Microelement Nutrition of Forest Trees: A Review

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Our present information on microelement nutrition of forest trees is fragmentary and, on the whole, unsatisfactory. The reasons for this are implied by its several origins: (a) From seedlings grown for a few weeks or months in nutrient cultures, generally in chemical and physical environments quite alien to those encountered in nature; (b) From nursery investigations, which also deal with juvenile plants, and usually with nutritional environments and treatment possibilities remote from the field; (c) From preliminary accounts of deficiencies or toxicities in planted trees; (d) From foliar and other analyses of normal or suspect trees — a source rapidly increasing in volume, and in technical and sampling reliability; (e) From the main body of horticultural and agronomic science, which has now established a measure of generalization about microelement relationships; furthermore, it deals with some of the same soils and climates, and occasionally with cultivars of the same genera met with in forestry.

In preparing this review, I have, of necessity, drawn heavily upon recent major summaries of horticultural crop nutrition (22, 29, 32, 113, 125, 137, 143). I am particularly indebted for much subject matter and an organizational framework to the several authors of H. D. Chapman's masterful guide, "Diagnostic Criteria for Plants and Soils" (29). Though forest species are seldom mentioned in it, this work is indispensable for serious students of forest tree nutrition.

From the several sources mentioned above we know something about forest tree nutrition, but very little indeed, in any specific sense, about the nutrition of forests. There are essentially no accounts of overt micronutrient deficiencies from natural forests or, for that matter, from the great areas of moderately disturbed forests still composed of native species growing on intact forest soils. It is instructive to consider why this may be so, as background for evaluating applicability of the information presented later.

Some part of this state of affairs is surely due to difficulties or disinterest in observation and will change as more plant scientists study or even learn to recognize the multiplicity of forest species. A more significant reason, of course, is the efficient and conservative operation of the forest ecosystem. Not only does the system have accumulated reserves in the biomass and soil organic matter, but thorough and often deep exploitation of the soil and external and internal cycling of absorbed nutrients minimize losses and sometimes enrich the surface soil (e.g., 68).

The quantities of micronutrients required by forest stands are small, although not known with any reasonable exactness. The small magnitudes contained in the biomass are suggested by the estimates of Young *et al.* (184). Their values are based on the contents found in entire single sample trees — foliage, branches, stems, and roots — which in size approximate the 8-inch dbh, 50-foot-high standard dimension to which the values below apply (184):

	B	Zn	Cu	Mn
	g/tree (8" dbh; 50' high)†			
Abies balsamea	.9	3.8	1.4	56
Picea rubens	1.0	3.8	1.0	64
Pinus strobus	.6	3.6	.9	12
Tsuga canadensis	1.3	1.0	.7	60
Acer rubrum	1.0	7.5	1.3	
Betula papyrifera	1.1	9.4*	1.6	19
Populus sp.	1.4	6.8*	1.3	12

†As a very rough indication of amounts on an area basis these values may also be read as lbs/acre or kg/ha, for pole stands with basal areas *ca* 150 sq. ft./acre.

*Underestimate; content of some component exceeds maximum range of method (185).

But cycling and conservation cannot ensure even moderate levels of nutrient supply on many soils. As the geneticist and ecologist together would remind us, however, natural ecosystems have the capacity, over time, of selecting species and individuals adapted to a competitive existence within the totality of their environment, including its chemical attributes. The emphasis on textbook examples of deficiencies sometimes overshadows Beeson's (11) caution that "Only a limited number of plant species has so high a requirement for a specific element as to exhibit deficiency symptoms or substandard yields where that element occurs in limited quantities." Sensitivity of a species or individual to moderate deficiency or excess obviously handicaps it in competition with more tolerant neighbors, which thus tend to predominate on particular soils. The shaping influence of soil phosphate supply on Australian vegetation (7, 136) provides a striking example of such nutritional influences, and Winterholder (180) suggests that high levels of available manganese likewise affect species dominance in some landscapes.

Horticulture provides abundant examples of within-species variation in nutrient uptake or requirement (165), with some differences traceable to single gene effects. Moderate differences in sensitivity to macronutrient supplies are beginning to appear in forest species (168) and similar differences in microelement sensitivity doubtless will be discovered. Actually, such differences are well foreshadowed by known variations in other wild populations (24, 78, 85) and by highly interesting evidence from the Michigan workers' demonstrating that provenances of the same species sometimes differ consistently in foliar micronutrient composition. Forty-five seed lots, representing a spectrum from the natural range of Scotch pine, showed differences in foliar B content attributable to provenance as well as soil when planted at three locations (141). Similar studies with ponderosa pine (D. P. White, pers. comm., 1967) show consistently higher foliar concentrations of B and Zn in West Coast origins as compared with those from the interior region. Such results not only demonstrate genetic differences in accumulation but suggest additional cautions in interpreting foliar analyses from plantation studies.

Thus there is good reason to suppose that the vegetation native to a soil area of some size must consist of species and genotypes fitted to the prevailing chemical environment. Several investigators have inferred mechanisms to obtain and efficiently utilize the nutrients in limited supply (125, 136, 165), or to exclude or minimize injury from those in excess (44, 52, 78, 180). Though such adaptations may have little bearing on the responsiveness or usefulness of the species in an economic forest, they strongly influence the appearance presented by indigenous vegetation, and hence the inferences drawn from this.

In decided contrast are young forest plantations and, to some extent, the volunteer stands of open lands. The planted trees are often exotics, but even when native they may not be truly indigenous genotypes. Their selection or occurrence is determined by factors apart from specific adaptability, and in many instances the chemical properties of open land are quite unlike those of the parent stands. The number of individuals or species is much too small for competitive selection, except in occasional dense sowings or old field stands. Death or retardation of spaced trees is conspicuous and invites attention. In such matters young plantations have much in common with orchard crops, and it is here that horticultural experience with micronutrient deficiencies proves most applicable.

In any case, assessment of micronutrient status of trees by visual symptoms, tissue analyses, or soil analyses involves a host of considerations and precautions — botanical, sampling, and analytical — which are now well set forth in the literature (21, 32, 58, 113, 134, 135). To violate these canons and cautions in future investigations would be foolish but, equally, we must admit, to delete all works now in violation would be disastrous to the present review.

Boron

At present writing boron (B) deficiency seems to be the most common micronutrient deficiency in forest plantations. Its occurrence in orchard species, including walnut, cherry, persimmon, and tung (23, 29) had been well studied before Vail *et al.* (156) reported it in wattle in Kenya and subsequently in pines (157). It is now known in *Grevillea* (132), eucalypts and other plantation species in Kenya, *Grevillea* in southern India (163, and planted pines in northern Rhodesia (123, 156, 157), New Zealand (147, 177), Australia (112), Brazil (158, 159), and presumptively, in Madagascar (J. Velley, pers. comm., 1967). In view of its wide occurrence in orchard and agricultural crops, many additional cases in forest trees may be expected. Thus far, however, the deficiency has not been found in natural forests.

Visual Symptoms of Deficiency and Excess

No specific symptoms mark the early stages. In pines bordering on deficiency, trees with impaired roots, as near ditches or vehicle tracks, may show symptoms sooner or more severely than the remainder.

Bradford's (23) tabulation of the specific symptoms in crop plants embraces the range thus far reported from forest trees. The dominant features are the result of death or impairment of meristematic tissues followed by secondary repair processes. Characteristic kinds of deficiency symptoms are:

Table 1. Specific Symptoms of Boron Deficiency (From field-grown trees except as otherwise indicated).

Acacia mearnsii (A. mollissima)	First symptoms are wilting and bending of apical shoot; this resembles moisture deficiency and is accentuated in bright weather. Small brown patches may be present in healthy phloem. Terminal and lateral growing points wither and brown, leaves drop. Discoloration in phloem and cambium spreads upward from lateral branch axils, and to root collar and roots. Whole tree may die, or remaining foliage is chlorotic with purplish cast. Lumps of discolored tissue on stem. Recovery from lower stem or root collar may occur in rainy season. Most severe in two-year trees (ca. 8-10′) (Vail et al., 156; Elmer and Gosnell, 46).
Betula verrucosa	In water culture: Growth of leaves at shoot apices inhibited; these and larger leaves appear blistered because of uneven mesophyll growth. Leaves dark green but few large chlorotic and necrotic spots on older. Root meristems injured, resulting in very short laterals (Ingestad and Jacobson, 75).
Eucalyptus spp.	First symptoms are crinkling and discoloration of unfolding leaves of apical buds; this extends to other upper buds. Unopened buds become brittle and dry. Mature leaves discolor, fall. Bark of mainstem becomes dark brown and necrotic, beginning at buds and working down. Progress halted by onset of rains. Diminishes as plants get older. Symptoms in all species similar except in severity. Also in Tectona, Aerocarpus, and Melia azedarach (Savory, 123).
Grevillea robusta	Five-month seedlings in water culture: First leaves normal, youngest leaves distorted with broad lamina on either side of midrib, pinnae very small and pinna segments not developed. Height and leaf weight significantly reduced (Moore and Keraitis, 101). Abnormal growth and dieback (Venkataramani, 163). Tips of terminal and uppermost laterals dieback, lower laterals healthy; the more seriously affected almost completely defoliated, usually also with bark cracking and gum exudation. Abundant sprouting from lower stems. No symptoms on adjacent tea bushes (A. N. Smith, 132).
Juglans regia	Dark brown spots between leaf veins; shoot tips die back, leaving leafless branches. Poor fruiting and premature nut drop (Chapman, 29).
Liquidambar styraciflua	In water culture: Seedlings stunted. Terminal buds died. Terminal leaves crowded, recurved, chlorotic. Roots dark, well developed, with swollen ends (Hacskaylo, 61).
Populus deltoides	Cuttings, 11 weeks in nutrient cultures: Plants dwarfed. Leaves closely spaced, dark green and normal except at shoot apex where underdeveloped (Hacskaylo and Vimmerstedt, 64).
Pinus radiata	Trees 1-30′: "Shoot dieback"—leading shoots die back during period of rapid elongation, while needles small, and often curl into J or U shape on drying. Needles of transition zone below fewer, shorter, with yellow green tip. White resin patches common. Pith of transition zone often has conspicuous brown spots. Intergrades to "tip dieback"—shoot tip, or only buds die; needles brown; needles below are shorter and closer with yellow tips. Resin flow common. Sometimes only terminal bud or upper part of it dies. Abundant new shoots from lateral or fascicle buds cause greater crown density or extreme bushiness. P. pinaster similar (Stone and Will, 147).

Table 1. Specific Symptoms of Boron Deficiency (From field-grown trees except as otherwise indicated) (Continued).

Pinus radiata	End of first or second season: Terminal dies back 3-12"; shoot may bend; some resin flow. Recovery by laterals or fascicle shoots. Repeated dieback makes bush with brown tips. All gradations to healthy plants. In some of fastest growing trees, 20-30', top dies back from few inches to several feet. P. patula similar (Proctor, 111).
Pinus caribaea Pinus elliottii Pinus roxburghii	Young trees, latter part of dry season: Terminal and sometimes lateral buds die. Surrounding needles short, may be bronzed. Resin flow from buds or needles.
Pinus patula Pinus leiophylla Pinus douglasiana	Terminal bud merely fails to shoot; later dies or may develop normally up to two years late (Savory, 123).
Pinus elliottii Pinus caribaea hondurensis	Two types of symptoms, dieback as above; crooked shoots as below.
Pinus patula Pinus khasya	No dieback; vigorous foliage; terminal shoots extremely wavy or crooked (Van Goor, 159).
Robinia pseudoacacia	In water culture: Seedlings stunted, terminal buds died. Terminal leaves recurved, chlorotic. Roots dark, well developed, with swollen ends; nodules small and abortive (Hacskaylo, 61).
Thuja plicata	In water and sand culture: Terminal shoot growth restricted, causing needles to bunch and approach a "rosette." Stems weak so tops bend. Younger foliage becoming bronzed. Roots short with ends of laterals somewhat bulbous (Walker et al., 167).

1. Death of apical shoots, or "rosetting" caused by progressive reduction in internodal (i.e., leaf-to-leaf) spacing and leaf size. Dieback of current year terminal shoots may be either more or less abrupt, preceded by wilting, or after some degree of reduced growth and abnormal foliage.

In pines, shoot, shoot tip, or bud dieback is general. Variation in detail seems due to time of onset or relative severity as well as to species. With exotic pines in Brazil, however, van Goor (159) has reported extreme crooking of leading shoots without any evidence of dieback.

2. Angiosperm leaves are dwarfed, discolored, or variously distorted by thickening, "blistering" or curling, especially in affected terminals. Interveinal chlorosis or browning occurs in some species. Shortened pine needles adjacent to dieback portions show characteristic dull yellow apical discoloration.

3. Petioles and stems show cracking, and necrotic or watersoaked spots, with corking, gum deposits or resin flow. In wattle, brown spots develop in the inner bark and eventually the entire cambial surface browns (46, 156). In pine, a conspicuous brown spotting in the pith below the dieback portion is presumptive evidence of B deficiency, although not always present (147).

In angiosperms, excess B is first concentrated in the leaf margins and apices, leading to marginal yellowing and burning (45, 106, 129). Chlorosis, followed by necrosis, progresses inward between the veins. Usually older leaves are first affected and may be shed prematurely. In lightly affected pines the needle tips become brown, with darker bands marking the successive boundaries between dead and live tissues (146). With greater excess a yellow transition zone intervenes, and severely affected trees show a gaudy contrast of basal green to yellow or bright brown before the needles die entirely and fall (147).

Plant species differ markedly in tolerance to excess (45).

Tissue Analyses

The usual range of B concentrations in mature first-year tissue of conifers and broadleaves alike is 15-100 ppm (Table 2), although higher levels

Table 2. Reported Foliar Boron Concentrations In Tree Species. (Except as otherwise indicated, all values refer to mature, green, first season foliage of large trees *in field conditions*, though *leaf age* and position are sometimes unknown. All values in tables and text are expressed as ppm of dry material.)

