red alder can be managed in pure stands or as part of a mixture with either other intolerant species such as Douglas-fir and black cottonwood (or *Populus* hybrids) or with more shade-tolerant species such as western redcedar or western hemlock. Knowledge of site-specific growth rates and relative shade tolerances of each component in a mixture is critical to achieving the potential benefits from mixed stands. Alder must receive adequate light to grow well in mixed stands. However, even if alder is shaded out in a mixed stand it may make substantial contributions to soil nitrogen prior to that time (Berg and Doerksen 1975).

Reaction of alder to competition is influenced by many factors including the size, species composition, and density of the competing vegetation (other alder stems, non-alder stems in the upper canopy, and plants in the understory) as well as soil and site factors. For example, growth of closely spaced, dominant alder was decreased with increasing density of subordinate Douglas-fir (Shainsky and Radosevich 1991). The high densities of Douglas-fir decreased soil moisture availability for alder. This caused alder to shift carbon from leaf area production to root growth, resulting in a more favourable light environment for the understory species that were less moisture-limited (Shainsky and Radosevich 1991). Thus, the interactions among plants can be complex and may influence both current growth rates of alder and long-term stand development and succession.

Damaging Agents

In natural stands red alder has relatively few significant problems with damaging agents, that is, there are relatively few instances where damaging agents kill enough trees to result in large openings in a stand. However, forest managers may be concerned with lower levels of mortality and when growth rates are depressed or tree form or wood quality is affected. In addition, problems will likely increase as management is intensified, particularly in nurseries and plantations.

Fungi

Red alder is fairly free from most disease problems, especially when young and uninjured (Worthington et al. 1962; Hepting 1971; Harrington et al. 1994). In another chapter of these proceedings, Eric Allen has summarized the decay and wood utilization problems of the species.

Red alder is immune to *Phellinus weirii* (a widespread conifer root rot) and has been planted on sites where *P. weirii* infection levels are high. It has been hypothesized that red alder alters the soil environment to the detriment of *P. weirii* (Nelson et al. 1978; Li et al. 1969; Li et al. 1972; Hansen 1979) and suggested that alder may serve as a biological control agent for *P. weirii* (Trappe 1972; Nelson et al. 1978). These ideas cannot be tested until we have the results from long-term trials currently under way to quantify the effects of alder stands on *P. weirii*. At this time it is only recommended that alder be considered as one of several species to plant on sites with high levels of *P. weirii*. However, foresters planting red alder on poor or unsuitable sites will encounter poor growth and problems with damaging agents.

Insects

Numerous insects have been reported feeding on or associated with red alder (Furniss and Carolin 1977; Gara and Jaeck 1978; Dolan 1984). Insect pests are not usually a major concern, but serious outbreaks of some defoliators can cause growth reductions. The forest tent caterpillar (*Malacosoma disstria*), western tent caterpillar (*M. californicum*), alder woolly sawfly (*Eriocampa ovata*), striped alder sawfly (*Hemichroa crocea*), alder flea beetle (*Altica ambiens*), and a leaf beetle (*Pyrrhalta punctipennis*) have caused substantial damage; but reports of mortality are rare (Worthington et al. 1962; Furniss and Carolin 1977; Briggs et al. 1978). However, mortality was observed when a forest tent caterpillar outbreak overlapped a drought period (Russell 1991); this mortality was probably substantially greater than would have occurred if only one stress was present. A flatheaded wood borer (*Agrilus burkei*) can kill twigs and branches (Furniss and Carolin 1977; Briggs et al. 1978). The alder leaf miner, *Lithocolletis alnicolella*, can cause necrotic spots up to 30 mm in diameter on leaves but does not apparently affect growth (W. Littke, pers. comm.). An epidemic of grasshoppers was reported to only slow growth slightly (Russell 1986). The fall webworm (*Hyphantria cunea*) will skeletonize or

consume leaf blades but its damage is usually minor (Furniss and Carolin 1977). The alder bark beetle (*Alniphagus aspericollis*) breeds primarily in slash and in young stressed trees; however, healthy trees can be attacked when bark beetle populations are high (Briggs et al. 1978).

The alder aphid (*Pterocaulis alni*) feeds on tender shoots (Furniss and Carolin 1977) and on foliage with high nitrogen content (Dolan 1984). Aphids are common associates in many young alder stands and are not generally considered to cause much damage. However, a severe aphid epidemic was reported in a young alder plantation (Dolan 1984). Under those epidemic conditions, plots sprayed with insecticide had diameter growth increases of up to 38% over unsprayed plots. Poor vigour was suspected of predisposing the trees to supporting an outbreak (Dolan 1984).

