Mineral Nutrition and Fertilization of Deciduous Broadleaved Tree Species in British Columbia

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Mineral Nutrition and Fertilization of Deciduous Broadleaved Tree Species in British Columbia

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There is increasing interest in the management and utilization of hybrid poplars and native deciduous broadleaved tree species (hardwoods) in British Columbia. This paper examines aspects of mineral nutrition and fertilization which are currently important or which may become important as management and utilization of the most important species increases. Gaps in knowledge about hardwood nutrition are also identified.

Maintaining nutrition to achieve the highest growth rates possible is more critically important for the culture of hybrid poplars than of native hardwoods. Hybrid poplars are grown under intensive management regimes, mainly to produce pulp, with rotations of 15 years or less. Plantations can be established where moisture is clearly sufficient. Under such management regimes, adequate nutrition and appropriate fertilization are essential for maximizing productivity and shortening rotations. The nutrition of native hardwoods is less important simply because native hardwood species are not heavily used at present. However, much of the standing volume of hardwood species in interior and coastal British Columbia is in near-mature, mature, or overmature stands. Therefore, it is prudent to assess how nutrient availability affects growth and whether fertilization may be useful in the long-term management of hardwood and mixed-wood stands.

Topics addressed in the review were: (1) the ecological roles and potential growth responses of hardwood species to fertilization as compared with the species' coniferous associates; (2) elements likely to be deficient in hardwoods; (3) growth responses of hardwoods to fertilization as affected by site conditions; (4) effects of fertilization on stress tolerance and mycorrhizal associates; and (5) tactics for ameliorating elemental deficiencies. Species-specific nutritional issues and operational contexts in which fertilization might be beneficial were also reviewed, and priority areas for research identified.

There is a considerable body of literature on the responses to fertilization by conifers, but virtually no published field studies of hardwood responses to fertilization in British Columbia. While principles developed from studies of conifer nutrition apply to hardwoods, site-specific growth responses to fertilization are likely much different in hardwoods than in conifers. The hardwood species of greatest importance generally predominate earlier in succession on wetter and more fertile sites than do coniferous species. These hardwood species also typically have greater growth rates when young, shorter lifespans, and greater annual nutrient requirements than do conifers of similar size. To achieve maximum growth rates, hardwoods may require greater quantities of nutrients than do conifers growing on sites of similar fertility.

Ongoing fertilization trials of hybrid poplar on Vancouver Island suggest that both N and P may limit growth. Growth responses may be considerable. A greater variety of options exist for delivery of nutrients than exist for native hardwood stands. Intensive breeding is producing numerous clones that differ in their growth rates and may differ in their abilities to grow on nutrient- and moisture-limited sites. Important still to do are

the following: (1) relating site characteristics and fertilization response; (2) assessing the advantages and disadvantages of establishment-year fertilization vs. later (3rd-year) fertilization; (3) determining which forms of nutrients are most appropriate (e.g., organic vs. inorganic); and (4) predicting how clones vary in response to site fertility and to added nutrients.

Stands of native hardwoods are much less likely to be managed at the same intensity as are hybrid poplar plantations. Virtually nothing is known of native hardwood growth responses to fertilization in British Columbia, except with respect to black cottonwood in the southwestern part of the province. It will be important to confirm what elements are deficient, to predict how growth responses to fertilization will vary with soil moisture and soil nutrient regimes, and to identify at what stand ages it is appropriate to fertilize in order to maximize tree value at harvest. Ongoing fertilization studies of red alder and trembling aspen may provide some of this information. Studies of aspen, alder, and paper birch are of the highest priority because of their extent and potential product value, while studies of black cottonwood, balsam poplar, and bigleaf maple are of lower priority.

Red alder is unique among native hardwood trees in that it fixes atmospheric N_2 in symbiotic association with the actinomycete *Frankia* sp. Fertilization trials and correlative studies of site:growth relations suggest that P may limit growth on some sites. Fertilization of young (1- to 4-year-old) stands has significantly increased growth, but various studies indicate the responses are sensitive to available soil P, soil moisture, and soil pH. Operational contexts in which nutrition may be an important factor include: (1) plantation management on sites considered appropriate for red alder; (2) management on *Phellinus*-infected sites that might normally be considered too dry and infertile for adequate growth of alder; (3) management on deactivated roads and landings; and (4) management of alder in repeated rotations on sites on which conifers are difficult to establish.

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The hardwood or deciduous broadleaved[1] trees considered to be of the greatest potential economic importance in British Columbia are the native *Alnus rubra* (red alder), *Acer macrophyllum* (bigleaf maple), *Populus trichocarpa* (black cottonwood), *Populus tremuloides* (trembling aspen), *Populus balsamifera* (balsam poplar), *Betula papyrifera* (paper birch), and hybrid poplars, primarily clones of *P. trichocarpa × P. deltoides*. Red alder, bigleaf maple, and black cottonwood occur mainly in coastal British Columbia, while trembling aspen and balsam poplar occur primarily in the Interior. Paper birch occurs in both regions. Hybrid poplars are being increasingly planted on the east side of Vancouver Island and in the Fraser Valley and, to a lesser extent, in the Interior.

Historically, native hardwoods have been an insignificant component of the British Columbia forest economy, though not of the forested landscape. It has been estimated that the harvestable area with significant volumes of hardwood species is about 3.9×10^6 ha, most of which contains trembling aspen occurring in the northern interior of the province. The potential annual harvest is 7×10^6 m^3 (Massie et al. 1994), i.e., 12–14% of the total annual forest harvest in British Columbia (B.C. Ministry of Forests 1994). Native hardwood species are therefore important for maintaining future fibre supplies from British Columbia forests. Species such as maple, birch, and alder are also desirable for the manufacture of high-value products such as veneer and furniture (Massie et al. 1994; Raettig et al. 1995). Demand has increased for chips and sawn wood products from native British Columbia hardwoods in recent years, in conjunction with decreases in the coniferous-dominated land base available for harvesting and with continued high world-wide demand for fibre.

A significant percentage of interior cottonwood, aspen, and birch is considered mature or overmature, while most of the volumes of red alder and bigleaf maple are near-mature or mature (Massie et al. 1994). Long-term supplies of native hardwoods may therefore be of concern. Similarly, concerns have been expressed over the diminishing quantity and quality of alder logs in Oregon and Washington, as demands for products from alder increase internationally (Raettig et al. 1995). In general, understanding how to maximize both productivity and log quality, while minimizing environmental impact, are important silvicultural research goals for native hardwoods.

Hybrid poplars have been increasingly planted on private lands, mainly in coastal British Columbia, as a fast-growing source of fibre for pulp. Rotations are expected to be less than 15 years. Understanding how to maximize juvenile productivity is a key to the economic viability of hybrid poplar culture, but issues such as log quality are of little concern.

My objectives in this assessment were to review existing knowledge and to suggest research directions pertaining to the nutrition and fertilization of native hardwoods and hybrid poplars. Growth responses to changes in nutrient supply and nutrient status were emphasized. Other important

1 Throughout this document, "hardwood" and "deciduous broadleaved" are used interchangeably.

aspects of fertilization and hardwood nutrition, such as the economics of fertilizing hardwoods, within-stand and within-tree nutrient cycling, and the impacts of fertilization on ecosystem components other than target trees, are not addressed in this review. Hardwood ecology and management in British Columbia have been recently reviewed (Peterson et al. 1989; McLennan and Mamias 1992; Peterson and Peterson 1992; Simard and Vyse 1992; Enns et al. 1993; Massie et al. 1994; Comeau et al. 1996), but nutritional concerns have generally been ranked as a low priority (e.g., McLennan and Mamias 1992).

Understanding the role of nutrition in maintaining or increasing productivity and the value of forested stands is important for several reasons:

- The growth potential of vegetation in natural environments is often limited by a low availability of one or more mineral nutrients (Ericsson et al. 1992) even when other factors, such as moisture, also limit growth. There are no conclusive data to suggest otherwise for British Columbian forests, although the responses to added nutrients are affected by the moisture available (Carter et al. 1998).
- Nutrient deficiencies can be minimized in a cost-effective manner when fertilization is used appropriately in combination with soil conservation and with the control of competing vegetation.
- An improvement in growth rates resulting from appropriate nutrient additions may decrease the time until a new stand is free-to-grow and may also reduce the age required for trees to reach minimum harvestable sizes. These changes may increase short-term or mid-term timber supplies (e.g., Pederson 1996a, b) and increase allowable annual cuts (AAC) per unit of available land area. For instance, fertilization increased basal area of coastal Douglas-fir by 49% relative to controls over 10 years (Weetman et al. 1997). In that study, the site index (50-year base) was increased from 33 to 35 m. Growth simulations projected an additional 62 m^3 ha^{-1} over the rotation if the increased growth rates could be maintained.
- Fertilization, properly timed and applied in conjunction with other silvicultural treatments, may increase product value in addition to growth rates. For example, an increase of 1 cm diameter in loblolly pine following fertilization can increase the value by 5–10% m^{-3} simply by increasing the proportion of wood suitable for higher-valued products (Binkley et al. 1995). This may be an important consideration for hardwoods used in the production of veneers and other value-added products.

Before maximum growth responses to fertilization can be obtained: (1) the elements that limit productivity in a given species on a given site must be correctly diagnosed, (2) the relation between site and stand characteristics and growth response to the added elements must be understood, and (3) the limiting elements must be applied in an appropriate form and at an appropriate time. In recent years, much of that information has become available for commercially important coniferous species in British Columbia, particularly coastal Douglas-fir (Weetman et al. 1997; Carter et al. 1998). Such information is not easily applied to hardwood species, however. In particular, the quantities of mineral nutrients

required for maximum growth may differ among hardwood species and their coniferous associates, as well as among hardwood species. In general, the dominant native hardwoods of British Columbia are early successional and most prominent on moister, more fertile sites (Klinka et al. 1990), compared with their coniferous associates. Potential growth rates of native hardwoods may be greater (and rotations shorter) than those of their coniferous associates, but the greater growth rates may also require greater irradiances and availabilities of moisture and mineral nutrients. Annual nutrient uptake requirements may also be greater in deciduous hardwoods because the entire canopy is replaced annually and the percentage of growth-enhancing elements supplied by retranslocation from senescing tissue is typically lower than in evergreen conifers (Cole and Gessel 1992). Thus, site fertility considered adequate for the growth of coniferous species may limit the growth of hardwoods naturally occurring on the same site.

2 FORMAT OF THE REVIEW

In this paper, ecological roles, site associations, and coniferous associates of the major hardwood species native to British Columbia are considered first. This is followed by a discussion of general questions concerning mineral nutrition and fertilization that will likely be important in the future management of native hardwoods and hybrid poplar:

1. How do the responses of native hardwoods to fertilization compare with those of their coniferous associates?
2. What, if any, mineral nutrients limit productivity on a given site? How can deficiencies be diagnosed?
3. What growth responses can be expected from increased nutrient availability? How will those responses be influenced by site and stand characteristics?
4. Will changes in the nutrient status of an individual tree affect the resistance to, or recovery from, abiotic stresses such as limited moisture availability and low temperatures, or biotic stresses associated with pathogens or herbivorous insects?
5. What are the most effective fertilization tactics for alleviating nutritional deficiencies?

Finally, relevant nutritional data and nutritional issues for each species, including hybrid poplars, are discussed.

An initial review of the literature revealed no published field studies of the relations between growth and mineral nutrition of red alder, paper birch, trembling aspen, balsam poplar, bigleaf maple, or hybrid poplar in British Columbia. As appropriate, I have summarized recent unpublished data from studies conducted in British Columbia, reviewed studies of the relevant species or genera conducted elsewhere, and reviewed relevant nutrition and fertilization studies of native conifers conducted in or near British Columbia.

3 ECOLOGY OF DECIDUOUS BROADLEAVED SPECIES: SITE ASSOCIATIONS, SUCCESSIONAL ROLES, AND CONIFEROUS ASSOCIATES

The native hardwoods of British Columbia are mainly seral species, usually dominating stands early in succession and eventually being over-topped by slower-growing conifers. Each of the major hardwood species occurs in one or more biogeoclimatic zones (Klinka et al. 1990). All of the major species occur primarily on rich to very rich sites. Balsam poplar, black cottonwood, and bigleaf maple occur primarily on moist sites, while paper birch occurs primarily on fresh sites. Aspen occurs commonly on both fresh and moist sites, while red alder may commonly occur in sites ranging from fresh to wet (Klinka et al. 1990) (Table 1). In general, a given deciduous broadleaved species is associated with richer sites than are the coniferous species that occur frequently within that zone.