	RANGE IN CONCENTRATION					
Sample Characteristics and Date	**Deficient**	**Low**	**Intermediate**	**High**	**Toxic**	**Ref.**
			B, ppm dry matter			
PINES						
Pinus banksiana; Mar.			31			51
Pinus contorta; upper crown, Nov.		4.3				8
Pinus echinata			7-10			121
Pinus elliottii	4-10		10-28			158
Pinus palustris; planted seedlings		4.4-6.5				147
nursery seedlings			7-12			147
Pinus patula; 4 yr pltn.	8-18		14-53			157
Pinus pinaster	5-6		16			147
Pinus ponderosa; lower branches, open stand, 1 + yr, June			15-135			108
Pinus radiata	3-7		11-13		<2500	147
	8-9		16-61			175
Pinus resinosa; pltn., 1+ yr needles, May-June			22-34		73-105	146
Mar.			21			51
Pinus strobus; pltn., 1+ yr needles, May-June			29-30		83-152	146
upper crown, Nov.-Feb.			18-19			1
Apr.			23			51
Pinus sylvestris; upper crown, Nov.-Feb.			12-21			1
4 yr pltn., means: 45 seedlots x 3 loc.			22-38			141
Pinus taeda; 4 yr pltn.		16	45			157
OTHER CONIFERS						
Abies balsamea; Mar.			22			51
Abies grandis; upper crown, Nov.-Feb.			29			1
Araucaria angustifolia			11-42			158
Larix leptolepis; upper crown, fall			52			1
Larix laricina; July			27			51
Picea abies			13-28			37
12 stands Site 1, upper crown, Nov.-Feb.			14-33			1
Picea glauca			16-30			51
Picea mariana			42			51
upper crown, Oct.			16-40			172
Picea sitchensis; upper crown, Nov.-Feb.			17-28			1
Pseudotsuga menziesii; upper crown, Aug.-Feb.		5	9-16			8
Nov.-Feb.			30-39			1

(Except as otherwise indicated, all values refer to mature, green,

Table 2. Reported Foliar Boron Concentrations In Tree Species. (Except as otherwise indicated, all values refer to mature, green, first season foliage of large trees in field conditions, though leaf age and position are sometimes unknown. All values in tables and text are expressed as ppm of dry material.) (Continued)

	RANGE IN CONCENTRATION					
Sample Characteristics and Date	**Deficient**	**Low**	**Intermediate**	**High**	**Toxic**	**Ref.**
			B, ppm dry matter			
young pltn., fall-winter		4	16			161
Sept.-Apr.			13-40			107
Thuja occidentalis; Mar.			53			51
Thuja plicata; seedlings, nutrient cultures,	10-15		32-104			167
Tsuga canadensis; Mar.			53			51
Tsuga heterophylla; Feb.-Apr.		5	17			8
ANGIOSPERMS						
Aceraceae						
Acer pseudoplatanus; fall			24-82			1
3 crown positions, Sept.			76-86			59
Acer rubrum; Oct			57			51
All leaves, one tree			30			185
Acer saccharum; Oct.			62			51
Corylaceae						
Betula alba; upper crown, fall			29-32			1
Betula nigra; Sept.			100			51
Betula papyrifera; all leaves, one tree			31			185
Aug.			41			118
Betula populifolia; range: 56 sites, older leaves, Aug. 15-26			21-42			35
Betula pumila; July			33			51
Betula verrucosa; 71-day seedlings, water culture	51	82	100		640	75
Carpinus betulus; fall			52-90			1
Ostrya virginiana; Sept.-Oct.			53-59			51
Fagaceae						
Fagus sylvatica; upper crown, fall			38-59			51
Quercus alba; June-Oct.			57-78			51
Quercus rubra (borealis); July-Oct.			55-74			1
Quercus borealis; upper crown, fall			38			51
Quercus velutina; June			19-47			1
Juglandaceae						
Carya ovata; Sept.			110			51
Carya spp.			23-64			118

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	RANGE IN CONCENTRATION					
Sample Characteristics and Date	Deficient	Low	Intermediate	High	Toxic	Ref.
			B, ppm dry matter			
Carya illinoensis; orchard, Aug.-Sept.			61-101	145-283	208-870	66
Juglans cinerea; Sept.			79			51
Juglans nigra; Sept.			50			51
June, Sept.			40-67			118
Juglans regia; orchard	9-25		16-378		360-1088	23
Leguminosae						
Acacia mollissima	7	11	20			157
Robinia pseudoacacia; fall			32-54			1
June-Oct.			32-77			118
Oleaceae						
Fraxinus americana; Oct.			38			51
Fraxinus excelsa; fall			27-34			1
Fraxinus pennsylvanica; Sept.			59			118
Proteaceae						
Grevillea robusta	13	17				132
Rosaceae						
Prunus serotina; June-Sept.			32-34			51
fall			28			1
Salicaceae						
Populus deltoides; Sept.			70-99			51
cuttings, nutrient culture	9		68			64
Populus grandidentata; Oct.			57			51
Aug.-Sept.			31-45			34
Populus tremula; fall			82	204		1
Salix nigra; Oct.			36			51
Tiliaceae						
Tilia americana; Oct.			79			51
Tilia cordata; Sept.			63			1
Ulmaceae						
Ulmus americana; Oct.			98			51
park; mid-Sept.			80-140			96

are common in park or orchard trees. Changes in concentration after the leaves or needles reach full size appear relatively small (1, 35, 118) in normal untreated trees, although accumulation may continue when soil supplies are high (106).

Foliar concentrations associated with deficiency symptoms are variable, though commonly less than 10-15 ppm. Although analyses of B-deficient plants usually show lower content than nearby healthy plants, content of deficient plants is sometimes higher. This lack of correlation is in part a sampling artifact. In many species, B already in the leaves is immobile, and interruption of the external supply soon affects meristems or developing tissues, regardless of content in adjacent leaves (45, 98). Normally, however, it is these nearby leaves that are sampled for diagnosis after dieback, and often they are compared with morphologically younger tissue of less affected plants. Contents as low as 5 to 9 ppm occur in the leaves of some conifers without overt symptoms, though it is possible that growth is reduced.

The great immobility of foliar B in some species has been demonstrated by transferring plants from high to zero B solutions; typical apical deficiency symptoms soon occur, although average B content of the foliage is high. Similar effects negate the applicability of most solution culture results (cf *Betula verrucosa* and *Juglans regia* in Table 2).

Excessive boron is concentrated in the chlorotic and dead portions of the leaf, often exceeding 1000 ppm. It is possible that the dead tissue serves as a "sink" inasmuch as greater than lethal concentrations occur there (106). Thus, content of the entire leaf or needle varies according to the proportion of affected tissue, and composite samples of foliage from lightly affected branches sometimes contain less B than the unaffected. Slight apical damage to foliage of slow-growing white pine has been found at gross concentrations of only 40 to 60 ppm (146). In rubber growing on soils naturally high in B the necrotic margins of the leaves contained about 250 ppm *vs.* 90-110 in the green portion (129).

Oertli and Kohl (106) found no major difference among species in sensitivity of leaf tissue to B concentration, and suggest that tolerant species simply accumulate at a slower rate.

Soil Criteria of Deficiency or Excess

Boron content of soils is affected by geological origin and degree of weathering. Beeson's (11) map shows that areas of known B deficiency in the U. S. are concentrated in the eastern third and portions of the Northwest. According to Bradford's (23) summary deficiency is most common on:

1. Soils from acid igneous rocks and from fresh water sediments.
2. Acid soils from which the original content has been removed by leaching.
3. Sands low in silts, clays or micas.
4. Acid peats and mucks.
5. Soils with free lime, including some acid soils after heavy liming.

All reported instances of deficiency in forest plantings concern sands or highly weathered soils.

Sea water contains 4 to 5 ppm B and in New Zealand it has been shown that open coasts are bordered by a narrow zone in which B uptake by grass is notably higher than inland.

Low organic matter content, which may result from erosion or prior cultivation, increases the likelihood of deficiency. Competition with grass, however, increased severity of deficiency in wattle, as compared with clean cultivation. In Tanganyika the deficiency in planted pine was slight or absent in valley positions but severe on upper slopes and ridges (111); similar physiographic effects have been noted in New Zealand (147).

The occurrence or intensity of deficiency is frequently, but not invariably, linked to drought or dry season. Thus over a 14-year period, dieback of young wattle in Kenya was correlated ($r = -.76$) with total rainfall during the four driest consecutive months of the growing season (46). Years of high and low seasonal rainfall were sometimes associated in consecutive "runs" of 3 or more, during which dieback might be less than 5 or more than 50%. Similarly, deficiency symptoms in sapling *Pinus elliottii* in Brazil intensified during the pronounced dry season (158, 159).

In Kenya wattle may suffer severely in its second year, but is free of deficiency after the fourth (46); spontaneous recovery after stunting has also occurred with *Pinus radiata* (111). Such instances suggest the effect of gradual root extension in deep, friable soils.

Though specific effects with forest trees are not known, studies with other species indicate that high internal concentrations of K, N, or Ca increase B requirements, whereas plants with low P also require higher B levels (23). Van Goor (159) considered that occurrence of a crooking syndrome, rather than dieback, of pines in Brazil was associated with higher N content and low temperature of the uplands.

Soil management influences in nurseries and seed orchards include land leveling, erosion, heavy fertilization and liming — which may be heavy enough to reduce uptake. Organic matter, manures and mulches add appreciable amounts. Though some arid zone irrigation waters contain substantial amounts of B (127), irrigation more often acts to reduce availability through leaching or residual alkalinity.

Toxic levels of B are known in arid zone soils and waters (127), volcanic hot springs, fresh marine sediments (23) and, in one instance, in a weathering granite (129). *Hevea braziliensis* (rubber) on this granite, and likewise on recent alluvial clay soils, showed marginal leaf scorch and premature abscission that were attributed to other causes but eventually traced to excess native B (129). Instances of toxicity in forest trees, however, are more likely to result from applications of borax as a soil sterilizant, fire retardant, wood preservative, herbicide, or as fertilizer on resistant crops. Unwitting use of fertilizers containing B supplements, intended for alfalfa or beets, has injured coniferous nursery stock on acid sandy soils. Orchard pecan trees 20 to 40 years old showed leaf injury when excess applications were made 26 to 36 feet away from the trunk (66).

Soil Analyses and Control of Deficiency

The most widely used procedure is extraction by refluxing or boiling with water. Threshold values for deficiency by this procedure commonly range between 0.15 to 0.5 ppm, varying with soil and crop (23). Wilde and Iyer (174) set a minimum level of 1.3 kg/ha water-soluble B (0.6 ppm) for *Pinus resinosa,* based on the lowest amounts actually found in six rapidly growing plantations.

"Biological assay" with a standardized sunflower test in pot cultures has also provided a reliable index (36).

Foliar sprays have a prompt effect and are useful for diagnosis or on small plants. Concentrations of 1-2% borax or boric acid are recommended for fruit trees; 0.25% borax (8 kg borax/ha) was effective on radiata pine (111).

Soil applications are likely to be easier and of longer effect (23). The principal materials are borax (sodium borate, 11.3% B); fertilizer borate (14.6% B) and "Solubor" (20.5% B). A borosilicate glass frit has also been advocated for continuous, slow availability. Rates recommended for most orchard crops are ¼ to 1 lb. per tree, depending on size, but up to 3 to 5 lbs. on large walnut trees. Applications less than 28 g per tree were wholly ineffective on young *Pinus radiata* on weathered volcanic ash (111), whereas this amount was fatal to some *P. patula.* A fraction of a gram in the planting hole has killed radiata pine seedlings in New Zealand.

The amounts required for effect in broadcast applications are in the range of 10 to 100 lbs. borax/acre; the lowest amount may be sufficient and the higher toxic (146) in acid sandy soils, whereas larger amounts are needed as clay content or reaction increases.

Consequences for Forestry

Grasses and other monocots grow well at lower tissue concentrations of B than dicots (19, 23) and probably most conifers also. Hence grass has a further advantage in competing with tree seedlings on deficient soils. Acute deficiency in planted seedlings delays height growth and reduces or negates the value of site preparation. Apart from outright death or stunting, dieback or wavy shoots deform the lower stem and increase branch coarseness. Suspected B, or B plus P, deficiency in large pole-size radiata pine has been associated with dieback of more than the current season's growth (111, 177).

It is reasonable to suppose that sub-acute boron deficiency affects root development and cambial growth in addition to the visible dieback effects. Pines without overt symptoms but within a deficient area increased height growth after boron application (147, 157). Death or delayed development of the terminal bud (123, 147) causes acute angle forks as well as affecting growth.

Boron deficiency causes reduced fruitfulness and fruit malformation in orchard crops; similar effects have been noted in *P. radiata* (147).

Boron application has been credited with reduced susceptibility to leaf rust and mildew in a few crop plants (cf. 143). Conifer seedlings sprayed with B are said to show greater resistance to frost (13, 77) but trials with *Eucalyptus cinerea* showed no certain effect (5). In the latter instance, however, the foliage was sprayed in July, some months before exposure to cold.

The cited instances of spontaneous recovery (46, 111) and the likehood that deficiency may fluctuate with "runs" of wet and dry years are too few for generalization but together suggest that B deficiency may be a highly variable or intermittent feature in young plantations on soils with marginal B supplies.

Differences in susceptibility between related species are likely. Savory (123) found young *Pinus khasya (insularis)* and *P. merkusii* unaffected. Van Goor (159) likewise noted that deficiency was less severe in *P. khasya* and *P. patula* and that these two tended to have higher foliar B concentrations than the associated pines.

Copper

Copper (Cu) deficiency in field-grown forest trees is known from only a few and mostly recent reports.

In 1940 Rademacher (*In* 126) reported that conifers planted on the sandy heath lands of northern Germany suffered from Cu deficiency whereas the native birch did not. Subsequent accounts relate to nurseries (15-17), peats (67), or humic sands (79, 99, 100, 107, 161), usually fertilized. Nevertheless, the deficiency is common in crop and orchard plants on leached sands, on calcareous soils, and on many cultivated peats and mucks. Though deficiency symptoms in poplar and willow (15, 16, 99, 100) agree with those described in orchard crops, symptoms in Douglas-fir and spruce (17, 107, 161) are less recognizable and suggest that other instances of deficiency in conifers may have gone unremarked or unidentified.

Visual Symptoms of Deficiency and Excess

In many crop plants the initial stages of Cu deficiency are not necessarily revealed by clearly marked symptoms, even though growth may respond to Cu additions (114). Symptoms of Cu deficiency are less specific than with other micronutrients. In general, woody species show marked disturbance of the terminal and leading lateral shoots, often followed by defoliation and/or dieback. In some species the foliage in the initial stages is unusually dark green or bluish green. "Bowing" or "cupping" and stunting of the upper leaves are common, and various degrees of marginal scorch or necrosis, marginal irregularity, and interveinal chlorosis occur. A rapid gradation, from unaffected foliage through leaves with increasingly severe symptoms to dwarfed terminal leaves, is common. The terminal internodes shorten abruptly and a rosette of small leaves may form, but premature abscission or withering and death of the terminal shoot seem more common. In some species or with less severe deficiency, the new shoots are soft and may curve in an S-shape. Numerous lateral buds or shoots resume growth from below and are similarily affected in the same or subsequent years; a stunted or bushy appearance often results. Roughened bark and excresences of the twigs are symptoms in some fruits and earlier led to the descriptive term "exanthema" (31, 114).

As Table 3 indicates, symptoms on poplar and willow agree with this general account. The few descriptions of conifers suggest that shoot curvature, growth retardation and overwinter death of tips may be the most significant evidences of moderate deficiency in larger plants (114).

Copper excess commonly induces foliage symptoms resembling or identical with those of iron (Fe) deficiency. In at least some instances the concentration of Fe in the foliage is actually reduced. Iron in needles and stems of loblolly pine seedlings was reduced from 137 and 169 ppm in the controls to 98 and 109 ppm, respectively, when Cu was added to pot cultures of soil at the rate of 14 pp2m (115). Roots are stunted and dark colored in cultures receiving excess Cu, and growth is markedly reduced.

Occurrences of excess in forest trees are few but Cannon (28) pictured a red or mountain maple leaf with typical Fe chlorosis which marked a Cu-rich outcrop in Vermont. Likewise, Dykeman and DeSousa (44) observed pale green or yellow mottled foliage, suggestive of Fe chlorosis, in seedlings of black spruce, balsam fir and tamarack that were unsuccessfully invading a sandy barren containing 3500-6700 ppm Cu.