Ambrosia beetles (*Gnathotrichus retusus*, *Trypodendron lineatum*, *Xyleborus saxeseni*) attack logs and slash left on the ground, causing a rapid degrade in quality. Insect holes can also serve as entry sites for fungi. Merchantable material should be removed rapidly, and large accumulations of slash should be avoided.

Animals

In general, animals cause only minor damage in alder stands; however, under some circumstances animal damage can be significant. Alder is not a highly preferred browse species for black-tailed deer (*Odocoileus hemionus columbianus*) or Roosevelt elk (*Cervus elaphus roosevelti*) during most of the year. Young trees are occasionally browsed by deer and elk, especially during the late summer and fall (Brown 1961), and browsing begins earlier in the growing season when weather conditions are dry or when other food sources are not available (personal observation). In the fall and winter, however, deer and elk preference for alder foliage increases. Abscising or freshly abscised alder leaves were documented as being a major component of deer and elk diets during the fall and winter in old-growth forests on the Olympic Peninsula (Leslie et al. 1984), and penned black-tailed deer have been observed eating freshly abscised alder leaves in the fall when other food sources were readily available (D. Campbell, pers. comm.). Seasonal changes in deer and elk browsing may be related to changes in foliar chemical composition; alder foliage in the fall is higher in crude fat content and lower in total phenols than during the summer (Radwan et al. 1978). Elk repeatedly browsed red alder planted on a debris flow

associated with the 1981 eruption of Mount St. Helens (Russell 1986); at that time alternative food sources were limited. Most browsed trees resprouted vigorously and very little mortality was associated with the heavy browse damage; however, the repeated browsing resulted in trees with shrub-like forms. Deer and elk can cause stem deformation, reduce growth, and provide entry sites for decay organisms when they rub antlers against tree trunks; in localized pockets this type of damage can be common.

Mountain beaver (*Aplodontia rufa*) clip small alder stems and branches; only the bark is eaten from stems 5–20 mm in diameter while the whole piece is consumed if less than 5 mm in diameter (D. Campbell, pers. comm.). Although mountain beaver clip only small-diameter pieces, they climb trees and can continue to clip branches and terminals as trees increase in size. Alder appears to be a regular item in mountain beaver diets (data on file, USDA APHIS Animal Damage Research Unit, Olympia, Wash.) and problems in stand establishment should be anticipated on sites with established mountain beaver populations (D. Campbell, pers. comm.). Mountain beaver use of alder foliage for food is minor except when other food sources are not available or in late September when use is fairly heavy (Voth 1968).

Observations of other animals damaging red alder are limited. Beaver (*Castor canadensis*) will cut any species of tree near their ponds to support their construction activities. As a food source, beaver prefer red alder over Douglas-fir, but other plants will be selected before alder if they are equally available (D. Campbell, pers. comm.). In years of high populations, meadow mice (*Microtus* sp.) girdle young stems; this type of damage has been most commonly observed in grassy or very wet areas. Deer mice (*Peromyscus maniculatus*) eat alder seed from the surface of snowpacks when other food is difficult to obtain (Moore 1949); however, alder seed is not usually a preferred food source. Individual trees can be heavily damaged by red-breasted sapsuckers (*Sphyrapicus ruber*); if the damage encircles all or most of stem, the top may break off during periods of wind or snow.

Extremes in Physical Factors

Extremes in physical factors—such as temperature, wind, or fire—can damage red alder. Mortality and top damage have been documented in natural stands after ice storms or unseasonable frosts (Worthington et al. 1962; Duffield 1956). Widespread cold damage was observed in bare-

root nurseries after a prolonged cold period in December 1990; this caused terminal dieback in many trees and some mortality, especially on trees in exposed areas. Recently planted trees are also susceptible to cold damage; late spring frosts and early fall frosts have caused top dieback and mortality (DeBell and Wilson 1978; Peeler and DeBell 1987; Dobkowski et al. 1994). The winter dormancy requirement for red alder has not been studied and the causal factors controlling timing of spring budbreak are not known. Presumably, once chilling requirements (if any exist) are met or day length is permissive, budbreak is temperature-dependent. This assumption is consistent with the observation of Peeler and DeBell (1987) that cold damage occurred when late frosts followed a period of warmer-than-normal temperature. Other temperature-related problems observed on alder are sunscald and frost cracks. As is generally true for other species, this type of damage is most common on the south and west side of exposed trees.

Fire is rarely a damaging agent because of the scarcity of flammable debris in alder stands; in fact, the species has been planted as a firebreak to protect adjacent conifers (Worthington et al. 1962). Alder bark is thin but sufficiently fire resistant to prevent damage during light surface fires (Worthington 1957).