TABLE 1 *Predominant biogeoclimatic zones, soil moisture regimes (SMR), and soil nutrient regimes (SNR) associated with the major deciduous broadleaved tree species native to British Columbia (adapted from Klinka et al. 1990 and Massie et al. 1994). Rankings of SMR and SNR are based on a total of 26 species characterized: a ranking of 1 indicates an association with the driest or least fertile sites, while a ranking of 26 indicates species most commonly associated with the wettest or most fertile sites.*

Species	BGC Zone	Soil moisture regime	Soil nutrient regime
Red alder	CDF, CWH	fresh to wet (22)	rich to very rich (26)
Bigleaf maple	CDF, CWH	moist (14)	very rich (25)
Black Cottonwood	CWH, CDF, ICH, SBS	moist (25)	very rich (18)
Balsam poplar	BWBS, SBS, SWB	moist (25)	very rich (18)
Birch	SBS, BWBS, ICH,	fresh (9)	medium to rich (13)
Aspen	BWBS, SBS, ESSF, SBPS, IDF, ICH	fresh to moist (13)	medium to rich (18)

4 GROWTH AND MINERAL NUTRITION OF DECIDUOUS BROADLEAVED VS CONIFEROUS SPECIES

No published data exist comparing the effects of fertilization on decidu-ous broadleaved trees with the effects on their coniferous associates on common sites in British Columbia. However, deciduous broadleaved species are often more responsive to nutrient additions than are conifers, at least when young. Greater growth responses may result from greater plasticity of biomass allocation to foliage (e.g., Chapin et al. 1983), and because photosynthetic rates increase more with nutrient availability (Reich et al. 1994; Brown et al. 1996a). Although both broadleaved and

coniferous species exhibit indeterminate patterns of shoot growth in the seedling stage (Kramer and Kozlowski 1979), species of many broadleaved genera—including *Populus* (Critchfield 1960), *Acer* (Critchfield 1971), *Alnus* (Oliver and Larson 1990), and *Betula* (Kozlowski and Clausen 1966)—continue to exhibit indeterminate shoot growth after the seedling stage. These genera may respond more rapidly to fertilization than do conifers (Linder and Rook 1984). Early successional forest habitats typically exhibit a greater availability of resources, including nutrients, than do later-successional habitats. Plants associated with those early successional habitats exhibit greater maximum growth rates as nutrient availability increases (Grime 1979; Chapin 1980). This response is more difficult to generalize for trees than for herbaceous plants because tree species may differ in their patterns of age-related growth rates (data cited in Greenwood 1989). In comparative studies of responses to increasing N and P availability, maximum relative growth rates or whole-plant masses of poplar, birch, and alder seedlings were greater than those of pine or spruce seedlings as N or P availability increased (Ingestad 1979; Chapin et al. 1983; Jia and Ingestad 1984; Ingestad and Kahr 1985; Brown and Higginbotham 1986). Thus, while growth rates may have been similar at lower nutrient availabilities, the deciduous broadleaved species required greater nutrient availabilities for maximum growth.

5   MINERAL NUTRIENTS LIMITING GROWTH

5.1 Limiting Nutrients

Nutritional deficiencies are most conclusively identified through field fertilization studies (Binkley 1986). At present, black cottonwood (McLennan 1993), trembling aspen,[2] and red alder[3] are the only native hardwood tree species that have been, or are being, subjected to fertilization trials in British Columbia. Several field studies of N and P fertilization effects on hybrid poplar growth are underway or recently completed on eastern Vancouver Island, as discussed below.

Ongoing field fertilization trials on Vancouver Island indicate that N and P deficiencies may limit the growth of hybrid poplar (data contained in van den Driessche 1997; van den Driessche [1999]), while deficiencies of P and other non-nitrogenous elements may limit the growth of red alder.[4] Nitrogen availability commonly limits the growth of conifers in British Columbia. While N is often limiting, erratic responses to N fertilization have been attributed to deficiencies of P, S, B, Fe, and Cu either inherent in the particular site or induced by N fertilization (e.g., Weetman et al. 1989a,b; Brockley 1990, 1991, 1992, 1995; Carter and Brockley 1990; Majid and Ballard 1990; Brockley et al. 1992; Weetman et al. 1992; Green and Carter 1993; Brockley and Sheran 1994; Carter et al. 1998). Potassium deficiencies have not been reported in native trees in British Columbia;

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2 Dave Coopersmith, poster presented at "Silviculture of Temperate and Boreal Broadleaf-conifer Mixtures" Workshop, February 28–March 1, 1995, Richmond, B.C.; pers. comm., November 1998.
3 Kevin Brown, B.C. Min. For. EP 1196.04, 1997.
4 Brown, unpubl. data, EP 1196.02, EP 1196.03, EP 1196.04.

however, deficiencies of K in Douglas-fir were induced by N fertilization in northern Idaho and western Montana (Mika and Moore 1990). The deficiencies were more pronounced over granitic parent materials than over basaltic parent materials (Moore and Mika 1997).

Optimal elemental balances in foliage are broadly similar in seedlings of a broad range of tree species, although the optimal balances of K, Ca, and Mg may be higher in deciduous broadleaved species than in conifers under optimal nutrition (Ingestad 1987). Why this is so is unclear, but deciduous broadleaved trees have a greater capacity to assimilate NO_3-N in foliage than do conifers (Smirnoff and Stewart 1985; Knoepp et al. 1993). The greater uptake rates of cations may be associated with uptake and assimilation of NO_3-N. Deciduous broadleaved species may be broadly predisposed to deficiencies of the same elements that limit conifer growth on a given site, but greater elemental requirements in hardwoods indicate they may be more prone to deficiencies on a given site.

5.2 Deficiency Diagnosis: Critical Concentrations and Elemental Ratios

Diagnoses of nutrient deficiencies in trees typically rely on published foliar concentrations associated with growth. Critical concentrations, defined variously as the lowest foliar elemental concentrations associated with maximum or near-maximum growth (see Timmer 1991), have not been developed specifically for hardwood species in British Columbia. The data that have been published (Table 2) are much less complete than are those compiled for native conifers (e.g., Ballard and Carter 1986) and they are extremely variable. Nonetheless, foliar concentrations of macroelements considered "adequate" appear higher than for those in associated native conifers (Ballard and Carter 1986). Toxic levels of essential elements are largely unknown. However, one study reported that foliar damage ascribed to boron toxicity occurred at lower foliar concentrations of B in bigleaf maple than in digger pine, California laurel, or madrone (Glaubig and Bingham 1985).

Applying critical concentrations is problematic. Critical foliar elemental concentrations associated with growth reductions may: (1) vary within a species; (2) decrease with increasing age of the tree, at least in coniferous species (Miller et al. 1981); or (3) vary with the availability of other resources such as moisture (Lambert 1986) or mineral nutrients other than the one of interest. It is assumed that if foliar elemental concentrations are less than previously published critical concentrations, the trees in question will respond to additions of those elements. However, an element thought to be deficient may be less deficient than other elements, in which case additions of the former will not increase growth. Consequently, foliar elemental concentrations may be combined with ratios of elements, such as N/P, N/K (Mika and Moore 1990), or N/S (Ballard and Carter 1986).

A diagnostic approach that relies solely on elemental ratios is the Diagnosis and Recommendation Integrated System (DRIS), which uses multiple two-way comparisons of foliar elemental ratios with established norms (Timmer 1991). Index values, based on elemental ratios, are calculated for each element of interest in foliage. The indices are compared with indices developed for plants growing under optimal conditions, and the relative deficiency of a given element is then estimated. The data set used for generation of the indices should be compiled under conditions

TABLE 2 *Adequate foliar macroelemental concentrations for deciduous broadleaved species occurring in British Columbia and for related species (derived from DeBell and Radwan 1984; van den Burg 1985; Fyles et al. 1994).*

Species	Element	Concentration (%)
Acer macrophyllum		?
Acer saccharum	N	1.6 –2.6
	P	0.13 –0.20
	K	0.6 –0.7
	Ca	0.7 –0.9
	Mg	1.0 –1.3
Alnus rubra	N	1.79 –3.16
	P	0.15 –0.21
	K	0.89 –0.99
Betula papyrifera	N	1.62 –1.79
	P	0.19 –0.32
	K	0.94 –1.45
	Ca	0.99 –1.07
	Mg	0.25 –0.30
Populus balsamifera	N	2.5 –2.6
	P	0.19 –0.24
	K	1.15 –1.45
	Ca	0.43
	Mg	0.21 –0.29
Populus tremuloides	N	2.1 –2.8
	P	0.15 –0.30
	K	0.77 –1.56
	Ca	1.25 –2.76
	Mg	0.14 –0.31
Populus trichocarpa	N	>2.5
	P	0.10 –0.44
	K	0.44 –1.76
	Ca	1.44 –2.14
	Mg	0.22 –0.37

(e.g., irradiance, humidity, soil moisture) representative of those to which DRIS will be applied. It is also important to know what elemental concentrations are associated with maximum growth. The basic data requirements are therefore as great as those required for determination of critical concentrations. DRIS has been applied to nutritional studies of hybrid poplars in Ontario (Leech and Kim 1981) and to field studies of black cottonwood in southwestern British Columbia (McLennan 1996), but there are no records in the literature of its application to other deciduous broadleaved trees in the province.

5.3 Vector Analyses

In contrast to the above approaches, foliar vector analysis combines measures of elemental concentration and foliar mass responses to treatments. In its most common form, changes in the concentration of the elements of interest are plotted against changes in content (the product

of elemental concentration and mass of a standardized number of leaves during the growing season following fertilization). Deficient elements are those whose concentration and standardized leaf mass both increase in response to a treatment (i.e., leaf mass is limited by that element). Recently, it has been suggested that changes in elemental concentration be plotted against changes in leaf mass, with the responses of elements that have been added plotted separately from those that have not been added (Valentine and Allen 1990; Brockley and Sheran 1994). The major advantages of the vector approach are that it facilitates tentative diagnostic interpretations about the nutritional status of foliage with respect to both added and non-added nutrients and allows simultaneous comparisons of several nutrients, sites, or treatments.

The vector analysis technique has most commonly been applied to conifers with determinate patterns of shoot elongation (i.e., those in which needle numbers on a shoot are predetermined the preceding fall). Increases in needle mass have been correlated with subsequent increases in basal area increment (Weetman et al. 1988). The technique has also been applied with variable success to species with indeterminate shoot elongation. In studies of hybrid poplar responses to liming and P fertilization during the establishment year (Timmer 1985; Teng and Timmer 1990), vectors were developed from foliar data collected from the entire stem. In another study, van den Driessche [1999] used newly expanded leaves along the stem. In western hemlock, Weetman et al. (1989b) assumed that fertilization did not affect needle numbers on the sampled lateral shoot[5]; in western redcedar, entire branchlets were sampled. The problem with the latter was that branchlet mass was not well correlated with height increment (Weetman et al. 1989b). Likewise, McLennan (1993) found little correlation between foliar mass on the terminal shoot and either height or basal area increment in fertilization studies of black cottonwood. In contrast, areas of newly-mature individual leaves were closely correlated with 1st- and 2nd-year stem growth in hybrid poplars (Harrington et al. 1997; van den Driessche [1999]), as did whole-plant leaf area (Larson and Isebrands 1972; Hinckley et al. 1989; Brown et al.[6]). *Populus trichocarpa* (Critchfield 1960), *P. tremuloides* (Kozlowski and Clausen 1966; Pollard 1970), *B. papyrifera* (Kramer and Kozlowski 1979), and *A. rubra* (Oliver and Larson 1990) all exhibit indeterminate shoot elongation. Shoot elongation patterns of *Acer* spp. vary with the species (Critchfield 1971), but those in *A. macrophyllum* have not been described. Furthermore, the percentage of shoots exhibiting indeterminate growth on a given tree may decrease with age (Kramer and Kozlowski 1979). The vector analysis technique deserves further attention as a means of detecting elemental deficiencies in deciduous broadleaved species. Consideration of the type of growth exhibited by the shoot sampled should be taken into account, and long-term measurements should be made to relate the magnitude of stemwood growth response to leaf size increases.