Tissue Analyses

The Cu content of small twigs, branch bark and stem bark frequently equals or exceeds that of mature foliage (116, 117, 185) although the data are too few to establish consistency or indicate the value of other tissues for diagnosis.

In the few species examined, Cu concentration is highest in developing leaves, but changes are slight in the months after full size is reached (1). Second year and older conifer needles may contain about the same or often progressively lower concentrations than younger foliage (1, 8, 37). The results of Guha and Mitchell (59) suggest that heavier leaves from the upper part of hardwood crowns may contain somewhat lower concentration but about the same absolute amount as the lower leaves. The extent of variability in gray birch foliage collected in mid-August and again from the same trees five to six weeks later is illustrated below (N = 6; each sample a composite taken from upper first year shoots of 10 trees (35):

	Date of sample	
	August 15-26	September 29-30
	ppm Cu	
Older leaves, from proximal half of shoot	7.2	6.0
Young leaves, from distal half of shoot	8.4	6.2

These several indications probably do not apply to plants on high Cu soils. Otherwise, it appears that the tolerance in sampling for foliar diagnosis may be somewhat greater than with other micronutrients. On the other hand, the low absolute concentrations and small differences between adequacy and deficiency place a high value on analytical accuracy and precision.

Table 3. Specific Symptoms of Copper Deficiency.
(From field-grown trees except as otherwise indicated)

Pinus contorta	First year seedlings in nursery: Slight indications of needle tip-burn as in Picea sitchensis (Benzian, 16).
Pinus strobus Pinus sylvestris	Nutrient cultures: Seedlings exposed to complete solution before transfer to —Cu solutions: No effect on height and diameter; fascicled needles long and wavy; primary needles with light yellow tips (Hacskaylo, 61, 62).
Picea sitchensis Also Tsuga heterophylla	First year seedlings in nursery: Needle tip-burn — Tips of upper needles shrivel during hot, dry weather; turn straw color, with sharp demarkation from healthy portion. Often a spiral twist to upper needles. If dry weather persists plants do not recover and growing point dies; if soil becomes moist most of newly emerged needles are free of injury (Benzian and Warren, 17).
Pseudotsuga menziesii Also Picea excelsa Also Picea sitchensis	Plantations: Shoot growth lax, weak, drooping, resulting in very crooked stems, recurved branches, and "pendula" form of larger trees. Needles at first full size, green, complete. Later in the season needles at top of shoot may become discolored and fall over winter. The terminal bud may also die (Van Goor and Henkens, 161; Oldencamp and Smilde, 107).
Populus deltoides	Cuttings in nutrient solution: Leaves near top of shoot gradually become smaller with gray-green mottled appearance; internodes shorten. Numerous slender secondary branches from lower axils, in contrast to non-deficient plants (Hacskaylo and Vimmerstedt, 64).
Populus robusta hybrids Populus maximowwiczii Berolinensis Populus trichocharpa x nigra Populus "canadense commune"	Nursery: Blackening of upper leaf tips, developing into general marginal scorch of younger leaves. Edges become taut, brittle, and irregular, forcing leaf into cup-like shape; marked interveinal chlorosis appears soon after blackening. The youngest leaves drop off severely affected plants, leaving shoot and branches bare (Benzian, 15).
Populus hybrid, "Gelrica"	Young plantation and pot cultures: Chlorotic spots and distinct cupping, often with marginal scorch. Elongation of upper shoots slows; younger leaves small and distorted; and dieback frequent. New shoots arise from axillary buds below, but may not harden enough to survive winter (van der Meiden, 99).
Robinia pseudoacacia Liquidambar styraciflua	Nutrient cultures: Plants exposed to complete solution before transfer to —Cu solutions: Dry weight reduced. No symptoms on upper shoot; lower leaves developed yellow-brown patches. Root nodules on locust sparse (Hacskaylo, 61).
Salix alba, "Liempde"	Young plantation: Beginning in July of first season, upper leaves develop necrotic tips and may lose pubescence. Retarded shoot elongation with production of small irregular leaves, and death of apical meristems. Twigs die back and are replaced by laterals which subsequently show same symptoms. A low shrubby plant results (van der Meiden, 100).

Reuther and Labanauskas (114) suggest that Cu concentration in a variety of horticultural plants normally ranges between 5 and 20 ppm, with deficiency characterized by levels less than 4 ppm. Table 4 indicates that this range is generally applicable to trees except that the threshold for visible evidence of deficiency seems to lie below 4 ppm for some species. Such inference is subject to the caution on sample treatment and analytical procedures mentioned at the beginning. Furthermore, the Dutch results (100, 161) suggest that growth response over a critical range is more significant than any single threshold value.

On the other hand, there are few values above

Table 4. Reported Copper Concentration in Tree Species. (See note in Table 2 for explanation.)

Table 4. Reported Copper Concentration in Tree Species. (See note in Table 2 for explanation.)

Sample Characteristics and Date	RANGE IN CONCENTRATION					Ref.
	Deficient	Low	Intermediate	High	Toxic	
			Cu, ppm dry matter			
PINES						
Pinus banksiana; Mar.			4.6			51
Pinus contorta; upper crown, 40-yr trees, Nov.		2.7				8
Pinus echinata			3.5			121
Pinus nigra (laricio)		2.7	5.1			175
Pinus palustris; natural seedlings, Aug.-Oct.			28-33			41
Pinus patula; 4 yr pltn			8-9			157
		2.8				175
Pinus ponderosa; lowest brs, open trees, 1-yr + needles, June		2.5	7.9			108
Pinus radiata		2.9-3.7	3.8-9.0			175
Pinus resinosa; Mar.			4.9			51
Pinus strobus; upper crown, Nov.-Feb.			5.1-7.9			1
Mar.			6.4			51
all foliage, 1 tree			5.3			185
Pinus sylvestris; upper crown, Nov.-Feb.			4.6-7.9			1
4-yr pltn, upper crown, Nov.-Dec., mean 45 seedlots x 3 loc.			7.5-9.5			139
young pltn			4.1			25
		2.6	12.			173
Pinus taeda; 4-yr pltn			5-22			157
OTHER CONIFERS						
Abies balsamea			4.9			116
all foliage, one tree			7.5			185
fine twigs, one tree			8.8			185
twigs and needles			40.	200-1120		44
Mar.			4.2			51
Abies grandis; upper crown, Nov.-Feb.			5.0			1
Abies pectinata; upper crown, Nov.-Feb.			5.5-9.5			1
Larix decidua; May			5.1			154
Larix laricina; July			5.8			51
			8.6			116
small twigs and needles			4.2	10.5-726		44
Larix leptolepis; upper crown, Nov.-Feb.			6.4			1
Picea glauca; Mar.			4.0-4.7			51
Picea mariana; twigs and needles		1		310		44
Mar.			3.6			51
upper crown, Oct.		0.8	5.0			172
Picea rubens; all foliage from one tree			7.0			185

Table 4. Reported Copper Concentration in Tree Species. (See note in Table 2 for explanation.) (Continued)

Sample Characteristics and Date	RANGE IN CONCENTRATION					Ref.
	Deficient	Low	Intermediate	High	Toxic	
			Cu, ppm dry matter			
Picea sitchensis; first-yr seedlings (tops)	2.3-2.8		7.0-10.8			16, 17
upper crown, Nov.-Feb.			4.5-6.6			1
Pseudotsuga menziesii; upper crown, Aug.-Feb.		2.9	4.9			8
upper crown, Nov.-Feb.			5.6-7.7			1
5-yr pltn, fall	2.4-3.9		4.2-5.9			107
3-yr pltn, fall, <5% crooked shoots			>5.1			161
3-yr pltn, fall, 5-16% crooked shoots	3.4-5.1					161
Thuja occidentalis; Mar.		2.8				51
Tsuga canadensis; Mar.			4.2			51
all foliage, 1 tree			4.5			185
Tsuga heterophylla, 60-140 yrs, upper crown, Feb.-Apr.			3.9-4.1			8
ANGIOSPERMS						
Aceraceae						
Acer pseudoplatanus; fall			6.5-8.1			1
3 crown positions, Sept.			5.7-7.6			51
Acer rubrum; Oct.			3.6			51
all foliage, one tree			9.0			185
Acer saccharum; Oct.			9.8			51
Sept.			12.			97
Anacardiaceae						
Corynocarpus laevigata			10.2			110
Corylaceae						
Alnus sp.			14.0			1
Alnus glutinosa			16.			155
Alnus rugosa; July			10.2			51
Betula sp., twigs and leaves				330		44
fall			8.6-9.2			1
Betula lutea			11.8			117
Betula nigra; Sept.			7.6			51
Betula papyrifera; all foliage, one tree			6.8			185
Betula pendula; May		2.3				154
Betula populifolia; distal-proximal leaves, Aug.-Sept.		2	3.5-12	18		35
Betula pumila; July			4.8			51

Table 4. Reported Copper Concentration in Tree Species. (See note in Table 2 for explanation.) (Continued)

Table 4. Reported Copper Concentration in Tree Species. (See note in Table 2 for explanation.) (Continued)

	RANGE IN CONCENTRATION					
Sample Characteristics and Date	**Deficient**	**Low**	**Intermediate**	**High**	**Toxic**	**Ref.**
			Cu, ppm dry matter			
Euphorbiaceae						
Aleurites fordii	2.3-3.4		4.0-12.4			39
Fagaceae						
Fagus sylvatica; upper crown, Oct.			5.2-10.5			1
3 crown positions, Oct.			3.3-4.2			1
			5.4	119		87
Quercus alba; June, Oct.			7.7-5.5			51
Quercus rubra (borealis); July, Oct.			5.1-3.1			51
Quercus borealis; fall			6.9-9.7			1
Quercus ilex and Quercus pyrenaica			26-85			86
Quercus palustris; Sept.			6.			97
Quercus petraea			7.8			155
Quercus robur			9.7			155
Quercus velutina; June			5.6			51
Sept.			7.			97
Juglandaceae						
Carya illinoensis; orchard			21-28			*In* 29
Carya ovata; Sept.			8.9			51
Juglans nigra; Sept.			10.7			51
Sept.			11.			97
Leguminosae						
Cladrastis lutea; Sept.			12.			97
Robinia pseudoacacia; Sept.			7.			97
fall			8.9-15.9			1
June — ?			4.0, 7.9			154, 155
Magnoliaceae						
Liriodendron tulipifera; Sept.			5			57
Magnolia macrophylla; Sept.			6			57
Magnolia virginiana; means: 5 x 3 sample dates			7.0-11.8			12
Nyssaceae						
Nyssa sylvatica var. biflora; means: 6 soils x 3 sample dates			7.1-12.9			12
Oleaceae						
Fraxinus americana; Oct.			19.2			51

Table 4. Reported Copper Concentration in Tree Species. (See note in Table 2 for explanation.) (Continued)

Sample Characteristics and Date	RANGE IN CONCENTRATION Deficient	 Low	Cu, ppm dry matter Intermediate	 High	 Toxic	Ref.
Fraxinus excelsa; fall			12.4			1
Fraxinus nigra			7.1			117
Fraxinus pennsylvanica			13.2			117
Fraxinus quadrangulata; Sept.			13.			97
Rosaceae						
Prunus serotina; June		2.9				51
Sept.			5.6			51
Sept.			8			97
fall			7.1			1
Salicaceae						
Populus, hybrid, "Gelrica"; pltn.,			7.8			99
pot culture	2.5-3.6	4.1-4.7				99
Populus deltoides; Sept.			5.2-8.8			51
cuttings, nutrient culture	Tr	2.2				64
Populus grandidentata			8.4			51
Populus robusta hybrids; nursery	1.3-1.8	3.1				15, 16
Populus tremula; fall			10.9-16.5			1
Salix alba, "Liempde"; 1 yr	1.4-<		<6.4			100
			7.9			154
Salix fragilis			8.5			155
Salix nigra			5.1			51
Salix purpurea			15.6			155
Tiliaceae						
Tilia americana; Oct.			7.8			51
Sept.			10.			97
Tilia cordata			4.5-6			154, 155
fall			9.9			1
Ulmaceae						
Celtis occidentalis; Sept.			7.5			51
Sept.			6.			97
Ulmus americana; Sept.			7.			97
Oct.			7.6			51
park, Sept.			9-32			96
Ulmus campestris			7.9			155

20 ppm, and Reuther and Labanauskas (114) suggest such concentrations may be "looked upon with suspicion," as indications of excess. Nevertheless, Dykeman and DeSousa (44) report no evidence of toxicity in black spruce, balsam fir, tamarack and the associated birch containing upwards of 200 ppm in the foliage and small twigs. Inasmuch as these are indigenous species occupying a naturally Cu-rich site, however, it is possible that tolerant ecotypes have arisen (24, 78, 85).

Other plant species differ markedly in sensitivity to Cu deficiency and excess, and similar differences will surely be found among forest trees and shrubs. Two angiosperm families, *Caryophyllaceae* and *Labiatae,* contain indicator species restricted to or dominant on soils high in Cu (114). There are also "copper mosses" but the common moss, *Pohlia nutans,* appeared as a dominant ground cover together with lichens on a high Cu bog and barren mentioned above (44).

Soil Criteria of Deficiency or Excess

Kinds of soil most subject to deficiency (114):

1. Leached sands, including those with an acid, organic or peaty surface.
2. Highly weathered soils from rocks low in copper.
3. Calcareous sands and other alkaline soils.
4. Peat and mucks of various botanic origins.
5. Soils enriched in P.

Hibbard's (68) study on zinc (Zn) accumulation in the surface soil beneath forests notes that unreported data show accumulation of Cu also.

Soils to which repeated P applications have been made seem prone to Cu deficiency (114). This group includes "old corral sites" and presumably similar areas enriched through biogenic additions (cf. discussion under Zn) as well as heavily fertilized soils. Moreover, direct effects of P on Cu status are known with crop plants. The Dutch findings with poplar and willow (99, 100), Douglas-fir and spruce (107, 161) demonstrate lower Cu content and stronger expression of deficiency symptoms in the presence of high P in tissue or soil. These effects are exemplified by Benzian's observations of needle tip burn, a symptom of Cu deficiency, on first year Sitka spruce seedlings in the nursery (16):

Phosphorus Added	Seedling Height	Visual Score for "Needle tip-burn"
g/sq. yd.	inches	
3	1.9	0.6
6	2.1	1.6
9	2.1	2.4
12	2.2	2.6

Similarly, Cu deficiency is induced or aggravated by high levels of available N when Cu supplies are low. A combined effect of N and P was found in young poplar (99). Nitrogen, or P at the lowest rate, applied separately reduced foliar Cu concentration but not to the point of deficiency. Application of both reduced foliar concentration further, and symptoms appeared. Van Goor and Henkens (161) attributed Cu deficiency in second generation plantations on Dutch heathlands to improved N nutrition of the second crop. In orchards, ammonium N is known to increase Cu deficiency to a notably greater extent than equivalent applications of nitrate N, and parallel results were observed with seedling Sitka spruce (16).