Windthrow is not common in alder because of the intermingling of roots and branches, the absence of leaves during winter storms when soils can be waterlogged, and the relatively deep-rooting habit of the species on well-drained soils. Uprooted trees are most commonly observed along cutting boundaries or where established root systems have been undercut by flooding or erosion. High winds, heavy snow, and ice storms will break alder tops and branches but these problems are generally less for alder than for associated species, which are foliated during the winter. However, exposed windy sites—such as those near the ocean or mountain passes—will have top breakage and reductions in height growth consistently enough to reduce site index (Harrington 1986).

Climate within the range of red alder is generally characterized by low summer rainfall, and the species has evolved to survive under those conditions. For example, the greater stomatal control of red alder as compared to black cottonwood (Harrington 1987) is probably a key feature that allows red alder to grow on upland sites. On the other hand, red alder is not as drought-tolerant as most of its coniferous associates. During the summer of 1987,

rainfall in the Puget Sound area was less than one-third of normal; in red alder stands this resulted in widespread leaf yellowing and premature abscission, terminal dieback, and—on droughty sites or new plantings—mortality (Russell 1991). Prior to 1987, the Puget Sound area experienced several decades without back-to-back dry summers and many years of above-normal rainfall. Combining these weather patterns with high levels of harvesting activity, which created seedbed conditions favourable to alder establishment, may have increased the percentage of alder stands growing on drought-sensitive sites (K. Russell, pers. comm.). From 1987 through 1992, every summer (June 1–September 30) in the Puget Sound region had below-normal precipitation. Thus trees stressed by the extreme drought in 1987 may have been further stressed in subsequent years; presumably these back-to-back dry summers are one of the causes of the widespread instances of alder top-dieback and mortality in the Puget Sound region in the late 1980s and early 1990s (K. Russell, pers. comm.).

The sensitivity of red alder to stress factors other than those discussed above is not documented. Alder is found on sites close to the ocean and presumably is fairly tolerant of salt spray. Alder has also been observed adjacent to pulp mills and other industrial plants and thus exhibits tolerance for at least some components of air pollution.

Conclusion

The purpose of this paper was to provide forest managers with basic information on the ecology of red alder and to alert them to potential problems. Almost 15 years ago, Minore (1979) commented on the surprising lack of information on autecological characteristics of red alder. Although we have learned a great deal since then, much of the knowledge base on the ecology of red alder is still based on casual or short-term observations and not on detailed life histories or controlled experiments. It is hoped that both future research on the silvics of red alder, and documentation and feedback from operational experience, can be combined to provide a more complete knowledge base from which to make future management recommendations.

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Literature Cited

- Ager, A.A. and R.F. Stettler. 1994. Genetics of red alder and its implications. *In* Biology and management of red alder, Proc. Symp. Oreg. State Univ., Nov. 18–19, 1992. D. Hibbs, D. DeBell, and R. Tarrant (editors). Oreg. State Univ., Press, Corvallis, Oreg. pp. 92–105.
- Ager, A.A., Y. Tanaka, and J. McGrath. 1994. Biology, ecology, and utilization of red alder seed. *In* Biology and management of red alder, Proc. Symp. Oreg. State Univ., Nov. 18–19, 1992. D. Hibbs, D. DeBell, and R. Tarrant (editors). Oreg. State Univ. Press, Corvallis, Oreg. pp. 159–169.
- Ahrens, G. 1994. Seedling quality and nursery practices for red alder. *In* Biology and management of red alder, Proc. Symp. Oreg. State Univ., Nov. 18–19, 1992. D. Hibbs, D. DeBell, and R. Tarrant (editors). Oreg. State Univ. Press, Corvallis, Oreg. pp. 170–185.
- Berg, A. and A. Doerksen. 1975. Natural fertilization of a heavily thinned Douglas-fir stand by understory red alder. School of Forestry, For. Res. Lab. Oreg. State Univ. Res. Note 56.
- Berntsen, C.M. 1961. Growth and development of red alder compared with conifers in 30-year-old stands. USDA For. Serv., Pac. NW For. and Range Exp. Stn. Res. Pap. 38.
- Berry, A.M. and J.G. Torrey. 1985. Seed germination, seedling inoculation, and establishment of *Alnus* spp. in containers in greenhouse trials. *Plant and Soil* 87(1):161–173.
- Binkley, D., K. Cromack, Jr., and D.D. Baker. 1994. Nitrogen fixation by red alder: Biology, rates, and control. *In* Biology and management of red alder, Proc. Symp. Oreg. State Univ., Nov. 18–19, 1992. D. Hibbs, D. DeBell, and R. Tarrant (editors). Oreg. State Univ. Press, Corvallis, Oreg. pp. 57–72.
- Bjorkbom, J. 1971. Production and germination of paper birch seed and its dispersal into a forest opening. USDA For. Serv., NE For. Exp. Stn. Res. Pap. NE-209.
- Bormann, B.T. 1983. Ecological implications of phytochrome mediated seed germination in red alder. *For. Sci.* 29(4):734–738.
- . 1985. Early wide spacing in red alder (*Alnus rubra* Bong.): Effects on stem form and stem growth. USDA For. Serv., Pac. NW For. and Range Exp. Stn. Res. Note PNW-423.
- Bormann, B.T., K. Cromack, Jr., and W.O. Russell III. 1994. Influences of red alder on soils and long-term ecosystem productivity. *In* Biology and management of red alder, Proc. Symp. Oreg. State Univ., Nov. 18–19, 1992. D. Hibbs, D. DeBell, and R. Tarrant (editors). Oreg. State Univ. Press, Corvallis, Oreg. pp. 47–56.
- Brayshaw, T.C. 1976. Catkin bearing plants (*Amentiferae*) of British Columbia. Occasional papers, British Columbia Provincial Museum. No. 18. 169 p.
- Briggs, D.G., D.S. DeBell, and W.A. Atkinson, (compilers). 1978. Utilization and management of alder. Proc. Symp., April 25–27, 1977. USDA For. Serv., Pac. NW For. and Range Exp. Stn. Gen. Tech. Rep. PNW-70.
- Brinkman, K.A. 1974. *Betula* L.—Birch: *In* Seeds of woody plants in the United States. C.S. Schopmeyer (technical coordinators). USDA For. Serv., Agric. Handb. No. 450 pp. 252–257.

