

MINERAL NUTRITION OF CONTAINER-GROWN TREE SEEDLINGS 1/

H. Brix and R. van den Driessch 2/

Abstract.—Aspects of mineral nutrition important to growth rate and quality of tree seedlings are discussed and some fertilizer regimes used for container stock in the Pacific Northwest are presented. Topics included are rooting media, pH, and major elements with respect to their ratios, concentration, amount and timing of application. Also considered are nitrogen source, interaction of mineral nutrition with other growth factors, micronutrients and mycorrhizal infection. Seedling quality is discussed in terms of drought and frost hardiness and potential for root and shoot growth.

INTRODUCTION

Fertilization of container plants has presented many problems not encountered in conventional nursery practices. To economize on space and reduce weight, we work with small containers in which reserves of nutrient and water are much less than in a nursery field. For example, the most widely used container in British Columbia (B.C.) has a volume of 40 cm³ (2.45 cubic inch), whereas plants growing in a nursery bed with a rooting depth of 20 cm (8 inches) have a soil volume of about 700 cm³ to occupy. As a result, most of the nutrients required by the crop can be in the seed bed at sowing. This is not possible in small containers because concentrations of some elements would be undesirably high. We have, therefore, to supply nutrients throughout the growing season that satisfy the requirement for optimum quantity and quality of growth.

ROOTING MEDIA

Natural soil is not used as a rooting medium because other media have more desirable physical characteristics, i.e., water-holding

capacity, aeration and bulk density. A mixture of peat moss and vermiculite is most widely used in the Pacific Northwest (PNW), but ground bark is the favorite with some growers; sand and pumice are used in small amounts in mixtures. The properties of these media of importance to mineral nutrition are water holding capacity, which determines their ability to contain nutrients in solution, and cation exchange capacity (CEC) which controls the retention of nutrients in an exchangeable form. The media are generally low in nutrient content, and some materials, such as ground bark, consume nutrients which must be replaced.

Peat and vermiculite have a high CEC based on dry weight compared to ground bark and sandy loam soil (Klougart and Olsen 1969a; Buckman and Brady 1969; Owston 1972). Owston (197²) gives figures for CEC in milliequivalent per 100 g dry weight of 103, 72 and 13 for 1:1 fine grind peat moss-vermiculite, 1:1 Douglas-fir bark-vermiculite and sandy loam soil, respectively. However, for our purpose, the CEC should be compared on a volume basis. If this is done, the CEC of sphagnum peat, and probably vermiculite, is not higher than that of soil (Klougart and Olsen 1969a). Work has been done to improve CEC by mixing granulated or powdered clay with a high CEC into rooting media, but many problems are still unsolved (Klougart and Olsen 1969a).

The water-holding capacity of sphagnum peat varies with its fineness, but it is generally very high, from 56% of volume in coarse grade to 84 in fine grade (Klougart and Olsen 1969a). Considerable amounts of nutrients can therefore be held in solution in peat mixtures but they are, on the other hand, readily leached out during rain and irrigation.

1/ Paper presented at North American Containerized Forest Tree Seedling Symposium, Denver, Colorado, August 26-29, 1974.

2/ Research Scientist, Pacific Forest Research Centre, Canadian Forestry Service, Victoria, British Columbia, and Tree Physiologist, Research Division, British Columbia Forest Service, Victoria, British Columbia.

pH

Optimum growth of many conifer seedlings occurs over a limited pH range (Benzian 1966b; Leyton 1952). Consequently, the pH of the rooting medium should be adjusted to some specific value which is usually within 4.5 to 5 for conifers. The rooting medium pH will change over the course of time, particularly as a result of differential removal of ions from the rooting medium and the nutrient solution. When nitrogen is added as nitrate, the pH tends to rise; when added as ammonium, it tends to become more acid (Hewitt 1966). Some container tree nurseries in the Pacific Northwest regulate pH during the growing season by the addition of $\text{Ca}(\text{NO}_3)_2$ or NaOH when pH has decreased, and with $(\text{NH}_4)_2\text{SO}_4$ or H_2SO_4 when it has increased. Adjustment of the water to pH 5.5 with phosphoric acid is another practice. Commercial fertilizers also have specific effects on pH (Wilde 1958). To avoid undesirable changes in pH during growth of container stock, it is desirable to use a rooting medium with adequate buffer capacity. Incorporation of peat moss and adjustment of initial pH with a sparingly soluble calcium salt is one approach to maintaining constant pH (Matkin and Chandler 1957).

FERTILIZER REGIMES

Incorporation of fertilizers in the rooting medium is, in many PNW operations, limited to lime for the purpose of pH adjustment, although some include a small amount of balanced fertilizer as a starter. Klougart and Olsen (1969b) found that, within the pH range of 3.5 to 7.0, 30 g of fine-ground limestone (97% CaCO_3) had to be added to 1 kg dry peat to change the pH one unit. Lime also serves as a source of calcium, gypsum as a source of sulfur, and dolomitic lime adds magnesium. In the B.C. styroblock system, only dolomite lime is added to the rooting medium; all other nutrients are supplied in solution with the irrigation water.