Copper is firmly complexed or chelated by organic matter and, in contrast to Zn, increased availability does not follow organic additions, green manures, or improved organic matter status. Indeed, Benzian observed that needle tip burn of young Sitka spruce was more severe following rye or rye-grass green manures than after fallow or seed beds, and still more severe after legumes.

Interaction between Cu and molybdenum (Mo), with high levels of either depressing uptake of or response to the other has been suggested by MacKay *et al.* (93) from a study of several crops on fertilized acid sphagnum peat. A somewhat parallel Cu-Fe interaction was observed by Richards (115) with seedling loblolly pine in pot cultures of a sandy lateritic podsolic soil. The main effects of the study included a positive response to N and an adverse effect of liming; neither Cu nor chelated Fe alone significantly improved overall growth, but the combination did.

Although these observations are no more than suggestive, they illustrate that adequate Cu nutrition may depend on factors other than soil supplies.

The extraordinary "copper bog" of New Brunswick has already been mentioned; only a few such rarities are known (44). Ore outcrop areas are more numerous (28) but still uncommon. Copper excess in agricultural soils usually results from long repeated Cu additions as fertilizers or fungicides (114).

Soil Analyses and Control of Deficiency

Reuther and Labanauskas' (114) summary indicates that total Cu content in a number of medium to fine textured soils ranges between 10 and 200 ppm, with the majority between 25 and 60 ppm. In contrast, most very sandy soils contain less than 15 ppm and sometimes less than 3 (131). The distribution of Cu with depth is variable; although the surface content is usually somewhat higher, some subsoils contain significantly more than the top soil.

A variety of extracting solutions including acids, neutral salt solutions, dithiazone and EDTA have been employed as measures of plant-available Cu (114). Removal by normal ammonium acetate, as in the conventional determination of exchangeable bases, is poor. Likewise, only a fraction of what may be regarded as "exchangeable" Cu is replaced by other neutral salt solutions, and Reuther and Labanauskas (114) conclude that 0.1 N HCl is as good or better than other extractants.

A biological assay procedure employing *Aspergillus niger* is also effective and is relatively simple and straightforward in application. Threshold values for crop plants appear at a level of about 2 to 2.5 ppm of fungus-extractable Cu.

Levels of extractable Cu indicative of excess vary with procedure and soil reaction, but appear to begin at 200 pp2m, or somewhat less in acid soils.

The most common Cu fertilizer is the sulfate, and rates of soil and spray applications are usually expressed in terms of the hydrated salt, $CuSO_4 \cdot 5\ H_2O$.

Soil applications are generally effective (114). Recommended rates for crop plants are commonly 5 to 25 lbs./acre on mineral soils and 50 to 200 lbs. on peats and mucks. Since Cu is strongly held in both mineral and organic soils, and only small amounts are absorbed, residual effects persist for many years. Present recommendations limit cumulative applications to perhaps 50 to 100 lbs./A on mineral soils and 250 on organic to avoid toxicity. Rates of 75 and 150 kg/ha have been used without harm to Douglas-fir on an acid sand high in organic matter (107). Copper slag at rates of 500 kg/ha was effective with poplar on a similar soil (99). Variable results were obtained from application of a trace element frit supplying 0.3 g Cu/square yard in a single nursery trial (16); Cu deficiency of Sitka spruce seedlings was unrelieved, whereas growth of poplar cuttings was increased and the symptoms reduced though not eliminated.

Copper sprays have a prompt effect and should prove useful in diagnosis or nursery treatments. Concentrations of .05 to .125% copper sulfate are common, but a 1% spray has been used on dormant Douglas-fir foliage (107). Mixtures based on equal weights of Cu sulfate and Ca hydroxide, or standard Bordeaux mixtures, are less likely to injure sensitive foliage. Copper oxychloride at 0.5% was effective on poplar (99).

Consequences for Forestry

Treatment of soils containing excess Cu includes liming acid soils to a reaction near pH 7 and/or correction of Fe chlorosis by Fe sprays or addition of Fe chelates. Heavy fertilization with P presumably would be effective (114), and addition of Mo as an antagonist has been suggested (93).

As already noted, there are but few known instances of Cu deficiency and response in forest trees, and these are chiefly from combinations of soil and treatment that are not widespread. Nevertheless, infertile sands and peats — on which crop plants are subject to Cu deficiency — are common enough in forestry, and increasing effort is made to accelerate growth on them through fertilization and drainage. Increased dry matter production, or the altered P and N status of soil and plant on such sites, may reduce adequacy of already low native Cu supplies (67, 79, 99, 161, 173). The growth-retarding effect of sub-acute deficiency in crop plants, together with the somewhat obscure disturbances of growth, form, and overwinter survival of shoots of conifers, suggests the need to consider evidences other than gross symptoms.

Concentrations of only 2-3 ppm have been found in several species of conifers without visible evidence of injury (Table 4.) Such values appear distinctly marginal, but it must be admitted that we do not know how well they characterize the Cu nutrition of large conifers.

The discussion of Zn deficiency on sites of biogenic P accumulation also applies in some unknown measure to Cu deficiency.

Copper deficiency is likewise a possibility wherever heavy N and P applications are made to sandy nursery soils (16, 17, 115). This possibility is countered in some nurseries, however, by use of Cu to control algae in irrigation waters, and by application of Cu-bearing fungicides.

Copper excess in natural forests or plantations is more likely to be puzzling than consequential. Inasmuch as Cu intake and Cu-Mo interactions are important in animal nutrition (114), however, unusually high or low contents of range and browse species may be of concern.

IRON

Iron deficiency is the most widespread, conspicuous and best known micronutrient deficiency in forest trees. Nevertheless, it is chiefly a problem of nurseries, shelterbelts, shade trees, poorly sited plantations, or pioneer vegetation on fresh surfaces — wherever unadapted species are placed on alkaline or calcareous soils. Its symptoms sometimes resemble those of manganese (Mn) deficiency and may be confounded by concurrent deficiencies of other elements.

Species within the same genus vary greatly in susceptibiltiy (e.g., Austrian and Ryuku pines *vs.* red and jack; white oak *vs.* pin oak); and even within a planting of a single species variations in severity are often marked. A general relationship of deficiency to high lime soils is evident, but the exact effects of pH, salinity and bicarbonate content are not well understood (151).

Visual Symptoms of Deficiency

Iron deficiency symptoms in angiosperm leaves present a continuous series in severity, wherein the midrib and even the finest veins remain green while the interveinal tissue assumes various shades of lighter green, yellow-green, yellow or even white. The sharply etched network of green veins against a light background is typical of the early to moderately severe stages of the uncomplicated deficiency, and is the usual basis for preliminary diagnosis. Small veins lose their green color only after adjacent intraveinal areas are devoid of chlorophyll. Such wholly chlorotic tissue slowly dies, producing an apical or marginal scorch. In species with marginal venation, however, like eucalypts, necrotic spots and blotches form inside the margin.

Wallihan (170) emphasizes that this apparent progression in symptoms represents production of increasingly more deficient leaves, and is not a time sequence within a single leaf. Green leaves remain green and the usual tendency is for individual leaves to become greener with time. Young leaves, however, may expand faster than Fe is translocated to them and so become more chlorotic; further, bleached out yellow leaves may fail to recover when Fe becomes available.

Iron deficiency may appear in any degree of severity. Characteristically the youngest leaves on a branch are the more severely affected. In open grown trees, individual branches or portions of the crown are often seen to be affected unequally. Lightly affected foliage often recovers in time or becomes less conspicuous. Severely chlorotic leaves drop prematurely, and twigs or entire branches often die back when the occurrence is perennial.

Iron chlorosis is sometimes complicated by concurrent deficiencies of other elements, such as Mn or magnesium (Mg), which modify foliage symptoms. Wallihan (170) points out that uncomplicated Fe deficiency in orchard crops is distinguished by the sharp contrast between the green vein and the less green, or yellow, interveinal tissue immediately adjacent. In the superficially similar chloroses due to Zn or Mn deficiencies, however, there is a gradation of color *within* the interveinal area, with green or darker green occurring near the vein. (Compare Mn deficiency.) Illustrations and descriptions of Fe deficiency in angiosperms are so numerous (3, 31, 32, 61-64, 89, 137) that no table of symptoms is given here.

Moderately severe deficiency in conifers shows as uniformly pale green or yellowish-green new foliage, which contrasts with the darker green or brownish tips of older needles. Very chlorotic needles brown back from the tips, or entirely, and are lost; slightly affected needles or portions gradually become greener. Nevertheless, dull yellow and brown colors mark severely deficient trees for much of the year, in contrast to the green appearance of Mg deficient trees in mid-summer.

Seedling conifers respond to Fe deficiency by a more or less uniform paling or chlorosis of the new foliage. This occurs in all degrees, from perceptibly less green than normal to yellow or near white; dwarfing of needles and plant follows. Variations in intensity within this basic pattern make up most of the descriptions of foliage symptoms reported from nurseries and nutrient cultures (61, 62, 80).

Visual evidences of deficiency are usually easily confirmed by sprays or dips of Fe salts, or by keeping cut twigs for some days in weak iron solutions.

Symptoms of Fe excess are not known in forest trees.

Tissue Analyses

The literature contains a moderately large number of Fe analyses of the foliage of forest species. Unfortunately almost all values are derived from unwashed leaves and hence subject to an unknown degree of soil contamination. This problem was discussed by Bennett (14) and others since (26, 151, 169), but is still commonly unrecognized. Wallihan (170) points out that whereas most micronutrients in plants occur at concentrations approximating or greater than their concentration in soil, the concentration of Fe in dry foliage is usually of the order of 10^{-2} or 10^{-4} times that of the soil in which the plant grows. Hence soil dust is a serious source of contamination with this element and Wallihan, in compiling a table of concentrations critical for deficiency, rejected all data obtained from unwashed leaves.

It may be argued that the atmospheric dust load over forests is much less than over agricultural lands; in fact, however, the majority of literature values represent foliage exposed for several months on trees in or near open land or other sources of dust. Though Guha and Mitchell (58) reported only moderate reduction in apparent Fe concentration upon washing leaves of beech, the generally high values obtained by these (59) and other workers (1, 8, 37, 51, 80, 86, 97, 155) suggest the likelihood of contamination.

Table 5. Some Minimal Values for Foliar Iron Concentration. (Except as indicated, all values represent unwashed leaves from plants having no indication of Fe deficiency. See explanatory note in Table 2.)

	Minimal Values Fe, ppm. dry matter	Ref.
Pinus banksiana; field	73	102
(tops) nutrient cultures, variable Mn	*ca* 50	102
Pinus contorta	58	8
Pinus nigra (laricio)	15-84	175
Pinus palustris	59	41
Pinus patula	22	175
Pinus radiata; (tops), nutrient cultures	40-50	176
field	21-52	175
Pinus sylvestris; nutrient cultures, complete	110	73
" " Fe deficient	40	73
Picea abies; field	*ca* 70	37
Picea *mariana; field*	35-40	102
field, Oct.	12-36	172
nutrient cultures, variable Mn	51	102
Pseudotsuga menziesii; field	39-51	8
Tsuga heterophylla; field	39-59	8
Betula verrucosa; nutrient culture, variable Mn	90	75
Fagus sylvatica; field	84	58
Populus deltoides; nutrient culture, complete	90	64
" " Fe deficient	33	64

Accordingly, Table 5 presents only selected minimum foliar concentrations, chiefly from normal plants. There is no assurance that these results are from leaves wholly free of contamination. They suggest, however, that the critical range for deficiency in orchard crops, indicated as 25 to 40 ppm by Wallihan (170), may well apply to many forest species.

Analyses of unwashed chlorotic leaves have frequently shown concentrations equal to or even greater than those from green leaves nearby. Thus one such comparison in pin oak indicated 450 ppm Fe in chlorotic leaves and 180 ppm in normal foliage (97). Other paired comparisons may show somewhat higher apparent concentrations in green foliage, but differences within pairs are greater than between (e.g., 80). Such results obtained from unwashed foliage have generated various physiological interpretations and hypotheses. In fact, however, the apparent concentrations of chlorotic leaves in such studies are often severalfold greater than the 25 to 40 ppm level suggested above and by Table 5.

Soil Criteria of Deficiency

Kinds of soils most subject to deficiency are:

1. Calcareous soils, either natural or overlimed.
2. Weathered soils high in Mn.
3. Gleyed soils either low in soluble Fe or high in soluble Mn.
4. Leached acid sandy soils from siliceous materials low in Fe-bearing minerals.

Of the above, the first group is by far the most common source of Fe deficiency problems in forest trees, justifying the usual description of "lime chlorosis." It is essential to recognize, however, that the general category of calcareous soils contains diverse root environments. In humid regions calcareous forest soils are usually characterized by acid to neutral surface organic layers, by admixtures of humus particles between fragments or in crevices, or by mineral surfaces high in organic matter. The latter may be acid or calcareous, but on a fine scale they are heterogeneous in reaction and carbon dioxide pressure. Any of these features provides root environments more favorable for Fe availability than do the homogeneous surfaces of alkaline cultivated or grassland soils.

Iron deficiency is often seen to be more severe in dry periods (170). In marginal occurrences symptoms may appear only during droughts; in climates with pronounced contrasts in growing season rainfall, chlorosis may regularly diminish during wet seasons. Such effects have been attributed to availability of Fe in moist surface horizons containing organic matter (81).

Erosion of the surface horizon of calcareous soils removes organic matter and the least limy soil. Susceptible species planted in such situations sometimes respond to small differences in the erosion-deposition pattern by large variations in severity of symptoms. Similarly, other natural differences in soil reaction due, for example, to drainage or limestone outcrops may cause variations in severity.

The Fe chlorosis problem of semi-arid regions is complicated by salinity and reactions above pH 8.3. Neuman and Waisel (105) comment that *Eucalyptus camaldulensis* may be green and healthy until the time that the roots penetrate a layer "of unfavorable ionic composition," after which chlorosis ensues.

Poor drainage, or water logging from excess irrigation usually increases the severity of deficiency symptoms (170). Chlorosis of *Eucalyptus* in Israel was less in poorly drained sites, however, possibly because of higher organic matter (80).

Iron chlorosis of sensitive conifers in forest nurseries has frequently followed increases in soil pH brought about by liming cover crops, application of lime-rich compost (103), irrigation with "hard" water or use of calcareous sand for seedbed covering (16). Heavy P fertilization also has been implicated in Fe chlorosis, even on acid soils. Shoulders and Czabator (130) reported on a chlorosis that affected more than 10 acres of southern pine seedbeds and was completely remedied by three applications of Fe chelates. The soil of the most severely chlorotic areas had a reaction between pH 4.1 and 4.6, with high levels of available K and P, but some portions had received as much as 2¾ tons of 20% superphosphate during the previous 4 years. Subsequent experiments with loblolly pine on less acid, less fertile soils showed little chlorosis after treatment with either 2 tons of lime/acre, which raised the reaction to pH 6.1-6.2, or with a mixed fertilizer containing 240 lbs. P_2O_5/acre. A combined treatment, however, caused a chlorosis affecting 10% of the seedlings.