- Brown, E.R. 1961. The black-tailed deer of western Washington. Washington State Game Department, Biological Bull. 13. Olympia, Wash.
- Brown, S.M. 1985. A study of reproductive biology of *Alnus rubra* along three elevational transects in Washington and Oregon. Report on file, USDA For. Serv., Pac. NW Res. Stn., Olympia, Wash.
- _____. 1986. Sexual allocation patterns in red alder (*Alnus rubra* Bong.) along three elevational transects. M.S. thesis, Coll. For. Resour., Univ. Wash., Seattle, Wash.
- Carlton, G.C. 1988. The structure and dynamics of red alder communities in the central Coast Range of western Oregon. M.S. thesis, Dep. For. Sci., Oreg. State Univ., Corvallis, Oreg.
- Chambers, C.J. 1983. Empirical yield tables for predominantly alder stands in western Washington (4th ed.). State of Washington, Dep. Nat. Resour. DNR Report 31.
- Chan, S.S. 1990. Effects of light and soil moisture availability on Douglas-fir and red alder sapling development, carbon allocations, and physiology. Dissertation, Dep. For. Sci., Oreg. State Univ., Corvallis, Oreg.
- Cwynar, L.C. 1987. Fire and the forest history of the North Cascade Range. *Ecology* 68(4):791–802.
- Davis, M.B. 1973. Pollen evidence of changing land use around the shores of Lake Washington. *Northwest Sci.* 47:133–148.
- DeBell, D.S. 1972. Potential productivity of dense, young thickets of red alder. Crown Zellerbach, Forest Res. Note 2. Camas, Wash.
- DeBell, D.S. and P.A. Giordano. 1994. Growth patterns of red alder. *In* Biology and management of red alder, Proc. Symp. Oreg. State Univ., Nov. 18–19, 1992. D. Hibbs, D. DeBell, and R. Tarrant (editors). Oreg. State Univ. Press, Corvallis, Oreg. pp. 116–130.
- DeBell, D.S., M.A. Radwan, C.A. Harrington, G.W. Clendenen, J.C. Zasada, W.R. Harms, and M.R. McKevlin. 1990. Increasing the productivity of biomass plantations of cottonwood and alder in the Pacific Northwest. Annual Technical Report submitted to U.S. Dep. Energy.
- DeBell, D.S., R.F. Strand, and D.L. Reukema. 1978. Short-rotation production of red alder: some options for future forest management. *In* Utilization and Management of Alder, Proc. Symp., April 25–27, 1977, Ocean Shores, Wash. D.G. Briggs, D.S. DeBell, and W.A. Atkinson (compilers). USDA For. Serv., Pac. NW For. and Range Exp. Stn. Gen. Tech. Rep. PNW-70: 231–244.
- DeBell, D.S. and T.C. Turpin. 1989. Control of red alder by cutting. USDA For. Serv., Pac. NW Res. Stn. Res. Pap. PNW-RP-414.
- DeBell, D.S. and B.C. Wilson. 1978. Natural variation in red alder. *In* Utilization and Management of Alder, Proc. Symp., April 25–27, 1977, Ocean Shores, Wash. D.G. Briggs, D.S. DeBell, and W.A. Atkinson (compilers). USDA For. Serv., Pac. NW For. and Range Exp. Stn. Gen. Tech. Rep. PNW-70: 193–208.
- Dobkowski, A., P.F. Figueroa, and Y. Tanaka. 1994. Red alder plantation establishment. *In* Biology and management of red alder, Proc. Symp. Oreg. State Univ., Nov. 18–19, 1992. D. Hibbs, D. DeBell, and R. Tarrant (editors). Oreg. State Univ. Press, Corvallis, Oreg. pp. 186–201.
- Dolan, L.S. 1984. The cultural treatment of selected species for woody biomass production in the Pacific Northwest. Final report prepared by Seattle City Light Department for U.S. Dep. Energy. Grant DE-FG-79-78BP35773.
- Duffield, J.W. 1956. Damage to western Washington forests from November 1955 cold wave. USDA For. Serv., Pac. NW For. and Range Exp. Stn. Res. Note 129.
- Elliot, D.M. and I.E.P. Taylor. 1981a. Germination of red alder (*Alnus rubra*) seed from several locations in its natural range. *Can. J. For. Res.* 11:517–521.
- _____. 1981b. The importance of fertility and physical characteristics of soil in early development of red alder seedlings grown under controlled environmental conditions. *Can. J. For. Res.* 11:522–529.
- Eyre, F.H (editors). 1980. Forest cover types of the United States and Canada. Soc. of American Foresters, Washington, D.C.