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5 Note: Kramer and Kozlowski (1979) cite data from Owens and Molder (1973) indicating that western hemlock exhibits determinate growth.

6 K.R. Brown, F.D. Beall, and G.D. Hogan. Biomass accumulation in hybrid poplars during the establishment year. Unpubl. manuscript. Can. For. Serv., Sault Ste. Marie, Ont.

5.4 Elemental Form

Alternatives to measuring total concentrations of elements in foliage have been suggested in the literature. One is to combine the elemental determinations with determinations of chlorophyll concentrations (Oren et al. 1993). A second is to measure concentrations of specific forms of elements, for example, inorganic P as a measure of P status (Sun et al. 1992), NO_3-N or specific amino acids and amides as an indicator of relative N status (Nasholm and McDonald 1990), SO_4–S as a measure of S status (Turner et al. 1977), and active-Fe (that Fe extracted with dilute acids or chelators) as an indicator of Fe status (DeKock et al. 1979). A lack of SO_4–S has been related to a lack of growth response to N fertilization in several coniferous species (Ballard and Carter 1986). Active-Fe is thought to be of the form Fe(II), as opposed to Fe(III). Although neither the composition nor the cellular location are conclusively known (Abadia 1992), active-Fe is often a better indicator of Fe deficiency, especially in plants grown in calcareous soils or subject to high availabilities of P (Marschner 1995). In general, vacuolar concentrations of elements (or the elemental forms that accumulate in the vacuoles) may be the best indicator of relative status of elements because they represent an accumulation of an element in excess of immediate needs for growth (Chapin and van Cleve 1989).

The difficulties in extraction and quantification of labile forms of elements may negate their advantages as diagnostic tools, although they may be easier to extract from deciduous hardwood foliage than from coniferous foliage. In Douglas-fir, concentrations of soluble N compounds showed greater changes in response to increased N availability than did total N. However, analytical precision was less for soluble N compounds than for total N, possibly because of a greater sensitivity to temperature and moisture stress (van den Driessche and Webber 1975). In birch seedlings, the ratio of amino acid-N (mainly citrulline, glutamine, y-aminobutyric acid, and arginine) to total N increased with N supply (Nasholm and McDonald 1990). However, soluble N compounds were not a more sensitive predictor of growth response to N fertilization than was total foliar N in sycamore plantations (Tschaplinski and Norby 1993). At this time, including measures of SO_4–S in routine foliar nutrient analyses for native broadleaved species, as recommended for conifers (Ballard and Carter 1986; Weetman and Wells 1990), seems reasonable. Active-Fe might be a useful measure of Fe deficiency in those species occurring in calcareous soils.

5.5 Non-Destructive Probes of Elemental Deficiencies

Procedures for the collection of foliage and its analysis for total elemental concentrations are well established for trees, including deciduous broad-leaved species (e.g., Weetman and Wells 1990). The preparation of tissue samples to determine elemental concentrations is labour-intensive, time consuming, and expensive. It remains a major impediment to routine screening of vegetation for elemental deficiencies. Alternative approaches for this assessment are therefore of interest.

The spectral characteristics of tissue may have promise for indicating nutrient stress (Powers 1992). In contrast to traditional wet chemistry techniques, there is no need to determine sample masses, no reagents are required, and the analytical time is relatively short. Near-infrared reflectance spectroscopy (NIRS) has been used with some success for

estimating foliar concentrations of Kjeldahl-N and organic constituents such as lignin and proteins, occurring in concentrations greater than 0.1% (dry mass) (Westerhaus 1985 cited in Wessman et al. 1988) in tissues that were dried and ground. However, deficiencies of Ca and P were difficult to detect (data cited in Wessman et al. 1988). The technique may be most effective in assessing specific elemental deficiencies if one or very few deficiencies predominate. Measurements of other compounds may indicate whether a plant is under stress, for example, by showing a shift in the ratios of N, lignin, carbohydrates, and protein (Waring et al. 1985).

Remote sensing of plant stress associated with elemental deficiencies would be particularly useful in assessing limitations to productivity in the widespread forested areas of British Columbia. There is some evidence that nutritional changes in the canopy can be detected by remote sensing techniques. For example, reflectance in the visible red spectrum decreased and that in the near-infrared region (NIR) increased with increasing rates of N application (Al-Abbas et al. 1974). Laser-induced fluorescence (LIF) is a non-destructive technique that may have some promise for use in identifying elemental deficiencies as part of remote sensing surveys. In one study, deficiencies of N, P, and Fe decreased fluorescence at one wavelength, while a deficiency of K caused a three-fold increase at the same wavelength (Jackson 1986).

There are numerous problems in obtaining interpretable foliar nutrition data from airborne sensors, ranging from problems in analyzing fresh intact leaves to problems in scaling from individual leaves to canopies. The analysis of fresh intact leaves may be more difficult than that of dried, ground tissue because: (1) the waxy cuticle of leaves may cause high specular reflectance, (2) the distribution within leaves of chloroplasts and of compounds associated with nutrient status (e.g., pigments, proteins) is not uniform, and (3) the high absorbance by water of infrared radiation and the presence of air and water interfaces with varied refractive indices may obscure variation in absorption associated with biochemical changes (Yoder and Pettigrew-Crosby 1995). Problems in scaling from individual leaves to canopies include the difficulty in accounting for varying leaf area index (LAI), which alters the contribution of the background to overall reflectance and affects the scattering of light (Yoder and Pettigrew-Crosby 1995). In addition, other stresses (e.g., moisture stress) may influence canopy reflectances by affecting leaf reflectance, leaf orientation, and canopy architecture (Jackson 1986). While problems clearly exist, it is worth noting that N concentrations of fresh tissue have been predicted from reflectance data, with the use of shortwave infrared bands (data cited in Yoder and Pettigrew-Crosby 1995). As well, canopy N concentrations have been predicted from Airborne Visible /Infrared Imaging Spectrometer (AVIRIS) data in forests in Massachusetts, Wisconsin, and Oregon (Martin and Aber 1993 and Johnson et al. 1994, both cited in Yoder and Pettigrew-Crosby 1995). Remote sensing techniques may have long-term applicability in assessing health and nutrition of British Columbia forests, whether those forests are dominated by coniferous or deciduous broadleaved trees. The techniques deserve further attention.

Appropriate measurements of photosynthesis may provide an assessment of elemental deficiencies. Photosynthetic rates of trees have been

associated with foliar concentrations of numerous elements, including N (Field and Mooney 1986; Reich et al. 1994), P (Conroy et al. 1986; Raaimakers et al. 1995), and Mg, S, Fe, Mn, Cu, and Zn (see reviews by Linder and Rook 1984; Marschner 1995). Because photosynthetic rates are also limited by factors such as moisture availability, CO_2 fixation rates alone appear to be of little use in indicating any elemental deficiencies, let alone specific deficiencies. However, patterns of chlorophyll fluorescence may vary with changes in the concentration of those elements associated with specific components of the light harvesting and electron transport reactions—elements such as Mn, Mg, Fe, and Cu (Kriedemann et al. 1985; Baillon et al. 1988; Fodor et al. 1995; Gorge et al. 1985). Phosphorus deficiencies may be inferred by fluorescence patterns and by the response of photosynthetic rates to increasing internal CO_2 concentrations (Conroy et al. 1986). The utility of photosynthetic probes in identifying nutrient deficiencies should be tested in well-designed experiments under field conditions.

6 GROWTH RESPONSES TO FERTILIZATION AS AFFECTED BY SITE CONDITIONS

Some minimum level of irradiance, soil moisture, and temperature must be reached before fertilization can increase tree growth (e.g., Brockley et al. 1992; Chappell et al. 1992), but fertilization may increase tree growth even when factors other than nutrient availability are less than optimal (e.g., Brix 1993). Attempts to relate site conditions to fertilizer response for a given species have not always been successful because site conditions are difficult to quantify in a manner meaningful for the understanding of tree growth. Characteristics of the site may affect nutrient availability or nutrient utilization. Nonetheless, the ability to select responsive stands and to predict the magnitude of the response to fertilization has important implications for the economic viability of fertilization programs. To date, black cottonwood is the only deciduous broadleaved species native to British Columbia in which such relationships have been examined (McLennan 1993).

6.1 Regression Approaches

Most attempts to relate site conditions to fertilization response have used regression approaches. In British Columbia, such attempts have been confined to studies of Douglas-fir (e.g., Carter and Klinka 1992; Carter et al. 1998). Site index was correlated with both continuous variables (mineralizable-N, site moisture balance) and categorical variables (soil moisture regime and soil nutrient regime), as defined in the biogeoclimatic ecosystem classification. Carter and Klinka (1992) concluded that the continuous variable model was not as portable as the categorical variable model, primarily because of difficulties in applying the water balance model used. Later analyses showed that 3rd- and 6th-year relative basal area responses generally decreased with increasing mineralizable-N, with increasing moisture deficit, and with increasing site index. However, large increases occurred on sites of high site index with low soil mineralizable N concentrations, low foliar N concentrations, adequate foliar P

concentrations, and an absence of soil moisture deficits. These sites were identified as having the greatest potential economic gains from fertilization.

In Washington and Oregon, the relative response of Douglas-fir to N fertilization decreased linearly with increasing foliar N concentration of unfertilized trees at a range of sites (Hopmans and Chappell 1994). Foliar N was a better predictor of response to N fertilization than was soil N concentration or C/N ratio. Miller et al. (1989) attempted to predict periodic annual increment in Douglas-fir stands in Oregon fertilized with either 224 or 448 kg N ha^{-1}, using a combination of stand variables (50-year site index, age at breast height, relative density), site and climatic variables (average annual precipitation, solar radiation, effective soil depth, available water-holding capacity), and soil variables (anaerobically mineralized N, total N, organic matter). An initial core equation incorporated stand variables known to be relevant predictors of growth and response; the stepwise procedure thereafter was based on ease and cost of measurement (soil test variables went in last). Core equations predicted the growth of unfertilized stands, but not fertilizer response. The best additional variable was surface soil C/N. The lack of effect from site variables suggested that the effects of site were already incorporated into stand variables. In other studies, incorporation of S/N improved predictions of growth responses to fertilization in Douglas-fir (Blake et al. 1990), and initial foliar concentrations of SO_4–S improved predictions of growth responses in lodgepole pine (Brockley 1991).

Findings from studies of Douglas-fir have suggested a number of variables that might be used to identify which stands are likely to be responsive to fertilization. Other species have not been similarly examined. However, site factors have been related to site index in western hemlock (Kayahara et al. 1995), Sitka spruce (Kayahara and Pearson 1996), lodgepole pine and interior spruce (Wang et al. 1994), and red alder (Courtin 1992) in British Columbia, and in red alder in Washington and Oregon (Harrington and Curtis 1986).

The studies highlight the difficulties in using site classification schemes such as soil nutrient regime (SNR) (Kabzems and Klinka 1987a) to predict the growth (and the growth response to fertilization) of different species. For example, the site index of western hemlock increased as SNR increased from very poor to poor, but did not increase further in medium and rich sites, even though mineralizable soil N increased (Kayahara and Pearson 1996). Site index of Douglas-fir, in contrast, increased as SNRs increased from medium to rich to very rich (Kabzems and Klinka 1987b). Site indices of interior spruce were lower than those of lodgepole pine in sites classified as nutrient-poor, but higher than those of lodgepole pine in sites classified as nutrient-rich. The site index of red alder increased with site productivity class for Douglas-fir, but the highest site indices for red alder were on sites considered unsuitable for growing Douglas-fir (Harrington and Curtis 1986). The poor relationship between red alder site index and Douglas-fir site productivity class was attributed to different requirements for mineral-N and differences in the growth of the two species on wetter and drier sites. Similar principles might apply to other hardwood associates of Douglas-fir that also do not fix N_2. If site classification is associated primarily with nutrient supply rate, a species with

greater requirements for nutrient uptake would be nutrient-limited (hence, more responsive to fertilization) in a more productive site class than would a species with lesser requirements (Binkley 1986).