The action of excess Zn and Cu in inducing Fe deficiency is mentioned in the discussion of those elements. Liming acid soils containing excess amounts of these or other heavy metals reduces their availability and may improve Fe nutrition. Studies with crop plants in calcareous soils show that nutrient balance involving P, Zn, and Fe has a strong influence on growth. Yields decreased as the Fe/Zn ratio fell below 1.5 (171).

Soil Analyses and Control of Deficiency

Since Fe deficiency is rarely due to insufficient Fe in the soil, analyses for the element provide no index of deficiency. A possible exception is an extraction procedure using polyamine polyacetate chelating agents. In limited tests Fe removed was correlated with uptake by plants (*In* 170).

Soil reaction is obviously an indication of soils on which deficiency may occur although, as already mentioned, nursery soils below pH 7 are not immune; severe chlorosis of red pine has occurred at reactions of 6.8-7.1. In other cases, however, susceptible species such as red pine may grow well on gravelly soils that effervesce with acid in the surface. Accordingly, Wallihan (170) and Karschon (80) consider that Drovineau's estimate of "active $CaCO_3$" (measured by the removal of oxalate from an ammonium oxalate solution) may be a better measure of deficiency hazard. Karschon's data with eucalypts in Palestine do not show this measure to have much predictive value.

Three avenues of control have been widely used or advocated in the past: Reduction of soil pH; addition of Fe to the soil; direct addition of Fe to the plant through sprays, injection or trunk implants.

Acidification of soils containing appreciable amounts of free carbonates is seldom feasible except in very small areas. On the other hand, nursery soils rendered alkaline by overliming or irrigation with lime-bearing water can be returned to an acid reaction by addition of S. The theoretical S requirement to lower soil reaction from one pH level to another is one-third the lime requirement for the reverse change, and can be measured or estimated in a similar manner. Aluminum sulfate is prompt in effect but costly; the amount of the anhydrous salt required approximately equals the lime requirement for the reverse change.

Broadcast application of inorganic Fe salts is seldom of large or lasting benefit because the added Fe is soon rendered unavailable. Concentrated addition of Fe sulfate or Fe sulfate solution (1 lb $FeSO_4 \cdot 5\ H_2O$ per gal; minimum treatment ½ gal) in holes or trenches, however, maintains localized zones of availability for large plants. This treatment, as well as deficiency symptoms, is well described by Locke and Eck (89, see also 63). Iron sulfate presumably would be effective in the few instances of deficiency in acid soils. In any case, Fe chelates are highly effective with a variety of plants and soils, and at much lower concentrations, though not necessarily at lower cost, than inorganic salts. Wallihan (170) indicates that the effectiveness of various chelates varies with soil reaction in the following order: Fe EDTA $<$ pH 7; FeHEEDTH; FeDTDA; FeEDDHA in highly calcareous soils.

Foliar sprays were more widely used in the pre-chelate period. The usual rate is ½ or 1% ferrous sulfate in water, with a spreader or wetting agent; concentrations up to 3% have been used on cottonwood and other less sensitive species. Iron sprays were early used on young conifers (84) and are effective on a variety of conifers and broadleaf species, including cottonwood, willow, acacia, and eucalyptus (89, 139, 169). Some species benefit little, however, and in any case the effect is short-lived. Perhaps the greatest use of such spray is for diagnosis or to hasten recovery while soil treatments are taking effect. Iron chelates are also applied as foliage sprays but their chief merit seems to be the somewhat higher concentrations tolerated without injury to foliage (170).

A number of injection and implant treatments have been employed in shade and orchard trees. A generally effective treatment for cottonwood, maple, box elder and some fruit trees is ferric phosphate or citrate, applied as the dry salt in drilled holes 1 to 3 inches deep, spaced 4 to 6 inches apart around the circumference; the holes are subsequently sealed (139). The effect of such treatment persists for some years. This form of treatment was not effective on ponderosa pine, however.

Significance for Forestry

The indicated control measures are valuable for shade trees, windbreaks and nursery beds but only occasionally will be feasible in large-scale forest plantings. Rather, recognition of the hazard and selection of resistant species are required. Such action is relatively straightforward in most forest climates where differences in the lime tolerance of species is well known, but requires greater consideration wherever forest planting is advanced into more arid climates, often with exotic species. Species of pines and eucalypts (80), for example, vary greatly in susceptibility to chlorosis and striking differences within species have been found in some crop plants. These facts suggest that selection or breeding can provide varieties that are less susceptible to this deficiency (26).

It is abundantly evident that most of the iron chlorosis problems (83, 84, 124, 130) in forest nurseries can be avoided through control of soil reaction and fertilization. Automatic equipment for neutralizing the bicarbonate content of irrigation waters is in use in some nurseries. In any case, prompt use of chelates can minimize losses from this hazard.

Iron deficiency usually is considered wholly in terms of the conspicuous chlorosis, but the effect of sub-acute deficiency on growth may deserve attention. In nutrient culture studies seedlings are usually restricted in height or weight before appreciable symptoms appear (61, 73, 183).

MANGANESE

Manganese is a relatively abundant element in the foliage of many temperate zone forest trees. In some the normal range of concentration regularly exceeds levels regarded as toxic in many horticultural species. In conifers, concentration often exceeds that of Mg and can interfere with analytical determination of the latter by chemical procedures.

Reports or even indications of Mn deficiency in trees in forest situations are rare, but the deficiency in shade trees and shelterbelts on calcareous soils and orchards is well known. It is likely that some instances of sub-acute deficiency are overlooked; in general, however, the possibility of Mn toxicity in forests has excited much more attention than deficiency. Few occurrences of toxicity in natural vegetation have been demonstrated, but much is yet to be learned about the accommodation of native species to the high level of available Mn found in many forest soils.

Visual Symptoms of Deficiency

The few descriptions of foliage deficiency symptoms in forest trees (Table 6) agree well with those from orchard crops (88), with the exception of pecan. As Cain and Shear (27) point out, the pattern of chlorosis is often somewhat intermediate between that caused by Mg deficiency and that due to Fe deficiency. With few exceptions, chlorosis begins near the margin (in species not having marginal veins) and develops along the margin and as V-shaped areas extending inward between the major veins. Even when chlorosis is severe, bands of normal green color remain next to the main veins and midrib, and near their junctions. Necrosis is not general but in some species gray or brown necrotic spots appear in the chlorotic areas.

Commonly the symptoms are distinguished from those due to Fe by these features (27): The finest veins do not remain green in chlorotic areas; broad bands of normal green occur next to major veins, even in severely affected leaves; on growing shoots symptoms appear after the leaves are fully expanded and persist unchanged, affecting some or all mature leaves on a tree; terminal leaves commonly are not affected until shoot growth stops. Hence, usually there is no general gradient in severity of symptoms from the basal to near-terminal leaves on a shoot, unlike Mg deficiency, where the most severely affected leaves occur near the base of the current shoot or on spurs. Because the symptoms develop late, leaf size and internode length are not generally reduced unless deficiency is severe. Strongly affected leaves

Table 6. Specific Symptoms of Manganese Deficiency.

Acer platanoides	Nursery: Only older leaves show typical chlorosis; broad green stripes remain along the main veins (Gruppe and Seitz, 56).
Betula verrucosa	71-day seedlings in nutrient culture: Chlorosis in mesophyll, especially in older leaves, followed by necrosis beginning at margins and in spots in the chlorotic areas (Ingestad and Jacobson, 75). 35-year forest trees: Discoloration most marked in older leaves; terminal leaves often remain green. Light green or yellow chlorosis in interveinal areas with larger veins and nearby tissue remaining green; the basal-midrib portion is least affected. Leaf size not reduced unless chlorosis acute (Ingestad, 72).
Grevillea robusta	Seedlings in nutrient cultures: Leaves at first pale, not chlorotic, then brown necrotic areas develop at tips of pinna segments on some leaves (Moore and Keraitis, 101).
Picea excelsa	Natural seedlings, $<$ 1 meter high, understory: New needles slightly chlorotic from outset, becoming pale green during the following winter and dark green by end of second year (Ingestad, 72).
Pinus strobus	Seedlings in nutrient cultures exposed to complete solution before shifting to—Mn solution: Height and weight not affected; fascicled needles with light yellow tip and light yellow-green base (Hacskaylo, 62).
Pinus sylvestris	35-year-old forest trees: No specific symptoms; in late autumn young leaves occasionally are pale green or yellow (Ingestad, 72).
Populus deltoides	Cuttings in nutrient cultures: Deficiency slight; height normal but weight reduced. Leaves lighter green, fine roots sparse (Hacskaylo and Vimmerstedt, 64).
Prunus serotina	Nursery: Very sensitive to deficiency at high soil reaction. Characteristic symptoms begin mostly on lower leaves throughout. Leaf margins and interveinal areas are pale green to yellowish while tissue near the veins and midribs remains as green stripes. Yellowed leaf margins sometimes turn brown (Gruppe and Seitz, 56).
Robinia pseudoacacia Liquidambar styraciflua	Plants in nutrient cultures exposed to complete solution before shifting to—Mn solution: Terminal leaves light yellow, grey spotting between veins. Unfolding terminal buds became yellow and died. (Hacskaylo, 61).

are often shed early, whereas lightly affected foliage, with only pale green or lightly chlorotic margins, persists normally and may escape recognition.

Present description of symptoms in conifers does not allow certain distinction from Fe deficiency. Further, in nutrient cultures symptoms in young conifers, especially spruce, may not be distinct from those caused by Mg deficiency (56). Young spruce growing on a moist calcareous soil had shoots that were chlorotic upon emergence; in older pine the new foliage or only the needle base was pale green to yellowish. In both species the needles became greener in later months (75).

Tissue Analyses

Manganese contents of mature foliage vary enormously in many species, as several writers have noted (1, 37, 60, 90, 173), with wider ranges among locations and greater maxima than occur with other micronutrients. It is clear that species, or even cultivars growing together, may differ in foliar concentration (52, 102), though less is known about differences in other tissues. On the basis of foliar concentration Gerloff *et al.* (52) suggest that some species possess mechanisms for selective absorption or exclusion of this element. Oaks, generally with 300 to 400 ppm, were higher than most of the associated species with which they grew, whereas the genus *Cornus* was materially lower, between 37 and 149 ppm. Other values for the genera agree (155).

In most studies, however, differences among species are confounded with differences due to habitat. The effect of soil on Mn concentration seems well shown by Ahrens' (1) comparison of European beech on two sites; the upper crown leaves were approximately full size at the first sampling:

	Sampling Date		
	May 29-June 1	July 23-25	Oct. 15-18
		% Mn	
"Lime-rich"	.058	.098	.095
"Lime-poor"	.342	.498	.530

Late season concentrations at other locations are .022 (59) and .437% (1), thus indicating nearly a 25-fold range in apparently normal trees.

Similar, though less extreme edaphic effects, free of climatic or genotypic differences are demonstrated by grey birch on two types of anthracite coal spoils in Pennsylvania, collected from the same trees on two dates. (N = 3; each sample a composite taken from upper first year shoots of 10 trees. pH of Type 1 spoils, usually 3.0 to 3.4; of Type 2, 4.3 to 7.0) (35):

Spoil Type and Leaf Position	Date of Sample	
	Aug. 15-26	Sept. 29-30
	% Mn	
Type I		
Older (Proximal)	.103	.150
Younger (Distal)	.089	.158
Type II		
Older (Proximal)	.257	.319
Younger (Distal)	.219	.325

The continued accumulation in late summer and disappearance of leaf position effects are evident. In this instance foliar content is higher on the less acid materials. Still higher concentrations occurred on a third type of lithology intermediate in reaction.

Variation due to site in conifers is abundantly evident from the great range of foliage content within species (Table 7). Steinbeck's (140) examination of five widely separated provenances of Scots pine, each planted at five locations in Michigan, revealed no significant effect of provenance or provenance-location interaction; by contrast, the differences associated with location ranged from 27 to 170% of the mean concentration of Mn.

The foregoing tables also serve to illustrate the change in Mn concentration with season (59), but allow no generalization about existence of a late summer "plateau" in concentration. Similarly, no firm generalization about increases in conifer needles during the second and following years is possible, although most studies show a strong tendency for increase (1, 37, 70, 71, 145).

Variation from year to year within species and site has not been studied though it is reasonable to suppose that large annual variations in available Mn supply must occur on some soils; for example, those subject to prolonged saturation in occasional years. In the pear, Mn accumulated during one episode of soil saturation maintained the foliar content at a high level for at least three years (55). The likelihood of similar effects in forest ecosystems deserves attention.

Occurrence of Deficiency and Excess

The few accounts from forest trees agree well with deficiency levels in orchard species (32). As Table 7 indicates, leaves showing deficiency symptoms seldom contain more than 40 ppm. Values less than 20 seem more usual, but probably represent more extreme deficiency.

Manganese toxicity in forest trees has been often postulated, but seldom demonstrated in nature. In view of the large numbers of species and the great variety of soils on which they grow or are planted, however, it is reasonable to expect more well substantiated instances of toxicity. Labanauskas' (88) suggestion that growth of horticultural species is likely to suffer when foliar concentrations exceed 1000 ppm (0.1%) probably will apply to some susceptible forest species. Yet numerous other species, oaks, beech, birches, and conifers, frequently contain from 1000 to 5000 ppm in the mature foliage (Table 7), with no visible evidence of toxicity. Speculation about differences within or among species seems fruitless until more is known about the forms in which these gross concentrations exist in the leaf.

In horticultural species excess Mn gives rise to a variety of symptoms, among which smaller leaves, severe chlorosis and appearance of yellow or necrotic spots are common (88). In apple a "distinctly purplish tint" was seen in leaves with interveinal chlorosis (18). This coloring may be indicative, for in nutrient cultures of young birch having foliar contents of 1700 ppm Mn, the only symptom, apart from reduced growth, was increased anthocyanin coloring (74).

Small seedlings of silky oak *(Grevillea)* transplanted into a soil high in manganese died within three weeks, apparently too rapidly to display characteristic symptoms. Foliar concentrations from 1900 to 3600 ppm Mn pointed to toxicity (30).

Eucalyptus gummifera (red bloodwood) apparently suffering from Mn toxicity showed "vigorous but unhealthy" growth in pot cultures, with small chlorotic leaves, often distorted in shape. Death of the terminal bud on leader and major laterals was

Table 7. Reported Manganese Concentration in Tree Species. (See Note in Table 2 for explanation.)