Fertilizer regimes must be adjusted throughout the growing period to meet the changing requirements for optimum growth in rate and quality. Nutrient requirement for good growth has been studied in sand and water culture for many tree seedlings (Table 1). Both concentration of nutrients and nutrient ratios affect seedling growth. It is important to provide an adequate supply of all known nutrients at concentrations as low as are compatible with adequate rates of absorption in relation to the container soil volume, frequency of replacement, and stability of pH (Hewitt 1966). Ingestad (1971) has stressed that the nutrient requirement is satisfied when the following criteria are met: (1) all

essential minerals are present in the plant in optimum proportion; (2) the ratio of the nitrogen sources NH_4^+ and NO_3^- in the nutrient solution is at its optimum, and (3) the total nutrient concentration in solution is optimum. Different plants may have different requirements and different tolerance to variation from the optimum.

An examination of recent sand culture experiments shows that concentration of nutrients used tends to increase with lower frequency of nutrient solution application (Table 1). Consideration of sand-culture nutrient solutions gives some guide to composition of solutions for use on container installations although chemical properties of the container rooting medium should also be considered. Furthermore, sparingly soluble nutrients, such as P and Ca, can be incorporated into the rooting medium used in containers. This is seldom done in sand cultures. In sand cultures with frequent irrigations (every 1 to 6 hours), concentrations of nutrients are in the ranges 28 to 100 ppm N, 1-24 ppm P, 20-126 ppm K, 40-150 ppm Ca, 10-50 ppm Mg and 20-150 ppm S. With less frequent irrigations (every 8 hours to once a week), optimum results are obtained with higher nutrient concentrations as follows: 56-300 ppm N, 31-250 ppm P, 50-320 ppm K, 75-320 ppm Ca, 48-173 ppm Mg and 50-280 ppm S.

Although it is difficult to determine optimum nutrient ratios from an examination of sand-culture experiments, it seems clear that the ratio N/P is > 1 and the ratio P/K is nearly always < 1 . Good growth of north temperate zone conifer seedlings can likely be obtained when nutrients are in the proportions N 4-10, P 1, K 1.5-2, Ca 5-10, Mg 1-4, and S 2-4. As growth continues the proportion of N can possibly be reduced (Loustalot et al. 1950). This may be desirable for hastening the onset of dormancy (Cheung 1973) and for control of seedling quality, as discussed later.

The total nutrient concentration must be watched to avoid detrimental and even toxic levels. The range of optimum level may be wide especially if nutrients are present in the right proportions (Ingestad 1971), but the small rooting volume we use accentuates the problem. Frequent conductivity tests, using Solu-bridge or other means, and chemical analysis of plant and soil should become routine practice for any large-scale container operation.

Nutrient solutions, recommended for use by the British Columbia Forest Service for growing-season production of BC/CFS Styroblock-2 container stock, are based on commercial fertilizers and contain relatively high proportions of P in the beginning and toward the end of the

Table 1.--Summary of some recent sand cultures

N	P	K	Ca	Mg	S	pH	N Source		Irrigation frequency	Species	Authority
							NO ₃	NH ₄			
ppm						ppm N					
100	10	20	50	10	20		50	50	2 hours	<i>Picea glauca</i> <i>Picea rubens</i>	Swan 1971
100	1	126	40	24		5.5	50	50	1 hour	<i>Pinus taeda</i> <i>Pinus virginiana</i>	Fowells and Krauss 1959
280	93	273	200	73		4.6- 4.9	238	42	7 to 28 days	<i>Pinus strobus</i>	Schomaker 1969
250	250	50	100	100		4.5- 5.0			8 hours	<i>Pinus radiata</i>	Leyton 1967
300	100	50	75	50	50	3.5			24 hours	<i>Pinus serotina</i> <i>Pinus taeda</i>	Woodwell 1958
28	23.5	44	40	18	30	5.5	24.5	3.5	6 hours	<i>Pseudotsuga menziesii</i> <i>Tsuga heterophylla</i> <i>Thuja plicata</i> <i>Pinus contorta</i>	Krajina <u>et al.</u> 1973
50	15	20	150	50	149	3.7- 5.1	25	25	3 hours	<i>Pseudotsuga menziesii</i> <i>Picea sitchensis</i>	van den Driessche 1968
112	31	156	80	48	150		56	56	24 hours	<i>Pinus contorta</i> <i>Picea glauca</i>	Hocking 1971
56	186	78	320	97	128		56	0	2xper week	<i>Pinus contorta</i>	Etter 1969
203	151	320	244	173	280		102	102	2xper week	<i>Pinus banksiana</i>	Giertych and Farrar 1961