If improving the productivity of hardwoods is important, then there is a pressing need to understand species-specific responses to fertilization, to relate these responses to site classification systems, and to refine soil fertility classifications. For operations, it is important to be able to identify elements that are deficient and to predict growth responses to fertilization across the range of soil moisture regime and soil nutrient regime combinations occupied by a given species. To this end, a well-replicated set of fertilization trials should be established in a range of site series or site associations within a given biogeoclimatic zone, since these provide the ecological framework for silvicultural prescriptions. Additional measurements relating to site characteristics (e.g., pH, nutrient and moisture availability) would be required, because the native hardwoods may exhibit a wide range of productivities over sites classified as rich to very rich (e.g., Courtin 1992). In addition, appropriate detailed growth and physiological measurements (e.g., plant moisture status) may be necessary if we are to understand why responses to nutrient addition vary with site series, as discussed below.

Moisture availability and nutrient uptake and utilization are linked. Low soil moisture contents may reduce the effective diffusion coefficient of elements in the soil solution, and plant moisture stress may reduce transpiration rates and the permeability of roots, thereby reducing the mass flow and uptake of elements. Water stress reduces the uptake of Ca and Mg less than that of N, P, and K (Sands and Mulligan 1990), and the uptake of B is sharply reduced under moisture stress (Marschner 1995). Although N uptake may be reduced by drought, in one study, moisture-stressed individuals of six clones of *Populus deltoides* had higher foliar N concentrations than did control plants (Broadfoot and Farmer 1969), possibly indicating that N uptake was less affected by water stress than was plant growth.

Fertilization with P increased the growth of red alder more in water-logged or relatively dry soils than in well-drained soils with optimal moisture contents (Radwan and DeBell 1994). Likewise, fertilization with P had a greater effect on the growth of hybrid poplars under mild water stress than on those trees that were well irrigated (DeBell et al. 1991). Greater responses to P fertilization by water-stressed trees may indicate that (1) higher P supply rates are needed to maintain P uptake and adequate tissue concentrations of P when moisture is not at optimal levels, (2) increasing P supply is associated with increased rooting and moisture availability, or (3) increasing tissue P concentrations are associated with greater water use efficiency.

6.2 Simulation Models

The effects of stand and site conditions on yield responses to nutrient additions may eventually be best understood through the use of physiologically based growth models, such as BIOMASS (McMurtrie et al. 1990; McMurtrie 1993) and ECOPHYS (Host et al. 1990).

BIOMASS simulates the carbon and water balance of trees in relation to their mineral nutrition, and therefore requires the collection of meteorological, stand, and site data (e.g., soil moisture characteristics) and the

determination of photosynthetic responses to light and CO_2 as affected by foliar elemental concentrations. Canopy net photosynthesis is calculated as a function of: (1) the proportion of foliage in each of three canopy layers exposed to direct and diffuse radiation, and (2) the quantum yield and light-saturated rates of photosynthesis in each of the canopy layers. Stomatal conductance is estimated as a function of photosynthetic rate, humidity, and atmospheric CO_2, and is assumed to decline when soil water content declines to a threshold value. Values of photosynthetic parameters and partitioning coefficients are considered to be a function of foliar elemental concentrations. To apply the models, the relationships of foliar elemental concentration to biomass allocation and photosynthetic characteristics will likely have to be determined for a given species (e.g., Brown et al. 1996a,b). Such data do not currently exist for deciduous broadleaved species occurring in British Columbia.

ECOPHYS, developed for hybrid poplars, estimates growth during the establishment year. Growth is simulated as a function of photosynthate production, based on light interception and photosynthetic responses to light by individual leaves, photosynthetic and respiratory responses to temperature, and the partitioning of photosynthate as a function of leaf development. The initial versions of the model could not simulate branching and did not incorporate the effects of moisture or nutrient stress on photosynthesis or partitioning of photosynthate. Submodels of root growth and stomatal responses to moisture and nutrient stress and subroutines to incorporate branching were planned as the next major development in the model.[7]

Light interception, which is strongly influenced by leaf and branch distribution and growth, is recognized as a major determinant of tree productivity. In hybrid poplars, the amount of sylleptic branching may correlate with tree biomass (Ceulemans et al. 1990), presumably through its effects on light interception. Sylleptic branching may vary with clone (Ceulemans et al. 1990) and with nutrient availability.[8] Chen et al. (1994) presented a fractal-based canopy structure model for estimating light interception in hybrid poplar plantations. Such an approach might be useful in assessing the effects of nutrition on growth of different clones of poplar after the establishment year.

Use of the above models requires the collection of considerable data. To determine site characteristics, appropriate measurements must be made of photon flux densities, temperatures, and moisture and nutrient availability; determining plant characteristics requires the gathering of biomass and appropriate morphological (e.g., leaf and branch growth patterns) and physiological (gas exchange, water relations, photosynthate allocation) data. However, as the relationships between plant nutrition and physiological processes underlying growth responses become better understood, this process-based approach may ultimately provide the best way of predicting growth responses to fertilization. With respect to hybrid poplar management, the use of models such as ECOPHYS may be valuable in matching specific clones with specific sites. To make these approaches

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7 George Host, University of Minnesota-Duluth, pers. comm., May 1995.
8 Brown, unpubl. data, 1995.

usable operationally, it will be necessary to accumulate key physiological data for the variety of clones likely to be used in operational plantings. It will also be necessary to minimize the amount of site data required to simulate growth.

7 TREE NUTRITION AND THE TOLERANCE OF MOISTURE STRESS, FROST, HERBIVORES, AND PATHOGENS

7.1 Mineral Nutrition and Plant Water Relations

While the availability of water may affect nutrient uptake and tree growth responses to fertilization, tree water relations and tolerance of moisture stress may, in turn, be affected by tree nutrient status. Radiata pine fertilized with N had less negative shoot water potentials (implying less water stress) than did unfertilized trees (Carlysle 1998). A similar response, though less pronounced, was observed in Douglas-fir (Brix and Mitchell 1986). Roots in nutrient-deficient soil may be less effective at water uptake because of reduced root conductivity (Sands and Mulligan 1990). Higher foliar N concentrations may increase tissue elasticity (Tan and Hogan 1995) and increase photosynthetic rates and water use efficiency (Mitchell and Hinckley 1993; Brown et al. 1996a). However, increases in leaf area relative to root area could predispose the plant to increased water stress and offset an increase in leaf-level water use efficiency.

In studies of four clones of hybrid poplar, high rates of P addition decreased vessel pit pore diameters and cavitation when drought stress was imposed, whereas high rates of N addition increased vessel diameter and cavitation (Harvey 1997; Harvey and van den Driessche 1997). High rates of N addition also increased water use efficiency prior to droughting and increased osmotic adjustment after droughting (Harvey 1997).

7.2 Mineral Nutrition and Frost Damage

The severity of frost damage to trees may be associated with the nutritional status of the tree and hence be affected by fertilization. The relationship, however, has not been studied in deciduous broadleaved trees in British Columbia and is poorly understood in other species. In general, high tissue concentrations of N and P may be associated with delays in the onset of dormancy, leading to greater damage from late-season frosts, but fertilization after active growth has ceased may reduce frost damage (van den Driessche 1984). Nitrogen fertilization increased needle frost hardiness of red spruce seedlings, but decreased frost hardiness of the bud (L'Hirondelle et al. 1992). Greater frost damage to N-fertilized birch was associated with N-induced deficiencies of B (Brakke 1979 cited in van den Driessche 1984). A late spring frost resulted in a greater frequency of severe damage to red alder seedlings fertilized with triple super phosphate than was experienced by unfertilized seedlings (Peeler and DeBell 1987). The researchers did not present foliar nutrient concentrations as part of the study. Fertilization with K, after the cessation of growth, reduced frost damage to *Picea sitchensis* and *Tsuga heterophylla* seedlings in the nursery, and K fertilization at planting reduced winter frost damage to 10-year-old *Pinus sylvestris* and *Picea abies* (data cited in van den Driessche 1984). Conversely, K-deficient *Picea abies* were hardy to -20ºC 5 weeks before well-nourished trees and 10ºC hardier than well-nourished trees prior to

budburst (Jalkanen et al. 1998). Van den Driessche (1984) suggested that the apparent cold hardiness sometimes associated with K fertilization may instead reflect an improved drought resistance, at least under conditions where water stress and cold temperatures occur concurrently.

An understanding of relations between nutrition and frost damage may be important for managing red alder and hybrid poplar plantations. Newly planted red alder deharden quickly after thawing and planting and are especially prone to frost damage if located in cold air drainages (Dobkowski et al. 1994). Such damage may greatly reduce eventual sawlog quality and value. The rapid growth of the poplar hybrids most often planted in coastal British Columbia (crosses of the native *P. trichocarpa* with *P. deltoides* from the southern United States) is largely the result of a longer leaf area duration (Ceulemans et al. 1992). That extended leaf area duration, combined with intensive fertilization, may make hybrid poplar plantations particularly susceptible to frost damage if they are located on frost-prone sites.

7.3 Mineral Nutrition and Insect Herbivores

The nutritional status of broadleaved trees may influence their resistance to, and tolerance of, insect herbivores or pathogens. Outbreaks of tent caterpillars (*Malacosoma disstria*) may cause significant growth reductions in red alder, birch, and aspen (Gara and Jaeck 1978; Peterson and Peterson 1992), while the large aspen tortrix is primarily a defoliator of balsam poplar (Peterson and Peterson 1992). Sawfly (*Trichiocampus* spp., *Nematus* spp.) larvae may also be significant defoliators of red alder (Gara and Jaeck 1978). Nitrogen fertilization increased the nutritional value of aspen leaves for larvae of the large aspen tortrix, by increasing foliar N concentrations (from 25–45 mg g^{-1}) and by decreasing the concentrations of toxic or digestion-inhibiting metabolites (tannins and phenolic glycosides) (Bryant et al. 1987). The concentrations of secondary metabolites either before or following defoliation may vary with clone (Mattson and Palmer 1988; Robison and Raffa 1994). As well, nitrogen fertilization may affect the insect-induced production of defensive compounds (e.g., condensed tannins, proanthocyanidins) in paper birch (Bryant et al. 1993) and oaks (Hunter and Schultz 1995). Such differences in phytochemical induction between clones or species may be due in part to differences in nutrient availability to the particular trees.

Fertilization may also increase the ability of trees to recover after defoliation. Nitrogen fertilization of stands infested with spruce budworms reduced defoliation and increased growth of infested trees (Wickman et al. 1992). Fertilization increased the numbers of larvae, but presumably increased the growth of foliage even more. Weetman et al. (1989a) observed greater incidence of spruce weevil damage after N and P fertilization of Sitka spruce. Although gains in height growth more than compensated for growth reductions from weevil damage, stem form was still adversely affected. It is unknown what effect fertilization might have on the ability of deciduous broadleaved trees to tolerate insect infestation.

7.4 Mineral Nutrition and Tree Pathogens

How nutrition might affect the susceptibility of deciduous broadleaved trees to pathogens in British Columbia has not been determined. These tree species are susceptible to a variety of diseases. Poplars, for example, are particularly susceptible to damage from leaf rust (*Melampsora* spp.)

(Wang and van der Kamp 1992; Newcome et al. 1994) and a variety of fungi causing heartwood decay, cankers and galls, stem and butt rots caused by *Phellinus* spp., and root rots caused by *Armillaria* spp., in addition to others (Peterson and Peterson 1992; Simard and Vyse 1992). Paper birch is susceptible to *Phellinus* spp., *Armillaria*, and *Fomes* spp. in older stands, as well as a variety of sap rots, leaf rust and "dieback," which is a progressive dying of twigs and branches from the treetop outward (Simard and Vyse 1992). However, birch may be resistant to *Armillaria ostoyae* and the Douglas-fir variety of *P. weirii* (Massie et al. 1994). Red alder may be susceptible to *F. annosus*, but is known to be resistant to laminated root rot caused by *P. weirii* (Nelson et al. 1978).