	RANGE IN CONCENTRATION					
Sample Characteristics and Date	**Deficient**	**Low**	**Intermediate**	**High**	**Toxic**	**Ref.**
			Mn, ppm dry matter			
PINES						
Pinus banksiana; Mar.			412			51
natural stands, late Aug.			100-220			102
(tops) nutrient cultures, variable Mn		10	35-855		4445	102
Pinus contorta; upper crown 40-yr trees, Nov.			293			8
Pinus echinata			121-977			38
			100-700			121
Pinus elliottii			330-346			38
Pinus palustris;			170-334			38
natural seedlings, Aug.-Oct.			119-346			41
Pinus patula			>200			175
Pinus ponderosa; lowest branches, open-grown trees, 1+yr, June			38-102			108
Pinus radiata; mature			220-460			4
(shoots) nutrient cultures			140-800			176
various soils and locations			42-905			175
Pinus resinosa; Mar.			260			51
20 stands, Oct.-Nov.			200-900			145
Pinus strobus; Mar.			184			51
Nov.-Mar.			266-1536			1
Oct.			950			145
Pinus sylvestris; 9 m. high, Oct.-Nov.		7	78-160			72
4-yr pltn, upper foliage, 3 locality means 45 seedlots, Nov.-Dec.			276,898,1008			141
upper crown, Nov.-Feb.			610-1204			1
3- and 10-yr pltn.			220-2280			104
young pltn.			310-390			25
Pinus taeda			306-392			38
OTHER CONIFERS						
Abies balsamea; Mar.			862			51
all foliage, one tree			1155			185
Abies grandis; upper crown, Nov.-Feb.			2272			1
Abies pectinata; upper crown, Nov.-Feb.			2160-2276			1
seedlings			500-1700			122
Larix decidua; May			655			154
Larix laricina; July			310			51

Table 7. Reported Manganese Concentration in Tree Species. (See Note in Table 2 for explanation.) (Continued)

Sample Characteristics and Date	RANGE IN CONCENTRATION					Ref.
	Deficient	Low	Intermediate	High	Toxic	
			Mn, ppm dry matter			
Larix leptolepis; fall			1591			1
Picea abies; 15-19-yr, upper whorl, Dec.			300-2300			70, 71
33-yr, first and second whorls			270-5210			37
upper crown, Nov.-Feb.			1670-2630			1
1 meter high seedlings, Oct.-Nov.	4-15	20				72
pltn, 4th whorl, Aug.			327-402			95
Picea glauca; Mar.			672-1052			51
Picea mariana; Mar.			634			51
young trees, fall			474-618			49
12 natural stands, late Aug.		170	600-870			102
(shoots) nutrient cultures, variable Mn		27	45-1028			102
Picea rubens; all foliage, one tree			1400			185
Picea sitchensis; upper crown, Nov.-Feb.			1598-2043			1
Pseudotsuga menziesii; 13-49-yr, upper crown, Aug.			452-503			8
Oct.-Feb.			687-758			8
upper crown, Nov.-Feb.			390-1294			1
Thuja occidentalis; Mar.			94			51
Tsuga canadensis; Mar.			419			51
all foliage, one tree			1500			185
Tsuga heterophylla; upper crown, Feb.-Apr.			1583-1876			8
ANGIOSPERMS						
Aceraceae						
Acer platanoides; nursery	40	40				56
Acer pseudoplatanus; fall			310-1887			1
Sept., 3 crown positions			49-63			59
Acer rubrum; Oct.			444			51
all foliage, one tree			765			185
Acer saccharum; Oct.			805			51
Sept.			100			97
Corylaceae						
Alnus sp.; fall			422			1
Alnus glutinosa			208			155
Alnus rugosa; July			152			51
Betula sp.; fall			670-1436			1

Table 7. Reported Manganese Concentration in Tree Species. (See Note in Table 2 for explanation.) (Continued)

Sample Characteristics and Date	RANGE IN CONCENTRATION					Ref.
	Deficient	Low	Intermediate	High	Toxic	
			Mn, ppm dry matter			
Betula nigra; Sept.			73			51
Betula papyrifera; all foliage, one tree			315			184
Betula populifolia; Aug. 15-Sept. 15			594-4900			35
Betula pumila; July			500			51
Betula verrucosa; end Aug., first Sept.	7-17					72
nutrient culture	9-12		41-850		1700	75
Fagaceae						
Fagus sylvatica; upper crown, Oct.			610-5296			1
3 crown positions, Sept.			212-242			59
			11-751			87
Quercus alba; June-Oct.			815-1374			51
Quercus bicolor; Sept.			323			51
Quercus rubra (borealis); July, Oct.			763-1736			51
Quercus borealis; fall			890-4368			1
Quercus ilex and Quercus pyrenaica			33-3970			86
Quercus palustris; Sept.			560			97
Quercus petraea			564			155
Quercus robur			354			155
Quercus velutina; June			1459			51
Oct.			1870			97
Juglandaceae						
Carya ovata; Sept.			266, 727			51,52
Juglans nigra; Sept.			83			51
Sept.			190			97
Juglans regia; orchard	5-6.5		35-65			162
Leguminosae						
Cladrastris lutea; Sept.			70			97
Robinia pseudoacacia; Sept.			50			97
fall			70-261			1
May, June, ?			19,49,58			154,155
Magnoliaceae						
Liriodendron tulipifera; Sept.			90			97
Magnolia virginiana; means 5 soils x 3 sampling dates			86-244			12
Magnolia macrophylla; Sept.			290			97

Table 7. Reported Manganese Concentration in Tree Species. (See Note in Table 2 for explanation.)

Sample Characteristics and Date	RANGE IN CONCENTRATION					Ref.
	Deficient	Low	Intermediate	High	Toxic	
			Mn, ppm dry matter			
PINES						
Pinus banksiana; Mar.			412			51
natural stands, late Aug.			100-220			102
(tops) nutrient cultures, variable Mn		10	35-855		4445	102
Pinus contorta; upper crown 40 yr trees, Nov.			293			8
Pinus echinata			121-977			38
			100-700			121
Pinus elliottii			330-346			38
Pinus palustris;			170-334			38
natural seedlings, Aug.-Oct.			119-346			41
Pinus patula			>200			175
Pinus ponderosa; lowest branches, open-grown trees, 1+yr, June			38-102			108
Pinus radiata; mature			220-460			4
(shoots) nutrient cultures			140-800			176
various soils and locations			42-905			175
Pinus resinosa; Mar.			260			51
20 stands, Oct.-Nov.			200-900			145
Pinus strobus; Mar.			184			51
Nov.-Mar.			266-1536			1
Oct.			950			145
Pinus sylvestris; 9 m. high, Oct.-Nov.		7	78-160			72
4 yr pltn, upper foliage, 3 locality means 45 seedlots, Nov.-Dec.			276,898,1008			141
upper crown, Nov.-Feb.			610-1204			1
3 and 10 yr pltn.			220-2280			104
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Abies pectinata; upper crown, Nov.-Feb.			2160-2276			1
seedlings			500-1700			122
Larix decidua; May			655			154
Larix laricina; July			310			51

common, and followed by abundant shoots from the basal lignotuber. Similar symptoms were observed in the field and clearly associated with foliar concentrations above 1000 ppm. By contrast, *Eucalyptus saligna* (Sydney blue gum) tolerated the same soils and even higher foliar contents (to about 4000 ppm) without apparent injury (180).

Three decades ago, in comparing the foliar composition of green and chlorotic Scots pine, Nemec (104) found generally higher Mn concentrations (above 800 ppm) in the chlorotic foliage. He held that the yellow or yellow-green discoloration was due not only to lack of K and Mg, but especially to high Mn uptake. Madgwick (94) has reported significant inverse correlations between foliar Mn concentration and total height or current leader length of individual trees within small plots on a K deficient soil. The relationship was not consistent among adjacent plots, however, and he indicated a dominant effect of K nutrition, as shown by response to fertilization.

More recently, Duchaufour and Rousseau (43) attributed differential survival of European fir seedlings on various humus types to Mn excess. No symptoms were observed in the field, but potted seedlings grown on mull humus types with higher exchangeable Mn contents died sooner when water was withheld than those on a moder. Foliage of the dying seedlings on the mull type contained more Mn (1300 to 2500 ppm vs. 500 to 120, respectively) and the roots were blackened, resembling the appearance produced in high Mn nutrient cultures (122). As Table 7 indicates, however, these concentrations are within the range found in the mature foliage of *Abies*. Results from the nutrient cultures are somewhat equivocal; mortality at 53 days after germination clearly increased with Mn concentrations of 5.5 ppm or above in the nutrient solutions, reaching 90 to 100% at 110 ppm.

In contrast to these findings are Morrison and Armson's (102) results from a similar study with black spruce and jack pine seedlings in nutrient cultures containing up to 100 ppm Mn. Manganese concentrations in the seedling tops increased sharply with increases in solution concentration but the maximum in both species was about 4200 to 4400 ppm. At such concentrations growth was reduced to about 60% of the maximum but no mortality occurred.

Foliar Mn concentrations of jack pine ranged between 100 and 220 ppm in natural stands having humus layers with reactions of pH 3.4 to 4.1 (102). Concentration in black spruce foliage from the same stands was 640 to 870 ppm (with one low value of 170), similar to other findings with the species (49). The difference between the two species in nature contrasts with their similarity in foliar concentration when grown together in nutrient cultures.

These several accounts suggest the difficulties in establishing Mn excess as a consequential factor in natural vegetation, although the possibility merits critical consideration.

In apple and pear, excess Mn not only produces leaf symptoms as noted above, but results also in a disorder termed "internal bark necrosis" (18, 55, 179). Numerous small necrotic spots develop deep in the cortex and pericycle of young shoots; these become encysted by suberized cells and subsequently appear at or near the surface as raised points or pustules. This appearance of "measles" is grossly similar to some effects of bark fungi or B deficiency, but is produced only at bark concentrations above 300 ppm of Mn. More extensive disturbance results in cracking and rolling of the periderm, "papery bark," especially in one year and older shoots. Lesions within the cortex result in characteristically roughened, scaly bark and, in severe cases, in splitting and dying of the bark.

Such evidence suggests examination of forest species and Ross (120) has studied the association of Mn with bark cankers of unexplained origin in red oak. Manganese concentration was highest in bark over the cankers (*ca* 1200 ppm) and higher on affected trees than on unaffected, but he was unable to induce canker by Mn injections or soil treatments.

Gross concentration of Mn in stem and branch bark varies greatly with species and site (60, 109, 181, 185), as has long been known, but the form of its occurrence and its significance are largely unexplained.

Soil Criteria of Deficiency or Excess

Kinds of soil most subject to deficiency:

1. Soils uniformly neutral to calcareous in the surface horizons (as opposed to those with an acid humus layer, or with circumneutral to acid aggregates between calcareous fragments).
2. Organic soils, moist alluvial soils, and ill-drained soils that are neutral to calcareous in the surface.
3. Over-limed acid soils.
4. Leached acid sandy soils from materials low in Mn-bearing minerals.

Kinds of soil possibly subject to excess:

1. Strongly acid soils (exclusive of No. 4 above).
2. Especially, acid highly weathered soils, such as some tropical red soils, containing large total amounts of Mn (30).
3. Ill-drained soils and others subject to poor aeration during annual or occasional periods of saturation. May include some soils neutral in reaction (55).

Some fraction of the total soil Mn is subject to transformations that greatly increase or decrease its availability to plants. Thus the soluble manganous form is rapidly oxidized to insoluble manganic Mn, with an optimum for the reaction at pH 6-7.5 (e.g., 55). On the contrary, Mn availability remains high in most strongly acid soils. It also appears that Mn rendered soluble during decomposition of organic matter (33) or cycled by vegetation remains highly available in many kinds of forest humus layers, even though their reaction, in bulk, reaches pH 7 (60, 122).

Manganese oxidation is halted, and the manganic form often reduced to the soluble manganous in poorly aerated soils. Presumably this occurs commonly also in anaerobic microsites and moist subsoils of many soils. Saturation or "water-logging" of surface soil, however, may greatly increase soluble Mn, even in neutral soil, with resulting injury to sensitive species (55).

Liming acid soils reduces Mn solubility and may be required to grow species sensitive to excess. Increasing soil reaction to pH 7 or above, on the other hand, as by overliming, burning surface peat, irrigation with alkaline water, or eroding to or mixing in calcareous subsoils readily induces Mn deficiency in another group of species unable to absorb the element efficiently. Thus applications of ammonium sulfate, with its localized acid residue, may give better or poorer responses than other N carriers, depending upon plant Mn status.

Interestingly, Sherman and Fujimoto (128) observed that a mulch of board slats reduced exchangeable Mn of a Hawaiian soil from 67 to 13 ppm, with a resulting effect on lettuce growth approaching that of two tons of lime. The authors attribute the change to the greater solubility of Mn oxides upon dehydration, which the mulch largely prevented.

As mentioned, soluble Mn may increase sharply with natural or artificial saturation of surface soil. Slow oxidation of soluble Mn in acid soils, or storage of excess within a tree (55), may greatly extend the effect of intermittent saturation. Somewhat in contrast, Mn deficiency on trees on marginal soils, as with Fe deficiency, is aggravated by long dry periods, apparently because roots cannot exploit the more acid or organic surface layers.

Manganese deficiency in susceptible soils has been eliminated by soil fumigation (88).

Soil Analyses

Plant Mn content tends to increase with increasing soil acidity and within generally similar soils the correlation may be high. Such correlation becomes progressively poorer, however, as a wider range of soil materials, drainage, etc., is examined, and hence conclusions about the predictive value of pH are varied. Beattie (9), for example, has reported Mn deficiency and response in a silt loam with a reaction of 5.3.

Estimates of Mn availability commonly depend on one or another of three types of extraction, measuring water soluble, exchangeable, or easily reducible Mn. Though each has found use, their predictive value over a range of soils is limited or uncertain. Manganese concentration in spruce and hornbeam seedlings, for example, was unrelated to readily reducible Mn in nursery soils, whereas pH alone accounted for about half the variation found (57). More recently, Hoff and Mederski (69) have shown that, over a variety of Ohio soils, Mn extractable in 1 *M* $NH_4H_2PO_4$ correlated better ($r = .90$) with soybean leaf content than any other measure. Phosphoric acid (.1 *N*) soluble and easily reducible Mn by the Jones and Leeper procedure (alcoholic hydroquinone) also correlated reasonably well with concentration in soybean ($r = .85$, .81 respectively) and were superior in this respect to exchangeable Mn.

Studies on internal bark necrosis of apple on strongly acid soils revealed little relationship between the contents of exchangeable and easily reducible (Sherman procedure) Mn, nor between either and the occurrence of the disease (18). Perhaps the latter merely exemplifies the limitations of examining the surface soil when a deep-rooted plant is involved.

Control of Deficiency and Excess

Control measures parallel those for Fe deficiency, except that soil applications of Mn are generally useful when deficiency occurs in acid soils. Effective measures are spraying, inclusion of Mn in fertilizers, or localized applications of 2-4 lbs. of Mn sulfate per tree for a year or more with orchard crops. Injections of solid salts are effective in some trees, including English walnut (162). Manganese chelates may have some value for shade or shelter belt species on calcareous soils.

Acidification of nursery soils or irrigation water, as discussed for control of iron deficiency, ordinarily will improve Mn availability but, as noted, numerous instances of Mn deficiency are found on acid soils.

Liming is the usual means of reducing excess Mn in tilled soils, though not generally applicable except in nurseries. Toxicity to newly planted tree seedlings can be reduced by lime or basic slag in the planting hole, or potting seedlings in a favorable medium (30).

Sprays of Fe salts or FeEDTA seem to offset

Mn excess and may sometimes be useful in diagnosis or seedling treatment (180).

Significance in Forestry

Manganese deficiency must be reckoned as a possible hazard in shade tree or shelter belt planting on some arid regions where surface soil reactions are high, or in forest plantings on eroded limestone materials. In such locations it may readily be confused with Fe deficiency, which its symptoms resemble. Large differences in species adaptability are probable, as with Fe.