- Furniss, R. and V.M. Carolin. 1977. Western forest insects. USDA For. Serv., Misc. Publ. 1339. Washington, D.C.
- Gara, R.I. and L.L. Jaeck. 1978. Insect pests of red alder: potential problems. *In* Utilization and Management of Alder, Proc. Symp., April 25–27, 1977, Ocean Shores, Wash. D.G. Briggs, D.S. DeBell, and W.A. Atkinson (compilers). USDA For. Serv., Pac. NW For. and Range Exp. Stn. Gen. Tech. Rep. PNW-70. pp. 265–269.
- Granstrom, A. 1982. Seed viability of fourteen species during five years of storage in forest soil. *J. Ecology* 75:321–331.
- Gregory, S.V. 1979. Primary production in Pacific Northwest streams. Ph.D. dissertation, Dep. For. Sci., Oreg. State Univ., Corvallis, Oreg.
- Haeussler, S. 1987. Germination and first-year survival of red alder seedlings in the central Coast Range of Oregon. M.S. thesis. Oreg. State Univ., Corvallis, Oreg. 105 p.
- Haeussler, S. and J.C. Tappeiner. 1993. Effect of the light environment on seed germination of red alder (*Alnus rubra*). *Can. J. For. Res.* 23(7):1487–1491.
- Hansen, E.M. 1979. Survival of *Phellinus weirii* in Douglas-fir stumps after logging. *Can. J. For. Res.* 9:484–488.
- Harrington, C.A. 1984a. Factors influencing sprouting of red alder. *Can. J. For. Res.* 14(3):357–361.
- _____. 1984b. Red alder: an American wood. USDA For. Serv. Publ. FS-215.
- _____. 1986. A method of site quality evaluation for red alder. USDA For. Serv., Pac. NW For. and Range Exp. Stn. Gen. Tech. Rep. PNW-192.
- _____. 1987. Responses of red alder and black cottonwood seedlings to flooding. *Physiol. Plantarum* 69:35–48.
- Harrington, C.A., and P.J. Courtin. 1994. Evaluation of site quality for red alder. *In* Biology and management of red alder, Proc. Symp. Oreg. State Univ., Nov. 18–19, 1992. D. Hibbs, D. DeBell, and R. Tarrant (editors). Oreg. State Univ. Press, Corvallis, Oreg., pp. 141–158.
- Harrington, C.A. and R.O. Curtis. 1986. Height growth and site index curves for red alder. USDA For. Serv., Pac. NW Res. Stn., Portland, Oreg. Res. Pap. PNW-358.
- Harrington, C.A. and D.S. DeBell. 1980. Variation in specific gravity of red alder (*Alnus rubra* Bong.). *Can. J. For. Res.* 10(3):293–299.
- _____. 1984. Effects of irrigation, pulp mill sludge, and repeated coppicing on growth and yield of black cottonwood and red alder. *Can. J. For. Res.* 14(6):844–849.
- Harrington, C.A., J.C. Zasada, and E.A. Allen. 1994. Biology of red alder (*Alnus rubra* Bong.). *In* Biology and management of red alder, Proc. Symp. Oreg. State Univ., Nov. 18–19, 1992. D. Hibbs, D. DeBell, and R. Tarrant (editors). Oreg. State Univ. Press, Corvallis, Oreg. pp. 3–22.
- Harris, A.S. 1969. Ripening and dispersal of a bumper western hemlock-Sitka spruce seed crop in southeast Alaska. USDA For. Serv., Pac. NW For. and Range Exp. Stn. Res. Note PNW-105.
- Hepting, G.H. 1971. Diseases of forest and shade trees of the United States. USDA For. Serv. Agric. Handb. 386. Washington, D.C.
- Heusser, C.J. 1964. Palynology of four bog sections from the western Olympic Peninsula, Washington. *Ecology* 45:23–40.
- Hibbs, D.E. and A.A. Ager. 1989. Red alder: guidelines for seed collection, handling, and storage. For. Res. Lab., Oreg. State Univ. Special Publ. 18.
- Hitchcock, C.L., A. Cronquist, M. Ownbey, and J.W. Thompson. 1964. Vascular plants of the Pacific Northwest. Part 2: Salicaceae to Saxifragaceae. Univ. Wash. Press, Seattle, Wash. p. 74.
- Hook, D.D., M.D. Murray, D.S. DeBell, and B.C. Wilson. 1987. Variation in growth of red alder families in relation to shallow water table levels. *For. Sci.* 33(1):224–229.
- Johnson, F.D. 1968a. Disjunct populations of red alder in Idaho. *In* Biology of alder, Proc. Symp. Northwest Scientific Association's Fortieth Annual Meeting, April 14–15 1967, Pullman, Wash. J.M. Trappe, J.F. Franklin, R.F. Tarrant, and G.M. Hansen. USDA For. Serv., Pac. NW For. and Range Exp. Stn. pp. 1–8.