There is evidence that the resistance to some pathogens may be influenced by plant nutritional status. Obligate parasites such as rusts may be promoted either by deficiencies of K (Suzuki and Chiba 1973 cited in van den Driessche 1984) or excesses of N. The increase in infection severity with deficiencies of K or excesses of N may be mediated through increased accumulations of low-molecular-weight substances (Marschner 1995); it was not associated with decreased foliar concentrations of phenolic compounds (Hakulinen 1998). Sulphur-deficient *Pinus radiata* were subject to more severe infections by the needle cast fungus, *Dothistroma* spp. (Lambert 1986), in association with increased foliar concentrations of arginine. Thinning and fertilization with urea increased the infection by *Armillaria* spp. of Rocky Mountain Douglas-fir, compared with control or thinned, unfertilized trees (Entry et al. 1991). The greater incidence of infection may have been associated with higher concentrations of sugars in roots and decreased concentrations of lignin and tannins. Fertilization with N alone may also have predisposed the trees to infection by increasing leaf:root ratios and increasing water stress (Belanger et al. 1990; Miller et al. 1992). The susceptibility of aspen to stem cankers caused by *Hypoxylon* spp. increased with N fertilization, but decreased with P and K addition (Teachman et al. 1980). Clonal interactions with nutrient addition were also noted. Fertilization may affect the interactions between deciduous broadleaved trees and pathogens and insects. However, it is unknown how tissue elemental concentrations, productivity, and susceptibility to insects and pathogens are related.

8 FERTILIZATION AND MYCORRHIZAE

Root systems of temperate forest trees are commonly infected by mycorrhizae. The most consistently reported beneficial effect of mycorrhizal infection for trees is enhanced uptake of mineral nutrients. It is unclear how fertilization may affect mycorrhizal presence and function and the relationships among fertilization, mycorrhizae, tree nutrition, and growth.

There are two primary types of mycorrhizae found on deciduous broadleaved trees: endomycorrhizae, dominated by the vesicular-arbuscular mycorrhizae (VAM) and ectomycorrhizae (ECM). The native hardwood trees of British Columbia may host either, but one type or the other typically dominates, depending on the host species. In red alder (Molina et al. 1994), paper birch (Perala and Alm 1990; Jones et al. 1997), and trembling

aspen (Cripps and Miller 1995 cited in Pregitzer and Friend 1996), ECM dominate. Hybrids of *Populus deltoides*, which should include the *P. trichocarpa* × *P. deltoides* hybrids typically planted in coastal British Columbia, may have either mycorrhizal type, but are usually dominated by VAM (Godbout and Fortin 1985). Both may also occur simultaneously on the same root system (Lodge 1989).

Mycorrhizae are commonly reported to enhance the uptake of P, but they also increase the uptake of K, Ca, S, Cu, Zn, NH4-N, and organic N (Bowen 1984; Marschner 1995). The enhanced uptake of immobile elements may be associated with the extensive surface areas of hyphal strands, but VAM may also be able to utilize Al and Fe phosphates not otherwise assimilated by the host tree (Bowen 1984).

The effects of fertilization on mycorrhizal development are unclear. Fertilization with P did not affect ECM development in red alder seedlings (Koo 1989 cited in Molina et al. 1994). Elsewhere, the numbers of mycorrhizal root tips per unit volume of soil in an 11-year-old *Pinus taeda* plantation were reduced in plots fertilized with N only, compared with unfertilized plots or plots fertilized with P only or N+P+K (Menge et al. 1977). Fertilization with B well in excess of host plant demand enhanced root infection (Mitchell et al. 1990). Marschner (1995) suggested that infection was low at low availability of P, increased to an optimum, then decreased as P availability further increased. Rate of decline in infection with increasing P appeared to vary with the fungal species. It is unknown how fertilization might impact mycorrhizal development in hardwoods in British Columbia and how this, in turn, might relate to tree growth and nutrition. Presumably, fertilization would offset any declines in nutrient uptake associated with decrease mycorrhizal infection and vigour.

9 AMELIORATION OF MINERAL NUTRIENT DEFICIENCIES

Fertilization is the primary approach for correcting mineral nutrient deficiencies in forest stands. The efficiency of fertilization (i.e., the percentage of the applied element assimilated by the target trees) may vary with the form of the element and its frequency of application. The effects of elemental form on fertilization efficiency have been examined only in coniferous species in British Columbia, although the effects of P form are currently being examined in hybrid poplars (see below). Of the deciduous broadleaved species significant to forestry in British Columbia, the effects of fertilization frequency have been examined only in hybrid poplars (Zabek 1995).

9.1 N Sources Typically, only 10–30% of applied N is assimilated by the target trees, compared with efficiencies exceeding 50% in crop species (Nason and Myrold 1992). Nitrogen is generally applied in coastal forests as urea and in the Interior as a blend of urea and ammonium sulphate. The most appropriate form of N to add is not always obvious. Application of ammonium nitrate resulted in greater growth responses by Douglas-fir on Vancouver Island, but was no more effective than urea in trials in northern Idaho and western Montana (Mika et al. 1992) and the interior of

British Columbia (Brockley 1995). Ammonium nitrate may be generally more effective in cooler climates and on soils with low native fertility or restricted moisture (Bengtson 1976 cited in Ballard 1984). Although urea contains a greater percentage of N (46% vs 35% in ammonium nitrate), hydrolysis of urea produces NH_3, which may volatilize under conditions of restricted moisture availability. As much as 30–40% of N applied as urea may be volatilized and lost from the soil-plant system (Marshall and DeBell 1980). The losses may be reduced when the fertilizer is applied in conjunction with cool, wet conditions (e.g., fall-early winter) or when the urea is coated with S. Ammoniacal fertilizers (ammonium nitrate, ammonium sulphate) are mildly acidifying. Thus, NH_4 remains protonated and dissolved in the soil solution and is not prone to volatilization (Nason and Myrold 1992). The disadvantage of ammoniacal fertilizers is that significant percentages (e.g., 60%) of the added N may be immobilized.

Nitrate-based fertilizers are not used in fertilization of coniferous forests in the Pacific Northwest. Concentrations of N in nitrate fertilizer are lower than in ammonium- or urea-based N fertilizers and the added nitrate may be readily leached. However, less N is immobilized (e.g., 20%) when added as nitrate than when added as ammonium. Nitrogen fertilizers containing a significant portion of N as nitrate may be more appropriate as a source for N fertilization for fast-growing hardwood species (except for red alder) than for associated conifers. In intensively managed stands, greater uptake rates of N may minimize leaching losses. As previously mentioned, deciduous broadleaved species may have a greater capacity for assimilating NO_3 than do conifers, particularly in foliage (Smirnoff and Stewart 1985).

Controlled-release fertilizers (CRFs) have received increasing attention as a way of increasing efficiency of nutrient uptake, especially by young trees. In studies conducted in British Columbia to date, CRFs have not been more effective in increasing growth than soluble fertilizers. In studies conducted with two clones of hybrid poplar on Vancouver Island, four CRFs (Osmocote 10-26-10-2 MgO, Agroblen ff 14-7-10+trace elements, Agroblen 15-9-9-3 MgO, and Osmocote Poly-S 19-7-11) and two readily soluble fertilizers (Growers Standard 15-30-15 and diammonium phosphate) were dibbled into holes 15 cm from newly planted cuttings at rates supplying 0, 13.5, or 27g N per tree.[9] Stem growth increased linearly with N supply through two growing seasons, but there was no difference among fertilizers after one or two growing seasons.[10] Studies with coniferous seedlings have shown a similar lack of effect from release rate (van den Driessche 1988; Sandford and Andersen 1997 cited in van den Driessche 1997).

9.2 P Sources

Phosphorus fertilizers generally occur as either water-soluble forms (e.g., triple superphosphate, TSP) or water-insoluble (e.g., ground rock phosphate, GRP) forms. Fertilization of coniferous forests in British Columbia or surrounding regions has rarely included additions of P (Weetman et al. 1992) and the efficacy of the different sources has not been compared systematically. Studies of growth responses of red alder, black cottonwood,

9 R. van den Driessche and K. Brown, BC Min. For., EP 753.24, 1996.
10 K. Brown and R. van den Driessche, unpubl. data, 1998.

and hybrid poplars have also used TSP (DeBell et al. 1991). Triple super phosphate may be superior on soils of moderate acidity and P-retention capacity, whereas GRP may be more effective on acid soils of low P-retention capacity and basic soils of high P-retention capacity (Ballard 1984). The advantage of GRP is its longer duration of effectiveness, which presumably occurs because of lesser leaching losses on soils of low P-retention capacity and slower rates of transformation to unavailable forms of P on high P-retention capacity soils (Ballard 1984). However, GRP may not supply adequate amounts of P to fast-growing, intensively managed hardwood species such as hybrid poplars.

The effects of P sources, rate of P addition, method of application, and rate of N addition on hybrid poplar growth and nutrition are currently being examined in a factorial experiment on eastern Vancouver Island.[11] Through three growing seasons, mean stem volumes were about 30% greater in trees fertilized with diammonium phosphate or TSP than in trees fertilized with GRP.[12] It appears that readily-soluble forms of P are more effective in the short-term, although it is unclear if the advantages persist longer into a rotation.

9.3 Frequency of Fertilization

Operational fertilization of coniferous stands in British Columbia and the Pacific Northwest states typically consists of about 100 kg N ha^{-1} applied every 5–10 years (Diggle 1992; Olson 1992). The low fertilization efficiency of N by forest stands may lead to increased nutrient runoff and water pollution in situations requiring intensive rates of nutrient addition (e.g., in short-rotation intensive culture). Fertilizer efficiency may be increased by dividing the fertilizer application over several applications (i.e., fertilizing more frequently and in smaller amounts per application) while increasing added amounts over time to match plant growth (Tamm 1968; Ingestad 1988). Annual applications of fertilizer have increased the productivity of Scots pine and Norway spruce by 150–300%, compared with increases of 30–90% relative to that achieved by fertilization at intervals of 5–10 years (Axelsson 1985 cited in Binkley 1986). A potential problem is that nitrification may be promoted by small repeated applications of N. When short-rotation sycamore plantations were fertilized with 450 kg N ha^{-1} as urea, additions at constant rates at the beginning of each growing season (i.e., 150 kg N ha^{-1}) resulted in the greatest amounts of NO_3 leaching; applications three times per year (50 kg N ha^{-1} per application) decreased the amount of NO_3 leaching, but increasing the amount of N added at the start of each growing season (e.g., 50, 150, 250 kg N ha^{-1}) resulted in the greatest growth, a 2- to 3-fold increase in N fertilizer efficiency and the smallest amounts of NO_3 leached (van Miegroet et al. 1994). Conversely, the growth of hybrid poplars at a site on Vancouver Island was not improved when fertilizer applications were split over a growing season, compared with a single application at the beginning of the growing season (Zabek 1995). Moisture deficits late in the growing season probably limited elemental uptake and growth responses to the late-season applications.

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11 R. van den Driessche, BC Min.For., EP753.23, 1995
12 Brown and van den Driessche, unpubl. data, 1998.

9.4 Biosolids   Alternatives to fertilizing with chemical fertilizers include applying sewage effluent or biosolids and interplanting with N_2-fixing species. Interest in biosolids applications has increased partly because of its potential value as a soil conditioner (adding mineral nutrients and organic matter), and partly because of problems with disposal following completion of secondary sewage treatment facilities in Vancouver. Concerns centre around salt accumulation, groundwater contamination, and the possible induction of secondary deficiencies of elements such as Mg (Harrison et al. 1992). Consequently, the effects of sludge on nutrition and growth of cottonwood and hybrid poplars have been examined in several studies in British Columbia and Washington.