But on acid or coarse sandy soils Mn deficiency is probably more frequent than Fe deficiency. Thus, Schutte (125) demonstrated a combined deficiency of Mn, Mg and Zn in *Rhus tomentosa* on a very sandy soil "almost devoid" of clay and organic matter. He noted that destruction of organic matter by fire and land clearing must often lead to lowered micronutrient availability in the less fertile soils still occupied by native vegetation.

The relatively large return of Mn in tree foliage and other litter and its apparent availability in surface humus layers suggest that deficiency is unlikely when and wherever such layers develop. On moist chalks or calcareous soils, however, intense earthworm activity may maintain a wholly calcareous surface for some decades after reforestation; the instance of Mn deficiency described by Ingestad (72, 74) was on such a soil.

Concern about Mn toxicity is obviously tempered when one deals with indigenous species adapted to acid or ill-drained sites. High concentration in foliage and bark of healthy trees is better testimony for physiological accommodation than for toxicity. Nevertheless, levels of available Mn vary enormously in some landscapes, corresponding to lithology and soil development processes. Where these levels are high, tolerance of excess can affect survival of planted species (30) and competition among the native (180).

Measures to prevent Fe chlorosis in forest nurseries will usually aid Mn availability as well, except that over-application of Fe chelates has been known to induce Mn deficiency. The possibility of Mn deficiency even in acid soils should not be overlooked when well marked chloroses fail to respond to iron (40, cf. Wilson, 178). The elimination of Mn deficiency on susceptible soils after fumigation parallels the behavior of Zn and may have some bearing on the favorable growth responses that often follow.

Molybdenum

Molybdenum deficiency is rare or essentially unknown in most orchard crops, with the exception of citrus (32, 76), and is totally unreported from forest trees in the field. With the exception of N-fixing species, the foliar concentrations required are minute, usually well below 1 ppm; and clear deficiency is not easily produced in nutrient cultures without greater than ordinary precautions against chemical impurities and contamination (3, 61, 62, 64, 101). Hence, the symptoms, foliar contents, and soil relationships pertaining to forest trees can only be inferred from findings with other species (March 1956 Soil Science, 32, 76).

Nevertheless, Mo warrants special mention because of its relation to the N economy of forests. Molybdenum has a key role in the biochemistry of N fixation, and is required in relatively large amounts by free-living N-fixing bacteria, blue-green algae, legumes, and nodulated nonlegumes in order for these to utilize atmospheric N. Hence, we must suppose that Mo deficiency or adequacy would have a large influence on the N status of unfertilized wildlands and ecosystems, and so upon their productivity.

Although no investigations of nodulated leguminous forest trees, such as *Robinia, Leucaena, Albizzia,* etc., have been reported, there is every reason to believe that they respond to Mo deficiency in the same manner as other legumes. The symptoms of Mo deficiency in these are ordinarily those of N deficiency, for the fixation process is impaired at concentrations much above that sufficient for the legume itself. Nodules are not lacking on deficient plants; rather they are usually abundant, but small and ineffective.

The nodulated nonlegumes examined thus far show a predictably large requirement for Mo. Again, this requirement is to serve an efficient N-fixing system rather than the host tissue. The high tissue concentrations of Mo and its effect on fixation are well shown by parallel studies with *Alnus* and *Myrica.* Becking's (10) results with seedling *Alnus glutinosa* in pot cultures of a low Mo soil (a low moor peat at pH 5.2) are summarized below:

Mo Addition	Dry Wt. of Shoots	N Content of Leaves	Total N Fixed	Mo Content of Plant		
				Leaf	Stem	Nodule
ppm of Soil	g/pot	%	mg/pot		ppm	
0	2.4	2.3	46	<.01	.14	2.0
0.3	7.6	3.6	218	.27	19.	17.

Symptoms on the deficient plants were pale leaves and marginal scorch of the lower leaves, indicative of low N. Other examination showed very abundant nodules on deficient alder, in contrast to the fewer and larger nodules on plants with adequate Mo.

Table 8. Molybdenum Concentration in the Foliage of Selected Forest Species. (See note in Table 2 for explanation.)

Sample Characteristics and Date	Range	Ref.
	Mo, ppm of dry matter	
PINES		
Pinus banksiana; Mar.	.07	51
Pinus contorta; 40 yr, Nov.	.09	8
Pinus palustris; range seedlings, Aug.-Oct.	.10-.14	41
Pinus radiata	.03-.05	175
Pinus resinosa; Mar.	.12	51
Pinus strobus; Mar.	.08	51
Nov.-Feb.	.052	1
Pinus sylvestris; Nov.-Feb.	.05-.12	1
OTHER CONIFERS		
Abies balsamea; Mar.	.04	51
Abies grandis; Nov.-Feb.	.073	1
Larix decidua; Nov.-Feb.	.064	1
	.10-.16	1
Larix laricina; July	.07	51
Larix leptolepis; Nov.-Feb.	.054	1
Picea abies; 13 stands, Site Cl. I, Nov.-Feb.	.03-.13	1
Picea glauca; Mar.	.03-.04	51
Picea mariana; upper crown, Oct.	1.3-3.0	172
Pseudotsuga menziesii; upper crown, Aug.-Feb.	.05-.10	8
fall	.06	1
ANGIOSPERMS		
Aceraceae		
Acer pseudoplatanus; upper crown, fall	.19-.31	1
Sept., Oct., top	.08-.24	59
Acer rubrum; Oct.	.05	51
Acer saccharum; Oct.	.05	51
Corylaceae		
Betula sp.; fall	.06-.17	1
Betula nigra; Sept.	.33	51
Betula pumila; July	.07	51
Fagaceae		
Fagus sylvatica; top, Oct.	.08	59
upper crown; fall	.05-.25	1
Quercus alba; June, Oct.	.06-.05	51
Quercus rubra (borealis); July-Oct.	.07	51
Quercus borealis; fall	.06-.21	1
Juglandaceae		
Carya ovata; Sept.	.34	51
Juglans nigra; Sept.	.27	51
Salicaceae		
Populus deltoides; Sept.	.13-.16	51
Populus grandidentata; Sept.	.05	51
Populus tremula; fall	.01-.18	1
NITROGEN FIXING SPECIES		
Legumes:		
Robinia pseudoacacia; fall	.05-.28	1
Non-legumes:		
Alnus sp.; fall	.05	1
Alnus glutinosa; young leaves	.25	10
cultures; seedling leaves	<.01-27.	10
Alnus rugosa; July	.05	51
Ceanothus americanus	.05	51
Myrica asplenifolia; July	.23	51
Myrica gale; cultures; seedling shoots	.16-52.	20

These findings are similar to those obtained by Bond and Hewitt (20) with seedlings of *Myrica gale* in solution culture; a single example is shown below:

Mo Added	Dry Wt. of Plant	N Content	Total N Fixed	Mo Content of Plant	
				Shoot	Nodule
	mgm	%	mgm	ppm	
—Mo	97	1.6	1.5	.16	1.6
+Mo	557	2.8	15.	31.	79.

Nodulated nonlegumes are conspicuous members of some forest communities where legumes are few or lacking. There is abundant evidence that associated trees benefit from the increased N supply (e.g., 149, 182) paralleling the effect of legumes. It seems clear that the Mo status of legumes and nodulated nonlegumes, trees, shrubs, or herbs should be examined wherever N is found to be limiting in organic productivity.

Goldman's (54) studies of phytoplankton productivity in Castle Lake, California, indicate that fixation by adjacent stands of *Alnus tenuifolia* is a significant source of N for the lake. At the same time, low Mo limits fixation within lake waters. Evidence from bottom sediment cores indicates that Mo concentrations in the lake were formerly much higher, and he speculates (54) that competition for Mo by *Alnus* stands now abundant on the watershed may be reducing its content in drainage waters reaching the lake.

Soils consigned to the forester's care because of low fertility include some with very low levels of available Mo. Molybdenum response, or low content in plants, has been demonstrated with some serpentine soils (166), acid sphagnum peats (93), "ironstone" soils (where Fe released in weathering has formed secondary Fe deposits entrapping Mo), strongly acid soils, and laterites. Attempts to increase productivity in any of these environments likewise will require awareness of possible Mo deficiency. Moreover, the increasing recognition of deficiency in crop plants on acid soils (e.g., 65) suggests that the problem of limited supply is not restricted to "unusual" soils. The possibility of deficiency should be considered wherever black locust or alder, for example, are planted on acid soils.

Treatment of Mo deficiency in crop plants usually has required very small amounts — 1-4 ounces of sodium molybdate per acre or sprays containing .01% sodium molybdate (76).

Zinc

The most spectacular example of micronutrient effects in forest trees is the Zn deficiency of planted pines in western and southern Australia (144). Despite widespread knowledge of this occurrence, and the increasing frequency of Zn deficiency in crop and orchard species (29, 151), no additional instances in forests have come to light. Rather, Viets (164) comments that there is no record of Zn response in native vegetation, and only Schutte's (125) observations in South Africa stand in contradiction. Though this state of affairs doubtless reflects insufficient observation, it is a consequence also of the association between Zn availability and fresh organic remains, and of the possible role of accumulator plants in mobilizing soil supplies. Meanwhile, routine use of Zn sprays, with their remarkably persistent effects, have all but eliminated the problem in the susceptible areas of Australia (H. Waring, Pers. Comm, 1967; 112, 150).

Visual Symptoms of Deficiency and Excess

Zinc deficiency is more common in climates with high light intensities and symptoms are expressed more strongly on the sunny side of the tree than in the shade (164). The common symptoms in woody plants are marked chlorosis or bronzing of younger leaves, especially in the top or individual branches, loss of older leaves from leading shoots, "rosettes" or dwarfed leaves on crowded terminal nodes, and dieback of affected shoots. In orchard crops, Zn deficiency may first appear as a chlorotic mottling of interveinal areas; sometimes only a few leaves or branches are affected. Mottling or bronzing and defoliation often progress upward, leaving bare stems. The terminal rosettes have closely spaced, small and discolored leaves, which may be stiff, narrow, crinkled or ragged, and carried at an acute angle. Strongly affected shoots die back and foliage of replacement branches often appears normal for a time (27, 29). Detailed symptoms for a few species are given in Table 9.

The Australian accounts (144) of deficiency in pine emphasize the extreme stunting especially when plantations are affected early. Extreme shortening of branches, needles and needle spacing in the upper part of the tree are characteristic, together with general yellowing of foliage and loss of all but the first or second year needles. Dieback of tops is frequent; recovery processes may either maintain a single stem or produce "brush brooming." Despite the use of some of the same phrases in description, the syndrome is entirely different from that of B deficiency.

In crop and orchard plants excess Zn produces a chlorosis characteristic of Fe deficiency. So striking is this that Cannon (28) traced a till-covered Zn-bearing dolomite for a distance of 20 miles in

Table 9. Specific Symptoms of Zinc Deficiency.

Pinus radiata	In field. Rosetting — Lateral branches short and at an acute angle, with needles generally less than 5 cm; only late-formed needles of current year retained. Needle color varies from green to bright yellow or brown at tips, with reddish-brown dead foliage beneath live tufts. Height growth may continue, but stagnation and malformation usual. Dieback: Short needles, poor color and growth from beginning. Usually in 4th to 8th year the terminal and upper whorls of many trees die, while lower branches remain normal. In severely affected 15-year trees the upper needles were very short, occasionally only 1 cm., with only 2 years' foliage retained; upper branches short, lower branches normal with sparse foliage; needles yellow to green with yellow or brown tips. Tops die back and recover to varying degrees, but single stem usually maintained (Stoate, 144).
Pinus pinaster	In field: Outstanding characteristic is golden yellow color of many needles; base pale green, tips often bronze. Needles between 3.7 and 7.5 cm long and in severe cases only current foliage retained. Shoots short, with tufted foliage. Side branches retained though needles few (Stoate, 144).
Pinus strobus	Eleven-month seedlings in nutrient culture: Primary needles blue-green with yellow-orange tips becoming necrotic. Fascicled needles long, pale blue-green with light yellow tips. Root system short, dark colored (Hacskaylo, 62).

New York, guided by the recognizable chlorosis of crops in the nearby high Zn peats. She notes that yellowing of trees rooted in mineral soils high in Zn has been observed in New Hampshire and the Driftless area of Wisconsin and used in prospecting for Zn in the limestones of Missouri.

Ragweed *(Ambrosia)*, which accumulates high concentrations of Zn, is tolerant and grew well where other plants were stunted by excess (29, 119). Such behavior is not known for Zn-accumulating woody plants (Table 11) but may well be found in some.

Tissue Analyses

The foliar content of Zn ranges widely, influenced by both soil and species. Table 10 suggests a "normal" range of 15 to 125 ppm to embrace many nonaccumulating species.

Changes in Zn concentration with maturity were slight in first year foliage of Norway spruce and Scotch pine (1). The successively older needles of several coniferous species may contain either more or less Zn than mature first year foliage (1, 8, 27), but it is by no means certain that small changes indicate any net translocation.

Similarly, the Zn concentration in European beech leaves from two unlike soils remained relatively constant between June and September, followed by slight changes before leaf fall (1).

The evidence cited above would suggest that sampling date is not a highly critical factor in diagnosing Zn deficiency, although sample position may be. With grey birch, however, which is a Zn-accumulating species, late September samples from two types of anthracite coal spoils were markedly higher than those from the same trees in mid-August, as shown below. (N = 3; each sample a composite from the upper first year shoots of 10 trees) (35):

Spoil Type and Leaf Position	**Sampling Date**	
	Aug. 15-26	**Sept. 29-30**
	ppm Zn	
Type I		
Older (Proximal)	289	432
Younger (Distal)	205	408
Type II		
Older (Proximal)	430	572
Younger (Distal)	267	465

Critical foliage concentrations for deficiency in orchard crops have not been established but the levels associated with deficiency symptoms are mostly less than 20 ppm. Symptom-free foliage of the

Table 10. Reported Zinc Concentration in Tree Species. (See Note in Table 2 for explanation.)

Table 10. Reported Zinc Concentration in Tree Species. (See Note in Table 2 for explanation.)