- _____. 1968b. Taxonomy and distribution of northwestern alders. *In* Biology of alder, Proc. Symp. Northwest Scientific Association's Fortieth Annual Meeting, April 14–15 1967, Pullman, Wash. J.M. Trappe, J.F. Franklin, R.F. Tarrant, and G.M. Hansen (editors). USDA For. Serv., Pac. NW For. and Range Exp. Stn. pp. 9–22.
- Koski, V. and R. Tallquist. 1978. Results of long-time measurements of the quantity of flowering and seed crop of forest trees. *Folia Forestalia* 364. 60 p.
- Leslie, D.M., Jr., E.E. Starkey, and M. Vaura. 1984. Elk and deer diets in old-growth forests in western Washington. *J. Wildl. Manage.* 48(3):762–775.
- Lester, D.T. and D.S. DeBell. 1989. Geographic variation in red alder. USDA For. Serv., Pac. NW Res. Stn. Res. Pap. PNW-409.
- Lewis, S.J. 1985. Seedfall, germination, and early survival of red alder. M.S. thesis, Coll. For. Resour., Univ. Wash., Seattle, Wash.
- Li, C.Y., K.C. Lu, E.E. Nelson, W.B. Bollen, and J.M. Trappe. 1969. Effect of phenolic and other compounds on growth of *Poria weirii* *in vitro*. *Microbios* 3:305–311.
- Li, C.Y., K.C. Lu, J.M. Trappe, and W.B. Bollen. 1972. *Poria weirii*—inhibiting and other phenolic compounds in roots of red alder and Douglas-fir. *Microbios* 5:65–68.
- Lousier, J.D. and B. Bancroft. 1990. Guidelines for alder seed tree control. For. Can. and B.C. Min. For., FRDA Memo No. 132.
- McComb, W.C. 1994. Red alder: Interactions with wildlife. *In* Biology and management of red alder, Proc. Symp. Oreg. State Univ., Nov. 18–19, 1992. D. Hibbs, D. DeBell, and R. Tarrant (editors). Oreg. State Univ. Press, Corvallis, Oreg. pp. 131–138.
- McGee, A.B. 1988. Vegetation response to right-of-way clearing procedures in coastal British Columbia. Ph.D. thesis. Univ. B.C., Vancouver, B.C. 196 p.
- Minore, D. 1968. Effects of artificial flooding on seedling survival and growth of six northwestern species. USDA For. Serv., Pac. NW For. and Range Exp. Stn. Res. Note PNW-92.
- _____. 1979. Comparative autecological characteristics of northwestern tree species—a literature review. USDA For. Serv., Pac. NW For. and Range Exp. Stn. Gen. Tech. Rep. PNW-87.
- Mitchell, K.J. and K.R. Polsson. 1988. Site index curves and tables for British Columbia's coastal species. For. Can. and B.C. Min. For., Victoria, B.C. FRDA Rep. No. 37.
- Molina, R. 1979. Pure culture synthesis and host specificity of red alder mycorrhizae. *Can. J. Bot.* 57(11):1223–1228.
- Molina, R., D. Myrold, and C.Y. Li. 1994. Root symbioses of red alder: Technological opportunities for enhanced regeneration and soil improvement. *In* Biology and management of red alder, Proc. Symp. Oreg. State Univ., Nov. 18–19, 1992. D. Hibbs, D. DeBell, and R. Tarrant (editors). Oreg. State Univ. Press, Corvallis, Oreg. pp. 23–46.
- Monaco, P.A., T.M. Ching, and K.K. Ching. 1980. Rooting of *Alnus rubra* cuttings. *Tree Planters' Notes* 31(3):22–24.
- Moore, A.W. 1949. Forest tree-seed-eaters and methods used to measure their populations in the Pac. NW Douglas-fir region. *Wash. State Univ. Forest Club Quarterly* 23(1): 7–11, 25.
- Nelson, E.E., E.M. Hansen, C.Y. Li, and J.M. Trappe. 1978. The role of red alder in reducing losses from laminated root rot. *In* Utilization and Management of Alder, Proc. Symp., April 25–27, 1977, Ocean Shores, WASH. D.G. Briggs, D.S. DeBell, and W.A. Atkinson (compilers). USDA For. Serv., Pac. NW For. and Range Exp. Stn. Gen. Tech. Rep. PNW-70. pp. 273–282.
- Newton, M., B.A. El Hassan, and J. Zavitkovski. 1968. Role of red alder in western Oregon forest succession. *In* Biology of alder, Proc. Symp. Northwest Scientific Association's Fortieth Annual Meeting, April 14–15, 1967, Pullman, Wash. J.M. Trappe, J.F. Franklin, R.F. Tarrant, and G.M. Hansen (editors). USDA For. Serv., Pac. NW For. and Range Exp. Stn. pp. 73–84.