The city of Vernon, B.C., in conjunction with the B.C. Ministry of Forests and the University of British Columbia, has irrigated hybrid poplar plantations with municipal sewage effluent since 1985 (Carlson 1992). The Greater Vancouver Regional District (GVRD), in conjunction with Scott Paper and the University of British Columbia, applied sludge in 1994 to hybrid poplars at rates intended to supply up to 4000 kg N ha^{-1}. Sludge was operationally applied to 70 ha in 1994 and 90 ha in 1995 at rates supplying about 831 kg N ha^{-1}.[13] In eastern Washington, sludge has been applied to hybrid poplars in combination with irrigation in a study that began in 1994. Approximately 75% of the N initially added was lost to volatilization, probably as a result of alkaline soils and warm, windy conditions at the site. Losses from volatilization appeared to be partially compensated by increased mineralization rates under sludge application.[14]

Biosolids may be an appropriate means of fertilizing intensively managed cottonwood and hybrid poplar stands. It is unclear, however, whether biosolids are more effective in supplying nutrients to fast-growing tree species than are synthetic fertilizers, although other factors (soil conditioning, cost) may make their use advantageous.

10 SPECIES-SPECIFIC MINERAL NUTRITION-RELATED RESEARCH PROBLEMS

10.1 Red Alder   Several factors make red alder an appealing species to manage for in coastal British Columbia. It is the fastest-growing native tree species after black cottonwood and may be a source of relatively valuable wood for furniture, cabinets, and turned-wood novelties (Plank and Willits 1994). Red alder is unique among the major hardwood species of the province in its ability to fix atmospheric N_2 symbiotically, in association with the actinomycete *Frankia* spp. Consequently, the presence of red alder may significantly improve the nitrogen capital of a site over time and improve the growth of coniferous associates such as Douglas-fir that ultimately dominate the site. The combination of fast growth and an ability to fix atmospheric N_2 make red alder an appropriate species to plant for

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13 GVRD Nutrifor Newsletter, July 1995.
14 Notes from presentation by Chuck Henry, University of Washington, at Poplar Field Day 2, Prosser, WA, August 2, 1995.

revegetating deactivated forest roads and landings and for stabilizing slides. Finally, red alder is resistant to laminated root rot (*Phellinus weirii*), which infects many Douglas-fir stands on Vancouver Island.

Despite the apparent desirable characteristics of red alder, there has been little interest until recently in managing for red alder in coastal British Columbia. One company, Coast Mountain Hardwoods Inc., was awarded forest licences in 1996, permitting the harvest of specified volumes of alder in four timber supply areas. In late 1997, the four districts in the Vancouver Forest Region (Port McNeill, Campbell River, South Island, and Sunshine Coast) in which Coast Mountain Hardwoods held forest licences agreed to plant a total of 100 ha yr^{-1} in red alder for 5 years. This is a test program to evaluate growth on a range of biogeoclimatic units and site series considered to be of medium-good quality.[15]

Operational contexts in which nutrition and fertilization studies may be particularly appropriate for red alder include where there is: (1) plantation management either on sites generally considered as appropriate for red alder (e.g., Green and Klinka 1994) or on *Phellinus*-infected sites that would normally be considered too dry and infertile for alder growth; (2) management on deactivated roads and landings; (3) management of repeated rotations of red alder; and (4) management to improve site fertility for later rotations of coniferous associates.

A long-term issue is to determine what mineral nutrients limit the growth of red alder in British Columbia and what responses might be expected on a variety of sites. Site indices (25-year base) of red alder in coastal British Columbia ranged from 12–25 m on sites classified as rich or very rich. These indices were also correlated with foliar P concentrations in acidic soils (pH 4.0–4.4), indicating that some red alder stands might be responsive to fertilization with P or other elements. In one glasshouse study, the growth of seedlings in pots containing soils collected from 0–20 cm depth in mature alluvial alder stands on Vancouver Island increased with the addition of TSP. The effect of TSP was greater in soils of lower initial pH (4.5±0.1(sd)) than in higher pH soils (5.3±0.5), but there was no effect in soils with high extractable-P concentrations. The addition of dolomite increased foliar Mg concentrations, but did not affect growth.[16] Single-tree plot fertilization studies in young (age 2–4) alder plantations on Vancouver Island have produced mixed results. In one trial, stem volume after one growing season decreased with increasing P supply, but the negative effect was offset by the addition of elements other than N and P. In a second study, there was no effect of P or other elements, and in a third study, volume increased by 23% with the addition of P and other elements.[17] In field fertilization trials conducted with plantation-grown alder in western Washington, P increased (Radwan and DeBell 1994) or had no effect (Harrington and DeBell 1995) on growth. In the former study, optimal P application rates increased with available

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15 Minutes, Red Alder Management Committee Meeting, Vancouver Forest Region, November 27, 1997.
16 Brown, unpubl. data, EP1196.02.
17 Brown, unpubl. data, EP1196.04, 1997.

moisture. Seedlings grown in pots containing native soils from Washington and Vancouver Island responded to addition of P, S, and trace elements (Binkley 1986; Radwan 1987; Compton 1990). Grey alder seedlings were reported to require higher concentrations of P, relative to N, than did birch seedlings (Ingestad 1980). Red alder may respond to fertilization, but the potential growth response and its relation to site characteristics are unknown.

Nitrogen fixation rates depend on a continuous supply of newly fixed carbohydrates to the root nodules (Marschner 1995), suggesting that the availability of any essential element that is low enough to reduce plant vigour will also reduce N_2-fixation rates. However, N_2 fixation and nodule development may be affected differently than is whole-plant growth as the availability of a given element increases. Nodule initiation, but not later nodule growth, was sensitive to Ca supply in clover (Lowther and Longeran 1968 cited in Marschner 1995). An increasing P supply to soybeans caused greater increases in nodule mass than in whole-plant mass (Israel 1987) and the ratio of nodule mass:root mass in red alder seedlings may have also increased with addition rates of triple superphosphate.[18] A low availability of P to legumes may be associated with N deficiencies (Marschner 1995). Among trace elements, supplies of Mo and Fe may directly affect N_2-fixation rates. In peanuts, the addition of Mo increased nodule mass by 2.3-fold, nitrogenase activity (per unit mass) by 1.2-fold, shoot+pod mass by 1.4-fold, and N uptake (per hectare) by 1.7-fold (Hafner et al. 1992).

Because red alder is immune to laminated root rot caused by *Phellinus weirii*, it may be planted in disease centres of infected stands, typically of Douglas-fir, and often in conjunction with commercial thinning of the infected stand (Thies and Sturrock 1995). Such stands may be on sites considered too dry and infertile to sustain adequate growth rates of red alder. In these situations, appropriate fertilization may have a strategic role in maintaining adequate growth rates and in improving site N capital for a subsequent stand of Douglas-fir.

Fertilization may also have an important role in enhancing the growth of alder on slides or deactivated forest roads and landings in coastal British Columbia. Growth and N_2 fixation may be limited by inadequate nutrition associated with removal of upper soil horizons and with soil compaction. A commercial fertilizer blend called Alder-pak (Reforestation Technologies Inc.), designed for adding at the time of planting, has been applied to seedlings planted on deactivated roads and landings and slides in the South Island Forest District.[19] Small-scale screening trials quantifying the effect of such fertilizers and their effectiveness in the different soil environments of slides, roads, and landings would provide a useful assessment of this practice.

Finally, an understanding of red alder nutrition may be important for management of the species in repeated rotations on sites on which conifers may be difficult to establish. During the course of an alder rotation, N_2 fixation may decrease soil pH over time and the growth of alder

18 Brown, unpubl. data, 1997.
19 P. Ducharme, B.C. Min. For., pers. comm., May 1998.

seedlings planted on sites previously containing red alder may be reduced relative to seedlings planted on similar sites that previously contained Douglas-fir (van Miegroet et al. 1990). After 5 years, above-ground biomass of alder planted on an alder site in the Cedar River watershed of western Washington was 75% less than that of alder planted on a Douglas-fir site. The lower growth rates were associated with lower Bray-extractable P concentrations in the soil, decreased foliar concentrations of P, Ca, and Mg, and decreased leaf litter concentrations of N, P, K, Mg, and Fe (Compton et al. 1997). The observed declines in productivity and elemental concentrations of second-rotation alder may have been associated with nitrification-enhanced reductions in soil pH and enhanced leaching of Ca and Mg from the original alder stand (Binkley and Sollins 1990; van Miegroet et al. 1990). The soil in the Cedar River site was a gravelly sandy loam and it is unclear whether such dramatic decreases in growth and nutrient availability would be seen in second-rotation alder stands growing on better-buffered soils. Elsewhere, the presence of alder increased the availability of P, compared with that in adjacent coniferous stands (Giardina et al. 1995), although the availability of P may still have limited alder growth.

Repeated rotations of red alder may be a preferred management option on sites in which establishment of Douglas-fir is difficult (e.g., wet alluvial sites). Because of this, it is important to determine to what extent the results of the Cedar River studies apply to other sites. The following questions may be important to answer: (1) What elements limit alder growth in soils of different pH and buffering capacity? (2) Does the presence of red alder necessarily result in site acidification and, if not, on which sites does it not? (3) What effect might site acidification have on the nutrition and productivity of second-rotation alder seedlings and saplings? (4) Can appropriate fertilization allow site management for consecutive rotations of alder without resulting in appreciable losses in productivity? (5) Can the problems alluded to above be minimized by appropriate mixtures of red alder and Douglas-fir, rather than managing for pure stands?

As indicated previously, the effectiveness of different P fertilizer sources may vary with soil acidity. Liming of acidic alder soils is one possible approach to minimize multiple elemental deficiencies (Seiler and McCormick 1982; Ljungstrom and Nihlgard 1995). However, liming of acidic soils may increase, decrease, or have no effect on P availability, depending on the soil and timing of lime and P applications (Haynes 1982). Reviews of long-term liming trials in European forests suggest that while some soil characteristics are improved by liming (decreased acidity, increased cation exchange capacity), growth and foliar K concentrations may be reduced, acidification may be promoted in deeper horizons, leaching of NO_3-N may increase, and fine root growth may be concentrated in the uppermost soil horizons (Huettl and Zoettl 1993). If so, liming may not be an appropriate substitute for the readily soluble forms of specific elements.

Finally, improved nutrition of red alder in mixed stands may improve rates of N accretion and N availability to coniferous associates that later dominate the stand. Reported rates of accretion range from 25 to 320 kg N ha^{-1} yr^{-1} in pure stands and 0 to 130 kg N ha^{-1} yr^{-1} in mixed stands

(Binkley et al. 1994). Many factors other than nutrition, including differences in sampling technique, stand age, moisture availability, and stand density could contribute to this variation. Given the direct and indirect roles of various nutrients in enhancing N_2 fixation, as demonstrated in controlled studies (discussed above), it seems that fertilization with appropriate elements other than N could enhance N availability to coniferous associates during stand development. Currently, studies are underway in coastal British Columbia to assess the effects of various mixtures of alder and conifers on stand development and N accretion (Comeau et al. 1997). Fertilization, however, is not part of the study design.

10.2 Black Cottonwood, Balsam Poplar, Trembling Aspen, Paper Birch, Bigleaf Maple

The diagnosis of elemental deficiencies in relation to site associations of the biogeoclimatic ecosystem classification, and the prediction of growth responses to nutritional amendments, are both important nutritional topics pertaining to the operational silviculture of black cottonwood, balsam poplar, trembling aspen, paper birch, and bigleaf maple. Each species may occur in a variety of sites, but it is unknown how nutrient supply affects growth in relation to quantifiable measures of site fertility (e.g., mineralizable-N, foliar elemental concentrations), soil moisture and stand characteristics (e.g., stand density, leaf area index) or categorical soil moisture and nutrient regimes used in the provincial biogeoclimatic ecosystem classification. To date in British Columbia, growth responses to nutrient additions have been examined only in black cottonwood (McLennan 1993) and are currently being examined in trembling aspen, as indicated previously.

Black cottonwood is the lead species on approximately 20 000 ha of coastal forest land in British Columbia and slightly less in the southern Interior (Peterson et al. 1996). Balsam poplar is the lead species on approximately 215 000 ha in northern British Columbia, primarily in the northeast. Both are most commonly associated with alluvial sites, but may also occur on moist upland sites. McLennan (1996) observed that site index (15-year base; SI_{15}) of black cottonwood in alluvial stands increased from 11.7 m to 23.6 m as soil nutrient regimes increased from medium to very rich and was more strongly related to foliar concentrations of N and P than to those of other elements. DRIS was applied to identify elements that limited growth in different site associations. On low alluvial benches (cottonwood-willow association, mean SI_{15}=11.5 m), N was more limiting than P and K. On middle benches (cottonwood-red osier dogwood association, mean SI_{15}=21.6 m), P and K were more limiting than N, and on high benches (Sitka spruce-salmonberry association, mean SI_{15}=25.4 m), K was more limiting than P. Nitrogen was not considered limiting on the high benches. Short-term fertilization screening trials were employed to test the accuracy of the DRIS conclusions. In general, fertilization has not been considered an issue of strategic importance in the intensive management of native black cottonwood or balsam poplar stands, but McLennan's findings may be important in developing fertilization regimes for hybrid poplar plantations located on alluvial sites.