Sample Characteristics and Date	RANGE IN CONCENTRATION Deficient	Low	Intermediate	High	Toxic	Ref.
			Zn, ppm dry matter			
PINES						
Pinus banksiana; Mar.			74			51
Pinus contorta; upper crown, Nov.			52			8
Pinus echinata			25			38
Pinus elliottii			30-59			38
			15-75			158
Pinus palustris			33			38
range seedlings, Aug-Oct.			12-40			41
Pinus patula			28-41			157
Pinus radiata; pltn	1-5	5-11	19			144
nursery			32			144
various soils and locations			30-54			175
Pinus resinosa; Mar.			41			51
Pinus strobus; Mar.			66			51
upper crown, Nov.-Feb.			72-84			1
Pinus sylvestris; upper crown, Nov.-Feb.			36-80			1
4-yr pltn: 3 locality means for 45 seedlots, Nov.-Dec.			58,63,67			141
young pltn			32-33			25
Pinus taeda; 4-yr pltn			44			157
			50			38
OTHER CONIFERS						
Abies balsamea; Mar.			46			51
all foliage, 8″ tree			50			185
Abies grandis; Nov.-Feb.			79			1
Abies pectinata			47-49			1
Auracaria angustifolia			10-48			158
Larix decidua; upper crown; fall			23-71			1
Larix laricina; July			32			51
Larix leptolepis; upper crown; fall			48			1
Picea abies; first whorls			24-57			37
upper crown, Nov.-Feb., 13 stands—Site I			32-53			1
8 stands—Sites I-IV			13-87			1
pltn, 4th whorls, Aug.			14-21			95
Picea glauca; Mar.			59-117			51
Picea mariana; Mar.			44			51
upper crown, Oct.			16-39			172
Picea rubens; all needles, 8″ tree			45			185
Picea sitchensis; upper crown, Nov.-Feb.			42-57			1

Table 10. Reported Zinc Concentration in Tree Species. (See Note in Table 2 for explanation.) (Continued)

	RANGE IN CONCENTRATION					
Sample Characteristics and Date	**Deficient**	**Low**	**Intermediate**	**High**	**Toxic**	**Ref.**
			Zn, ppm dry matter			
Pseudotsuga menziesii, upper crown, Nov.-Feb.			46-63			1
upper crown, Aug.-Feb.			17-35			8
			25-55			161
Sequoia sempervirens			39			68
Thuja occidentalis; Mar.			30			52
Tsuga canadensis; Mar.			12			52
Tsuga heterophylla; upper crown, Apr.-Feb.		3	10			8
ANGIOSPERMS						
Aceraceae						
Acer pseudoplatanus; upper crown, fall			91-125			1
3 crown positions, Sept.			21-23			59
Acer rubrum; Oct.			22			51
all leaves, one tree			41			185
Acer saccharum; Oct.			42			51
Sept.			54			97
Corylaceae (See also Table 11 for Betula)						
Alnus glutinosa; fall			73			1
Alnus rugosa; July			34			51
Carpinus betulus; fall			40-71			1
Ostrya virginiana; Sept.-Oct.			17-22			51
Ebonaceae						
Diospyros virginiana; Sept.			36			97
Euphorbiaceae						
Aleurites fordii	10-24		26-36			39
Fagaceae						
Quercus alba; June, Sept.			17-22			51
Quercus rubra (borealis); July-Oct.			25-34			51
Quercus borealis; upper crown, fall			45-53			1
Quercus palustris;			88			97
Quercus velutina; June			32			51
Sept.			66			97
Hamamelidaceae						
Liquidambar styraciflua; Sept.			27			97
Juglandaceae						
Carya ovata; Sept.			62			51

Table 10. Reported Zinc Concentration in Tree Species. (See Note in Table 2 for explanation.) (Continued)

Sample Characteristics and Date	RANGE IN CONCENTRATION Deficient	Low	Intermediate	High	Toxic	Ref.
	Zn, ppm dry matter					
Carya illinoensis; orchard	Tr-7.0		66-202			47
Juglans cinerea; Sept.			58			51
Juglans nigra; Sept.			50			51
fall			42			97
Juglans regia; orchard, apical 6-8″	11-22		16-30			*In* 29
Leguminosae						
Cladrastris lutea; Sept.			36			97
Robinia pseudoacacia; Sept.			50			97
fall			34-49			1
June			24			154
Magnoliaceae						
Liriodendron tulipifera; Sept.			28			97
Magnolia macrophylla; Sept.			19			97
Magnolia virginiana; means 5 soils x 3 dates			12-16			12
Nyssaceae						
Nyssa sylvatica; means, 6 soils x 3 dates			12-15			12
Oleaceae						
Fraxinus americana; Oct.			15			51
Fraxinus excelsa; upper crown, fall			26-31			1
Fraxinus quadrangulata; Sept.			34			97
Rosaceae						
Prunus serotina; June-Sept.			26-27			51
Sept.			27			97
fall			49			1
Salicaceae (See Table 11)						
Tiliaceae						
Tilia americana; Oct.			49			51
Sept.			54			97
Tilia cordata; upper crown, fall			60			1
May			23			154
Ulmaceae						
Ulmus americana; Oct.			28			51
Sept.			20			97
park, Sept.			10-128			96

same species nearby may contain as little as 5 to 10 ppm (29).

Apart from pine, deficiency levels of forest trees in the field are unknown, except by inference from Table 10. In radiata pine acute deficiency was marked by foliage concentrations of 1-5 ppm. Trees returned to health by Zn treatment contained 5 to 9 ppm, about twice to five times the content of still deficient trees, whereas untreated healthy trees contained 10 ppm (144). Table 10 indicates that several conifers and some hardwoods may range as low as 10-15 ppm without showing deficiency symptoms.

Analyses of six tree species from NE U. S. indicate that Zn concentration in twigs, small roots, branch bark and stem bark very commonly equals or exceeds the average content of foliage (185).

Questions of Zn excess must take account of large differences among genera. As Table 11 shows, species of *Betula, Populus, Salix, Ilex, Clethra,* and *Taxus* attain much higher foliage concentrations of Zn than other species, even when growing together (12, 52, 90). Thus, although the mean values for *Ilex glabra* in Table 11 are not high in absolute terms, they are 2-3 times greater than those of the companion species, blackgum, sweet bay and broomsedge *(Andropogon glomeratus)* (12). Doubtless other such accumulators will be discovered as more woody species are examined. The lowest foliar concentrations of the above species fall well within the normal range of nonaccumulators; the highest frequently exceed the 400 ppm level which Chapman (29) suggests as indicative of excess in horticultural species. There is no real evidence that the above accumulators have any greater tolerance to excess soil contents, though this may prove true of some, especially birch (90). Willow used as a windbreak on the high Zn peats of New York State shows the same geographic pattern of chlorosis and poor growth as the adjacent vegetable crops. Black poplar hybrids survived moderately well and made excellent growth on sandy alluvium heavily contaminated with mine tailings high in lead and Zn (82).

Soil Criteria of Deficiency and Excess

Following Chapman's summary (29), the kinds of soils most subject to deficiency are:

1. Acid leached sandy soils low in total Zn.
2. Soils derived from acidic rocks, such as granites, and gneisses; e.g., a Cecil sandy clay loam averaged 4 ppm total Zn (2).
3. Neutral to alkaline soils in which Zn availability is low.
4. Subsoils, especially of the above, when exposed by erosion or grading.
5. High P soils (151) and, notably, areas enriched in P, such as old corral and barnyard sites, Indian burial grounds, etc. (29).

On some soils heavy P fertilization has reduced foliar Zn content and appears linked to the prevalence of deficiency in sensitive crops such as corn. The highly variable effect of "ashbeds" (sites where logs and slash were burned) on planted pines in Australia may well be linked to increased P availability in the heated soil. On some areas improved growth appeared to be a P response; in others, perhaps with lower Zn status, Zn rosetting was induced or intensified.

Zinc deficiency is more likely on exposed subsoils and is intensified by clean cultivation. Contrarily, Zn accumulated by weed fallows or green manures reduced deficiency in the succeeding crops (119).

Markedly higher Zn content has been found in the surface soil of forests, and is attributed to retention of Zn returned by vegetation. The only substantial demonstration of this effect, however, seems to be Hibbard's (68) observations in California, abbreviated below:

	Sequoia sempervirens	Pinus ponderosa (?)	Quercus sp.
		Zn, ppm	
Foliage, fresh green	39	37	40
Foliage, much decomposed	97	150	98
Soil, 0-1″ depth	41	56	68
Soil, 1-3″ depth	19	27	19
Soil, 11-17″ depth	8	8	10

The generality of such concentration requires examination. Tiller (153) found little or no accumulation of Zn and Cu in the litter of first generation of *P. radiata* on infertile sands. It would appear, however, that Zn availability in new plantations should improve materially after a forest floor is established, unless the total content of Zn is extremely low.

The possible consequences of continued heavy application of P fertilizers on Zn availability in sandy nursery soils deserve attention. Recent evidence from crop species (148, 171) suggests, however, that Zn-P interactions at the root surface or within the plant are more consequential.

Liming acid soils to above pH 6 may reduce Zn availability. On the other hand, cover crops

Table 11. Zinc Accumulator Species and Genera. (See explanatory note in Table 2.)

Sample Characteristics and Date	Range	Ref.
	Zn, ppm dry matter	
Aquifoliaceae		
Ilex glabra; means: 3 dates x 6 loc.	26-61	12
Ilex opaca	240	97
Ilex verticillata	363	52
Nemopanthus mucronata	327-711	51,52
Clethraceae		
Clethra alnifolium; means: 3 x 2 loc.	81-127	12
Corylaceae		
Betula sp.; upper crown; Flottsand	467	1
Alluvium	717	1
Betula alleghaniensis (lutea)	115	52
Betula nigra	212-237	52
Betula papyrifera	110	52
all foliage	77	185
Betula pendula	96	154
Betula populifolia; range, 150 samples, Sept.-Oct.	137-759	35
Betula pumila	164	52
Betula sandbergi	105	52
Salicaceae		
Populus alba	135	52
Populus balsamifera	331	52
Populus deltoides	81-199	52
Populus grandidentata	108-117	52
	254-480	35
Populus tremula	451-1501	1
Populus tremuloides	103-127	52
	62	38
Salix alba	83	155
Salix amygdaloides	154	52
Salix bebbiana	134	52
Salix nigra	55-213	52
Salix purpurea	134	155
Salix fragilis	98	155
Salix caprea	100	155
Taxaceae		
Taxus canadensis; 1-yr foliage, Apr.	109-111	145
3-yr " "	218-274	145
1-yr foliage, Mar.	209	51

seem to increase availability of native Zn, and certain types of organic addition, e.g., peat, bark (185) contribute moderate amounts. Of particular interest in nurseries is the increased plant uptake of Zn following fumigation of soils even on those subject to deficiency (29, 151).

Excess Zn in plants is known from three situations:

1. Soils from rock high in Zn, including some limestones and dolomites, ore outcrop areas, and probably sulfide-rich coal mine spoils.
2. Peats enriched in Zn from the groundwater, especially in the vicinity of the above. Toxicity is increased after drainage of the peat.
3. The vicinity of Zn and lead mines and processing areas. Alluvium from waste dumps may affect stream bottoms for long distances (82).

The high-Zn peats of New York contain up to 6% Zn, and even more at localized points (138). In the natural swamps the Zn occurs largely as the insoluble sulfide; drainage favors oxidation to the soluble sulfate form, greatly increasing toxicity.

Corrosion of galvanized iron containers, hardware cloth, etc., especially in contact with soil, may produce localized Zn toxicity (16, 29); this is most likely with acid sandy soils. On the other hand, traces of Zn from galvanized rabbit wire netting caused spectacular recovery of Zn-deficient pines in western Australia (144).

Soil Analyses and Control of Deficiency

Thorne (151) and Chapman (29) have reviewed soil analytical procedures useful in diagnosing deficiency or excess. In some soil areas total Zn content may be as useful as extractable Zn in predicting likelihood of deficiency (2, 151). Current procedures, however, usually depend on extraction with ammonium acetate (pH 4.6), ammonium acetate with dithiazone — carbon tetrachloride, or 0.1 *N* HCl. In neutral and alkaline soil, titratable acidity or pH may be incorporated as a variable to take account of reduced plant availability. Recently Stewart and Berger (142) have found excellent correlation ($r = .93$) between Zn concentration in Japanese millet, grown as a test crop, and Zn extractable in 2 *N* $MgCl_2$. The absolute quantities extracted were smaller than those obtained by other procedures, but the correlation with plant Zn was much superior.

The mold, *Aspergillus niger,* responds to available Zn and is used as a test organism in a biological assay procedure. The results are comparable with extraction by chemical procedures.

No threshold values for toxicity can be stated. Addition of from 80 to 400 ppm soluble Zn to acid mineral soils has produced toxicity in crops, but the symptoms were readily overcome by liming (29).

Broadcast applications of 10 to 25 lbs. Zn sulfate have remedied deficiency in several crop species in sandy soil. Much heavier applications have been required or used on orchard crops, often as localized additions around individual trees. Such applications are sometimes ineffective, however, or, contrarily, produce toxicity (29). Stoate (144) applied from 4 oz. to 4 lbs. Zn sulfate to individual young pines with favorable response.

Zinc chelates at rates of 1-2 lbs. per tree have proved effective with a few orchard crops on acid sandy soils (29, 32, 151); extent of usefulness on other soils is less certain (164).

In general, however, Zn sprays are the preferred means of treatment (29), since dosage and effect are more nearly independent of soil. Concentrations applied to orchard crops in leaf are commonly 1.1 to 2.2% $ZnSO_4$ with one-half the weight of $Ca(OH)_2$ added to reduce leaf injury. Dormant sprays are often 5.5%. Neither type of spray was very effective on English walnut.

Standard treatment for pine in the Australian areas of deficiency is 2.5% $ZnSO_4$ at the rate of 10 gal. per acre (144, 150). Coverage need not be entire. It appears that a single application is effective for the life of the stand, and carry-over effects have been seen in natural regeneration on treated areas that subsequently burned.

Trunk injection of Zn solutions or solid salts placed in bored holes overcome deficiency. Similarly, metallic Zn as galvanized strips, nails or glazier's points driven into the sapwood provide long-time effectiveness in many woody species, including pecan and English walnut. As a measure of the small amounts required, Stoate (144) reports that a single roofing nail restored a 2 inch diameter tree of ***P. pinaster*** to vigorous growth. In *P. radiata* such metal implants had much smaller and more temporary effect but, in any case, foresters presumably would be inclined to apply such treatments sparingly. Likewise, Stoate's observation of a kangaroo skeleton beneath the single green pine in an otherwise deficient plantation has somewhat limited implications for silvicultural practice.

Consequences for Forestry

Stunting of planted pine by extreme Zn deficiency is well illustrated by the response of "severely disordered" *Pinus pinaster.* At the age of nine years trees were treated with galvanized nails or Zn strips driven into the base, with the following results (144):

	Control	Galvanized roofing nails
Height at 9 years (ft)	6.4	4.8
Height at 22 years (ft)	11.5	21.2

The surviving controls were all on old ash beds.

Zinc deficiency is unreported in forest trees in the U. S. Its widespread occurrence in orchard crops both on weathered sands in the South and neutral to alkaline soils of the West suggests, however, that deficiencies may yet be found in plantations or shelterbelts. The symptoms of acute deficiency are sufficiently striking, and response to foliar sprays or metal implants is so marked that diagnosis should be simple. Localized biogenic concentration of P at old corrals, barnyards, habitation sites, and former bird roosting or nesting sites — such as of buzzards, passenger pigeons and, most notably, seabirds (48) — is a prospective source of deficiency long after its origin. It is possible that the ash bed effect may occasionally act similarly. Though none of these occurrences are likely to affect large areas, they are prospective additions to the puzzling irregularities sometimes encountered in young plantations.

The concentration of Zn within surface organic layers, and the relative abundance of known accumulator plants — *Ilex, Betula, Populus* — imply that deficiency in established stands will be uncommon. Yet the indications of greater cold resistance and increased growth in tung trees at concentrations much higher than needed for control of symptoms (6) may warrant investigation in forest species also.

Instances of Zn excess in nature are few but too widespread to be ignored when foliar symptoms suggest Fe deficiency.

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