- O'Dea, M.E. 1992. The clonal development of vine maple during Douglas-fir development in the Coast Range of Oregon. M.S. thesis. Oreg. State Univ., Corvallis, Oreg. 70 p.
- Owens, J.N. and S.J. Simpson. [undated]. Manual of conifer pollen from British Columbia conifers. Biology Department, Univ. Victoria, Victoria, B.C.
- Peeler, K.C. and D.S. DeBell. 1987. Variation in damage from growing-season frosts among open-pollinated families of red alder. USDA For. Serv., Pac. NW Res. Stn. Res. Note PNW-RN-464.
- Pendl, F. and B. D'Anjou. 1990. Effect of manual treatment timing on red alder regrowth and conifer release. For. Can. and B.C. Min. For. FRDA Rep. 112.
- Perala, D.A. and A. Alm. 1989. Regenerating paper birch in the Lake States with the shelterwood method. Northern J. Appl. For. 6:151-153.
- Radwan, M.A. and D.S. DeBell. 1981. Germination of red alder seed. USDA For. Serv., Pac. NW For. and Range Exp. Stn. Res. Note PNW-370.
- Radwan, M.A., W.D. Ellis, and G.L. Crouch. 1978. Chemical composition and deer browsing of red alder foliage. USDA For. Serv., Pac. NW For. and Range Exp. Stn. Res. Pap. PNW-246.
- Radwan, M.A., T.A. Max, and D.W. Johnson. 1989. Softwood cuttings for propagation of red alder. New Forests 3:21-30.
- Radwan, M.A., Y. Tanaka, A. Dobkowski, and W. Fangen. 1992. Production and assessment of red alder planting stock. USDA For. Serv., Pac. NW Res. Stn. Res. Pap. PNW-RP-450.
- Radwan, M.A., and D.S. DeBell. 1994. Fertilization and nutrition of red alder. *In* Biology and management of red alder, Proc. Symp. Oreg. State Univ., Nov. 18-19, 1992. D. Hibbs, D. DeBell, and R. Tarrant (editors). Oreg. State Univ. Press, Corvallis, Oreg. pp. 216-282.
- Reukema, D.L. 1965. Seasonal progress of radial growth of Douglas-fir, western redcedar and red alder. USDA For. Serv., Pac. NW For. and Range Exp. Stn. Res. Pap. PNW-26.
- Russell, K. 1986. Revegetation trials in a Mount St. Helens eruption debris flow. *In* Mt. St. Helens: five years later, Proc. Symp., May 16-18 1985, Eastern Wash. Univ., Cheney, Wash. pp. 231-248.
1991. Drought injury to trees related to summer and winter weather extremes. Washington State Department of Natural Resources, Forest Health Alert #3. Olympia, Wash.
- Safford, L.O., J.C. Bjorkbom, and J.C. Zasada. 1990. *Betula papyrifera* Marsh.—paper birch. *In* Silvics of North America-Vol. 2, hardwoods. R.M. Burns and B.H. Hakala (technical coordinators). USDA For. Serv. Agric. Handb. 654.
- Schopmeyer, C.S. (technical coordinators) 1974. *Alnus* B. Ehrh—Alder. *In* Seeds of woody plants in the United States. USDA For. Serv., Agric. Handb. 450. pp. 206-211.
- Shainsky, L.J., M. Newton, and S.R. Radosevich. 1992. Effects of intra- and inter-specific competition on root and shoot biomass of young Douglas-fir and red alder. Can. J. For. Res. 22:101-110.
- Shainsky, L.J., and S. Radosevich. 1991. Analysis of yield density relationships in experimental stands of Douglas-fir and red alder seedlings. For. Sci. 37: 574-592.
- Smith, J.H.G. 1964. Root spread can be estimated from crown width of Douglas fir, lodgepole pine, and other British Columbia tree species. For. Chron. 40:456-473.
- _____. 1968. Growth and yield of red alder in British Columbia. *In* Biology of alder, Proc. Symp. Northwest Scientific Association's Fortieth Annual Meeting, April 14-15 1967, Pullman, Wash. J.M. Trappe, J.F. Franklin, R.F. Tarrant, and G.M. Hansen (editors). USDA For. Serv., Pac. NW For. and Range Exp. Stn. pp. 273-286.
- Stettler, R.F. 1978. Biological aspects of red alder pertinent to potential breeding programs. *In* Utilization and Management of Alder, Proc. symp., April 25-27, 1977, Ocean Shores, Wash. D.G. Briggs, D.S. DeBell, and W.A. Atkinson (compilers). USDA For. Serv., Pac. NW For. and Range Exp. Stn. Gen. Tech. Rep. PNW-70. pp. 209-222.