It is important to understand where and how mineral nutrition limits the growth of aspen. Aspen is the most widely distributed hardwood tree species in British Columbia and is the species harvested in the greatest quantities. Aspen stands may be responsive to fertilization at least to ages

of 35 years (Coyne and van Cleve 1977; van Cleve and Oliver 1982; Nilsson and Wasielewski 1987; Yang 1991). For example, stem volume of a 35-year-old aspen stand (initial volume 145 m^3) increased by 37.3 m^3 ha^{-1} (111.3%) relative to the control stand when fertilized with 224 kg N ha^{-1} and 112 kg ha^{-1} of P and K (Yang 1991). In contrast, fertilization with up to 200 kg N ha^{-1} + micronutrients did not increase the growth of aspen on fertile sites.[20] There is some concern that the capturing of added nutrients by the abundant understorey vegetation associated with aspen stands will minimize any response to fertilization (Peterson and Peterson 1995).

Many of the aspen stands in northeastern British Columbia are 85–100 years old and are considered overmature (Peterson and Peterson 1992). If the harvesting of older stands is accelerated, factors affecting vegetative reproduction (i.e., suckering) and early growth must be understood. Poor aspen regeneration is often associated with herbivory and with soil compaction following harvesting, possibly because of poor drainage or poor aeration.[21] Soil temperature is felt to be a major influence on the initiation and development of suckers (Peterson and Peterson 1992). An improved mineral nutrient status of the parent stand could increase the post-harvest initiation of adventitious shoots on lateral roots by increasing cytokinin production, and might further affect the subsequent rate of sucker growth by affecting concentrations of soluble carbohydrates in the roots (Tew 1970; Schier and Zasada 1973). With respect to nutritional research, fertilization trials on a variety of sites are of high priority because of the obvious operational implications. At the same time, the relation of fertilization and tree nutrient status to vegetative reproduction may be of some importance. The effects of fertilization on tree growth and susceptibility to herbivores and diseases are of interest, but of lower priority.

Paper birch occurs throughout the Interior and, to a lesser extent, in coastal British Columbia. The highest concentrations occur in the northeastern part of the province on sites considered to be of low productivity (Massie et al. 1994). Lower concentrations occur in the central and south-central parts of the province on sites of medium productivity. In the Kamloops region, site index is strongly related to available moisture; site index at 50 years ranged from 12.8 m in subxeric sites in the ICHmw2 biogeoclimatic variant to 22.1 m in subhygric sites (Simard and Vyse 1992).

The response of birches to fertilization have not been examined in British Columbia, though it has been studied elsewhere. The growth of paper birch on medium- or coarse-textured soils in the northeastern U.S. is often limited by deficiencies of N and P. If fertilized after thinning, growth responses to fertilization last 5–7 years (Safford 1983; Hoyle 1984). Hoyle (1984) grew paper birch from seed for 10 years under plantation conditions in New Hampshire. Seedlings fertilized with N, P, and lime had basal areas 282% greater than did controls, whereas the basal area of yellow birch (*Betula alleghensis*) did not increase with fertilization. Protection of the plantation from deer was essential for successful plantation culture of paper birch. Viro (1974) studied the growth responses of

20 Dave Coopersmith, B.C. Min. For., pers. comm., November 1998.
21 Richard Kabzems, BC Min. For., pers. comm., January 1996.

seedlings and near-mature (ages 25–40) stands of warty and hairy birch (*Betula verrucosa* and *B. pubescens*, respectively) to fertilization in Finland. Fertilization the year after planting with ammonium sulphate increased heights 70–80% over controls; in older stands, fertilization with N+P increased stem diameters up to 50% over 10 years in one study and 20% in a second. In a study conducted on a site considered to be fertile, no response to fertilization was observed. Fertilization was determined not to be economically feasible even where growth responses were observed, because of the small tree size. However, the responses of pole-sized, well-stocked stands were not examined. In mixed stands, birch required greater application rates of N to achieve a given relative increase in yield than did the associated spruce (*Picea abies*), an interesting observation considering that hardwood species often respond more rapidly to fertilization (Linder and Rook 1984).

Clearly, and not surprisingly, the growth of birch may respond to the addition of limiting nutrients. It is therefore important, as with other species, to identify on which sites fertilization will evoke a growth response. Site moisture availability is likely to be important in determining the response of birch to fertilization, at least in the southern interior of the province. Safford (1983) suggested that a site index of 18 m at 50 years (equivalent to site indices observed in mesic-subhygric sites in the IDF and ICH zones of southern British Columbia) was the minimum to consider for intensive culture, which would include fertilization.

The most valuable birch logs are those that are both large and with few defects. While fertilization may be important for enhancing growth early in stand development, fertilizing well-stocked, productive, and near-mature stands may be desirable economically. It is important to identify the appropriate age and size of stands at which fertilization would be most beneficial.

Increasing interest in the planting of bigleaf maple has revealed some difficulties in the consistent production of high-quality nursery stock and in the growth attainable after outplanting.[22] Outplanted seedlings may exhibit little or no above-ground growth during the first growing season after outplanting; field observations suggested that seedlings planted in moist swordfern-dominated depressions outgrew those planted in coarse-textured soils derived from glacial till.[23] This suggests that either nutrient or moisture availability, or both, may affect biomass allocation and growth of bigleaf maple seedlings. However, the effects of plant nutrition and moisture status on biomass allocation and growth have not been studied. Rankings compiled by Klinka et al. (1990) suggest that bigleaf maple is relatively undemanding of moisture, compared with other coastal hardwoods. These rankings, however, may not apply to seedling requirements. The relationships between seedling growth, nutrition, and moisture availability should be examined. As with paper birch, the value of bigleaf maple logs increase with size, as long as defects do not also increase (Massie et al. 1994). Hence, fertilization trials with near-mature stands might be appropriate.

22 A. Luckett 1996. Big-leaf maple regeneration study. Progress report, Hardwood Silviculture Cooperative Meeting, January 8–9, 1996.
23 Phil Comeau, B.C. Min. For., pers. comm., January 1996.

10.3 Hybrid Poplars   The specific nutritional concerns associated with hybrid poplars differ from those of the native broadleaved species occurring in British Columbia forests. Site conditions, while variable, are likely much less so than are those associated with widespread species such as trembling aspen, black cottonwood, balsam poplar, or red alder. Intensive breeding programs are producing numerous clones that may differ in growth rates and their abilities to grow on nutrient- and moisture-limited sites. The greater growth potential of poplar hybrids, combined with their short rotations (e.g., less than 15 years) means that nutrient addition rates required to achieve maximum growth will be greater than those rates required by native broadleaved species. However, the plantation sites typically have shallow water tables, and the over-application of fertilizers early in the life of the stand (within 2 years following planting) could result in greater leaching of added fertilizer to subsurface waters. At the same time, a greater variety of viable options exists for the delivery of nutrients. These include the application of biosolids, varied frequencies in the application of inorganic fertilizers, and irrigation with municipal effluent (Carlson 1992), as discussed previously. Research on these different methods of nutrient delivery should be continued.

Clonal variation in response to site fertility and added nutrients is a major area of uncertainty. Optimum soil pH for growth varies among species and hybrids. For example, optimum pH tends to be lower in Tacmahaca, Tacmahaca × Aigeiros, and Aigeiros cultivars and hybrids with balsam poplar parentage than in Euramerican (*deltoides* × *nigra*) crosses (Heilman 1992). Clones sensitive to high pH may be prone to iron-chlorosis (Heilman 1992).

Clones of cottonwood and hybrid poplars may vary in their growth responses to N (Curlin 1967; Heilman 1985; Heilman and Xie 1993) and P fertilization[24] and therefore may differ in their ability to capture and use available nutrients. An understanding of those differences may be important for matching clones to sites and for developing new clones. Differences in growth responses to a given availability of nutrients may be due to differences in: (1) the amount of root growth; (2) acquisition efficiency, the amount of a given nutrient assimilated per unit of root; and (3) utilization efficiency—the amount of biomass produced per unit of nutrient acquired. Clonal or varietal differences in early root growth may be associated with later differences in biomass accumulation (Bloomberg 1963; Tschaplinski and Blake 1989; Brown et al.[25]), implying that the rate and total amount of early root growth is important for providing the plant with access to sufficient moisture and nutrients for establishment. Studies of herbaceous species suggest that the uptake of P, a relatively immobile element, is greater in varieties with larger or more fibrous root systems (Vose 1987). The distribution of root growth in relation to nutrient-rich patches may vary with clone (Friend et al. 1998). If so, clones may differ in the amount of photosynthate they must allocate toward nutrient acquisition versus the capture of light and CO_2.

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24 R. van den Driessche, K.R. Brown, EP753.23, unpubl. data 1997
25 K.R. Brown, F.D. Beall, and G.D. Hogan. Biomass accumulation in hybrid poplars during the establishment year. Can. For. Serv., Sault Ste. Marie, Ont., Unpubl. manuscript.

While clonal differences in root growth have been studied in hybrid poplars, it is unknown whether clones might also vary in their ability to solubilize and assimilate nutrients existing in forms that are not readily available. For example, some plants can hydrolyze organic phosphates through secretions of phosphatases (e.g., Li et al. 1997). Likewise, it is unknown if uptake capacity (i.e., uptake per unit root mass or surface area) varies with clone or if it is even important compared with differences in the amount of root growth. Variation of uptake capacity for NO_3 might be important, because NO_3 is likely to be the predominant form of available N in sites considered suitable for *Populus*, and because increased uptake capacity is likely more important for mobile elements such as NO_3 and K (Chapin et al. 1986; Garnier et al. 1989). Nitrate reductase activity was correlated with growth rate in clones of *Populus deltoides* (Gordon and Promnitz 1976), but it is unknown if NO_3 reductase activity and NO_3 uptake capacity are linked.

It is also unknown whether clones of hybrid poplar differ in the efficiency with which they utilize different elements. During a growing season, N utilization efficiency may vary with N partitioning between photosynthetic and other functions in the leaf, and with allocation between roots and foliage. Growth rates might be greater at a given whole-plant concentration of N if more assimilated N was allocated to foliage, and a further increase could occur if a greater proportion of foliar N was partitioned to photosynthetic functions (Hirose 1988; Evans 1989; Brown et al. 1996a,b). However, the highest whole-plant nutrient use efficiency should result when processes underlying growth (Bloom et al. 1985) are limited equally by a given limiting nutrient. Whole-plant N use efficiency could be increased if less foliar N needed to be partitioned to photosynthetic functions, thus allowing more N to be reallocated to support growth in other parts of the plant. Differences in P utilization efficiency have been attributed to differences in the utilization of stored Pi (e.g., in vacuoles) (Marschner 1995). Low apparent utilization efficiencies of elements may also result from deficiencies of other elements, moisture, or light (e.g., Brand 1991).

The relative importance of the components of nutrient use efficiency has rarely been assessed. In one study, family differences in N use efficiency of loblolly pine were due to different characteristics, depending on the availability of N (Li et al. 1991). At low N, uptake efficiency was more important than was utilization efficiency. Rooting efficiency was the most important component of uptake efficiency. At high N, utilization efficiency was more important. Conversion efficiency was the most important component of utilization efficiency.

Studies of nutrient efficiency have largely focused on short-term studies, typically during a single growing season. However, whole-plant nutrient use efficiency may also be affected by the efficiency of retranslocation of elements prior to leaf senescence. Retranslocation efficiency may vary with the species. For example, one study found that the percentage of foliar P removed before senescence was 44% in *Betula papyrifera* and 81% in *Alnus crispa*, and the percentage of foliar N removed was 75% and 62%, respectively (Chapin and Kedrowski 1983). In addition, retranslocation efficiency may increase with the "sink strength" in the plant (Pugnaire and Chapin 1992), suggesting that an improved nutritional status

might improve retranslocation efficiency. However, retranslocation efficiency of P in barley decreased with increasing N and P availability and decreased with water stress (Pugnaire and Chapin 1992), whereas the retranslocation efficiency of N and K in *Pinus radiata* increased with N fertilization (Nambiar and Fife 1987). Clearly, retranslocation efficiency may vary with several factors.

In broadleaved stands, the extent to which a high retranslocation efficiency is desirable depends on what happens to elements lost from the tree via litterfall. If nutrients contained in litterfall were rapidly cycled back into the crop trees, a greater retranslocation efficiency may be undesirable, in that more nutrients would be removed from the site at each harvest (assuming woody above-ground tissues only are removed). Such increased removals may be detrimental to the maintenance of site productivity. The problem would be exacerbated under the short-rotations typically used for producing wood chips. The problem would be minimized if the trees were harvested with the leaves attached and the leaves were then stripped and returned to the site (as is commonly practiced in western Oregon and Washington). If the poplars are being grown in riparian zones as a buffer to adjacent agricultural lands, an increased retention of assimilated nutrients may be desired. Some *Populus trichocarpa* × *P. deltoides* (T × D) hybrids may return 30% of N in litterfall annually, whereas *P. trichocarpa* may return as much as 60%. If nutrients in runoff are a concern (e.g., with agricultural runoff) the T × D hybrids may be desired.[26]

The identification and interpretation of differences in nutrient use efficiency is complicated by the number of underlying plant processes involved. When pot-based trials are used to elucidate clonal differences, interpretations may be further complicated by time-dependent declines in tissue nutrient concentrations associated with insufficient nutrient supplies (Ingestad 1982; Brown 1991). Thus, reports of greater N-use efficiency in fast-growing clones of *Populus deltoides* (Curlin 1967) may merely indicate that N supplies were insufficient to maintain constant tissue nutrient concentrations over time. Nonetheless, a better understanding of the processes underlying nutrient-use efficiency could provide a useful direction in poplar breeding and assist in the development of appropriate fertilization practices.

As indicated above, clonal differences in root growth may affect nutrition and growth. Conversely, the mineral nutrition of stool beds may be important in determining the rooting capability of poplar cuttings. Nitrogen deficiencies may enhance the rooting of cuttings, whereas deficiencies of K, P, Mg and Ca may decrease rooting (Haissig 1986). It is not clear whether mineral nutrition primarily affects root initiation (Lovell and White 1986) or subsequent root growth, and the underlying mechanisms are not yet understood.

Determining the most effective time to fertilize during a rotation is an area of considerable uncertainty. Fertilization, at least with N, is not recommended during the establishment year (Dickmann and Stuart 1983; Hansen 1994). The most conservative approach advocates delaying

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26 P. Heilman and J. Braatne. 1995. Ecological concerns in poplar conservation. Paper presented at International Poplar Symposium, Seattle WA, August 20–25, 1995.

fertilization until nutrient supply clearly limits growth (Heilman 1992). Root systems of the planted cuttings are more extensive during the 2nd and 3rd years following planting, and absolute growth rates (and nutrient demand) are greater as the stand approaches canopy closure. Thus, demands are greater and losses of N to leaching and denitrification are less likely. However, fertilization with N and P during the establishment year increased height growth by up to 100% during the establishment year.[27] It is unclear whether the advantages of increased growth during the establishment year are offset by a decreased fertilizer use efficiency and by increased losses of added nutrients off-site.

Finally, understanding the effects of hybrid poplar plantation establishment on long-term site productivity is important. The site preparation conducted in association with establishment of hybrid poplar plantations on previously forested land is intensive and commonly involves windrowing and forest floor displacement. There is some concern that site degradation may occur over time under such intensive management, although inputs of senescing leaves and fine roots during the life of a plantation may improve the productivity of the site. Conversely, the establishment of plantations on sites formerly used for pasture might well improve site quality. Long-term monitoring of relevant soil properties influencing site productivity, including nutritional aspects, should be initiated to quantify changes in both situations.

11 PRIORITIES FOR RESEARCH

Although fertilization clearly has the potential to increase the productivity and value of hardwood species, the relationships between mineral nutrition and the productivity of deciduous broadleaved tree species in British Columbia are largely unknown. There is information available from Washington concerning the nutrition and fertilization of poplar hybrids currently grown in coastal British Columbia, but few data exist on the responses of those hybrids to fertilization in the site conditions being used for poplar culture in the province. It is not yet clear how clones of hybrid poplar may vary in their growth responses to nutrient availability or what fertilization tactics are most appropriate to achieve maximum productivity, although such studies are under way.

Native species are even less well understood. It is unknown, for example, how foliar elemental concentrations relate to growth in bigleaf maple, how growth and nutrient uptake responses to fertilization differ between native hardwood species and their coniferous associates, and how fertilization responses in red alder, bigleaf maple, trembling aspen, paper birch, or balsam poplar vary with stand and site characteristics. There is no information on the soil-based or physiological mechanisms underlying responses to fertilization, or on how tissue nutrient concentrations affect plant responses to other abiotic stresses (such as drought or frost) or biotic stresses (pathogens, herbivores). Such information is essential for

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27 van den Driessche and Brown, unpubl. data 1995.

properly evaluating the potential productivity of hardwood trees in British Columbia.

Fortunately, some information from conifer fertilization studies in British Columbia can, with caution, be applied to hardwoods. This includes data suggesting which elements are most likely to be deficient in certain sites and soils, and data indicating which types of N fertilizer may be most effective as a source of N. Principles inferred from studies of the relationships among nutrient status, drought and cold stress, herbivores and pathogens, and productivity are applicable, even if the threshold concentrations of foliar nutrients associated with maximum growth rates and stress tolerance are not known for each species.

From an operations perspective, being able to predict growth responses of the predominant hardwood species to fertilization on a variety of sites and stand conditions is of the greatest strategic importance, as it is with conifers. Having the ability to predict responses implies understanding the processes affecting response. Which should be emphasized: intensively cultured hybrid poplars or less intensively managed (and presumably less desirable) native hardwoods? Both are important. The objective of hybrid poplar culture is to produce fibre. Fertilization has an immediate and obvious role in enhancing the growth of hybrid poplar plantations, with the clear likelihood of resulting in positive net economic returns. Conversely, the objectives of native hardwood management are much more variable and may not include fibre production. However, the potential area available for native hardwood management is much greater than that for hybrid poplar plantations, and the relationships between site, productivity, and potential responses to fertilization are more complicated. Hence, it is prudent to begin the appropriate research on nutrition of native hardwoods before demands increase substantially and supplies become limiting. That work should be largely extensive in nature (i.e., establishing fertilization trials on a variety of sites while measuring a minimal number of tree and site processes), with the intent being to examine soil and plant processes affecting nutrient uptake and utilization in more detail as field results become available. In this regard, information gained from process-oriented studies on fertilized hybrid poplar plantations should be useful in guiding more intensive studies of native hardwoods.

Several areas of research should be emphasized for intensively cultured hardwoods, such as hybrid poplars. These include:

1. Developing a better understanding of the constraints that nutrient limitations place on productivity, and of how best to alleviate those constraints.

    This focus would be part of studies designed to identify clones suitable for growing on marginal sites (e.g., less fertile, with shorter growing season, or moisture-stressed), such as those found on Vancouver Island. Some emphasis should be placed on determining the most efficient means of delivering mineral nutrients, including the use of controlled-release fertilizers, and on understanding how soil moisture and fertilization interact in affecting elemental availability and uptake. Also important to examine is how plant nutrient status affects water consumption. In the longer-term, assessments should be made as to the sustainability of repeated rotations of hybrid poplars.

2. Determining whether clones likely to be used operationally vary in their nutrient use efficiency to a degree sufficient to warrant consideration in planting decisions.

   This focus will require extensive collaboration with tree breeders. Several long-term opportunities for such collaboration exist in the region. The B.C. Ministry of Forests has committed to a hardwood breeding program, which will lead to the development of clones appropriate to British Columbian climates and soils. As well, researchers at the University of Washington have identified quantitative trait loci associated with rapid stem and root growth and stress resistance (Bradshaw and Stettler 1995), but factors contributing to clonal differences in the efficiency of elemental use are not understood. Identification of such traits could lead to the development of clones with greater growth potential at lower rates of fertilization.

3. As part of the two areas above, adapting appropriate simulation models and developing the required data base.

   Such work should be continued. Use of the models and data may provide managers with mechanistically based tools for matching clones to sites.

4. Better defining the relationships between clone, nutrient status, and susceptibility to abiotic (drought, frost) and biotic stresses (insect herbivores and pathogens).

   Research in this area is especially important, given the variety of insects and pathogens that attack hybrid poplars and the reported effects of nutrition on, and clonal susceptibility to, different pathogens and herbivores.

5. Developing improved protocols, using the above information, for the early (years 1 and 2) screening of new poplar clones.

The above studies will be much more intensive with respect to data collection and instrumental needs than are those suggested for native species. However, a better understanding of the processes limiting productivity of hybrid poplars should help researchers answer similar questions that arise in the course of more extensive studies conducted on native hardwood species.

Which native species are of the highest priority to study? Aspen is the most widespread species and is harvested in the greatest quantities. Several studies from outside British Columbia have related foliar elemental concentrations to aspen growth, but only two trials to date have been conducted in the province. Alder is less widespread than aspen, but is of considerable value. Management problems perceived to be of some importance (e.g., productivity in repeated rotations) almost certainly have some nutritional basis. Therefore, experiments addressing relevant aspects of nutrition and growth might have a larger impact on alder management practices than they would on aspen management.

Black cottonwood is of a lower priority to study. Growth has been studied in relation to site classification and fertilization on alluvial sites in

28 Peter McAuliffe, Scott Paper, pers. comm., August 1995.

southwestern British Columbia. Basic fertilization guidelines have been developed and are currently in use by Scott Paper[28] and other studies are examining responses to biosolid applications. Less is known of growth and nutrient relations of black cottonwood in more northerly sites, such as those in the Prince Rupert region. Balsam poplar is of some interest. Although less widespread than aspen, it is a potentially fast-growing species that can occur on alluvial or upland sites in the interior of the province. Relationships between growth and mineral nutrition have not been studied. Although balsam poplar is closely related to black cotton-wood, the information available about site classification, productivity, and responses to fertilization for black cottonwood may be of little direct value to those interested in managing balsam poplar, simply because of the differences in their ranges and associated climates and soils. If new hybrids are developed for the Interior that incorporate a balsam poplar parent, it would be useful to have information on nutritional require-ments for the balsam poplar parent as a guide in breeding.

Paper birch is relatively widespread and potentially of considerable value. It can also be a desirable species to grow in areas prone to root rot. Studies outside British Columbia suggest that paper birch can be respon-sive to fertilization on appropriate sites. It would be prudent to undertake fertilization studies on appropriate sites as part of refining silvicultural practices for birch.

Bigleaf maple is relatively restricted geographically and is of less overall economic importance than are the more widespread black cotton-wood or red alder. However, maple seedlings are increasingly being planted. The relationships between growth after planting and site quality are not well understood and it is unknown how growth varies with tissue elemental concentrations. Research should be initiated to define these relationships. As with paper birch, bigleaf maple may be most valuable (from a forest products perspective) as a source of sawn lumber. However, it is unclear how fertilization at different stages of stand development will affect the quality and value of such products (e.g., Cahill and Briggs 1992).

12   CONCLUSIONS

Intelligent management of the native hardwoods of British Columbia, combined with the increased culture of hybrid poplars on appropriate sites, can contribute significantly to future supplies of fibre and to the development of a value-added hardwood forest products industry in the province. Compared with their coniferous associates, the hardwood species may grow faster and have shorter rotations, but their growth rates may also be more sensitive to the availability of moisture and nutri-ents. Despite this, the responses of hardwoods to fertilization in British Columbia are unknown. Understanding the relations between growth and nutrition of hardwood species should provide a better basis for iden-tifying what sites are best suited to being managed as hardwood or mixedwood stands and what silvicultural treatments can best increase growth.

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