- Swartz, D. 1971. Collegiate dictionary of botany. Ronald Press Co., New York, N.Y. 520 p.
- Tanaka, Y., P.J. Brotherton, A. Dobkowski, and P.C. Cameron, P.C. 1991. Germination of stratified and non-stratified seeds of red alder at two germination temperatures. *New Forests* 5:67–75.
- Tappeiner, J., J. Zasada, P. Ryan, and M. Newton. 1991. Salmonberry clonal and population structure: the basis for a persistent cover. *Ecology* 72(2):609–618.
- Trappe, J.M. 1972. Regulation of soil organisms by red alder—a potential biological system for control of *Poria weirii*. In *Managing young forests in the Douglas-fir region*. (proc. symp.) A.B. Berg (editors). Oreg. State Univ. Sch. For. Res. Lab. Symp. 3. pp. 35–46.
- Voth, E.H. 1968. Food habits of the Pacific mountain beaver, *Aplodontia rufa pacifica* Merriam. Ph. D. thesis, Oreg. State Univ., Corvallis, Oreg.
- White, C.M. and G.C. West. 1977. The annual lipid cycle and feeding behavior of Alaskan redpolls. *Oecologia* 27:227–238.
- Williamson, R.L. 1968. Productivity of red alder in western Oregon and Washington. In *Biology of alder*, Proc. Symp. Northwest Scientific Association's Fortieth Annual Meeting, April 14–15 1967, Pullman, Wash. J.M. Trappe, J.F. Franklin, R.F. Tarrant, and G.M. Hansen (editors). USDA For. Serv., Pac. NW For. and Range Exp. Stn. pp. 287–292.
- Wondzell, S. 1994. Flux of ground water and nitrogen through the floodplain of a fourth-order stream. Ph.D. dissertation, Dep. For. Sci., Oreg. State Univ., Corvallis, Oreg.
- Worthington, N.P. 1957. Silvical characteristics of red alder. USDA For. Serv., Pac. NW For. and Range Exp. Stn. Silvical Series 1.
- Worthington, N.P., F.A. Johnson, G.R. Staebler, and W.J. Lloyd. 1960. Normal yield tables for red alder. USDA For. Serv., Pac. NW For. and Range Exp. Stn. Res. Pap. 36.
- Worthington, N.P., R.H. Ruth, and E.E. Matson. 1962. Red alder: Its management and utilization. USDA Misc. Publ. 881.
- Zasada, J. 1986. Natural regeneration of trees and tall shrubs on forest sites in interior Alaska. In *Forest ecosystems in the Alaska taiga: a synthesis of structure and function*. K. VanCleve, F.S. Chapin, III, P.W. Flanagan, L.A. Viereck, and C.T. Dyrness (editors). Springer-Verlag, New York, N.Y. pp. 44–73.
- Zasada, J., T. Sharik, and M. Nygren. 1991. The reproductive process in boreal forest trees. In *A systems analysis of the global boreal forest*. H.H. Shugart, R. Leemans, and G.B. Bonan (editors). Cambridge Univ. Press, Cambridge, U.K. pp. 85–125.
- Zasada, J., J. Tappeiner, and M. O'Dea. 1992. Clonal structure of salmonberry and vine maple in the Oregon Coast Range. In *Ecology and management of riparian shrub communities*. W. Clary, E. McArthur, D. Bedunah, and C. Wambolt (compilers). Proc. Symp. held in Sun Valley, Idaho, May 29–31 1991. USDA For. Serv., Intermountain For. and Range Exp. Stn. Gen. Tech. Rep. INT-289. pp. 56–61.