growing period 3/. After germination of the spring-sown seed, 10-52-10 is used to give concentrations of 62 ppm N, 141 ppm P and 52 ppm K for 1-2 weeks. 20-20-20 is then applied at concentrations of 100 ppm N, 44 ppm P and 82 ppm K until the end of August; thereafter, N is dropped from the nutrient solution and 0-52-34 is substituted to supply 141 ppm P and 176 ppm K for 1-2 weeks. In the beginning of September, the regime is changed to 10-52-10 and is continued until mid November. Fertilizers are usually applied to the drip-point twice a week during the growing season. Stock held in a greenhouse or shelterhouse is fertilized with 10-52-10 once or twice a month from mid November through January and this stock is usually packaged and cold stored in February. To avoid iron chlorosis, ferrous sulphate is supplied at weekly or biweekly intervals in concentration of 18 ppm Fe during most of the growing period. Other fertilizer solutions are applied to the drip-point twice a week. This regime is used for all container-grown seedlings, with only minor differences in timing and amounts applied for different

species. Application to the point at which the solution drips through the medium does not give a close control of the amount of nutrients supplied as this depends on the water content of the medium before fertilization.

To indicate the variety of fertilizer regimes used by growers in the PNW, some other regimes are given. One grower uses 20-20-20 as a starter and changes to 30-10-10 during the period of fastest growth. If stem elongation is too great, the schedule reverts to 20-20-20. Another grower uses a modified Hoagland solution applied in 5X strength. The working solution contains N, P, K in concentrations of 1400, 154 and 1170 ppm, respectively, plus other major and minor elements. Three ml of this solution are applied weekly throughout the growing season to Douglas-fir and hemlock seedlings growing in 44 cm³ containers, in addition to irrigation. A third regime is reported to this symposium by Peyton W. Owston ('Two-crop production of western conifers'). A solution of 20-19-18 plus chelated iron and trace elements is alternated with calcium nitrate from 2-3 weeks after germination until bud set, in amounts that vary with the growth rate. A 0-10-10 fertilizer is used during bud set and, when it is completed, 9-45-15 is supplied throughout the winter for seedlings to be planted in the spring.

3/ J.T. Arnott and E. van Eerden, Canadian Forestry Service, Victoria, personal communication.

NITROGEN SOURCE

Nitrogen source has a marked effect on growth of some species of conifer seedlings. Ammonium nitrogen results in greater growth than nitrate nitrogen under a range of conditions (McFee and Stone 1968; Swan 1960; Christersson 1972; Benzian 1965; Ingestad and Molin 1960; van den Driessche 1971). Under other conditions, greater growth may result from use of nitrate (Krajina et al. 1973; Radwan et al. 1971; Pharis et al. 1964). Frequently, mixtures of these sources result in greater growth than either of them alone (Evers 1964; Christersson 1972). Urea was an effective N source for *Pinus taeda* (Pharis et al. 1964), but not for *Pinus sylvestris* (Christersson 1972). The N source may affect different parts of the plant without influencing total growth; e.g. nitrate tended to have more effect than ammonium on root growth of *Picea sitchensis*, but the source did not affect total plant production (Leyton 1952).

The reasons for the apparently different effects of nitrogen source on conifer seedling growth may be partly related to species or to differences in moisture supply, concentration other nutrients, temperature and pH conditions. In view of this, it is advisable to supply nitrogen initially as a mixture of both sources. Further research and local experiments may show that better results can be obtained with one nitrogen source rather than with another under specific conditions.

MICRONUTRIENTS

Micronutrients are usually not added to rooting mixtures in the U.C. system for producing container-grown plants unless a specific deficiency is identified (Matkin and Chandler 1957). However, micronutrients are contained in commercial soluble fertilizers commonly used now for tree seedlings. Micronutrient deficiency symptoms for a number of important forest tree species have been described (Stone 1968; Chapman 1966; Hacskaylo et al. 1969) and, when detected, are most effectively overcome by treatment with metallic chelates, if these are available (Tiffin 1972). Spraying of micronutrients onto foliage often corrects deficiency very rapidly; otherwise, micronutrient fertilizers can be added to nutrient solutions. Lack of iron is the most common deficiency on artificial soils, due to high calcium concentrations, but it can be overcome with iron chelate (Matkin et al. 1957).

INTERACTION WITH OTHER GROWTH FACTORS

Fertilizer regimes must be adjusted to other environmental conditions affecting growth

and to other cultural practices. This becomes especially important with use of greenhouses for year-round production of two or more crops for which the environment is greatly different. Light intensity will influence mineral nutrient requirement by its effect on growth rate and, as a source of energy, it is likely to affect mineral uptake (McKee 1972; Rains 1967). For Douglas-fir, a decrease in light intensity will reduce the response of photosynthesis to nitrogen (Brix 1971). Temperature has been shown to affect mineral uptake and utilization. Uptake of ^{32}P by *Pinus elliottii* was more rapid at 10 to 15 degrees C than at 30 to 35 degrees C (McKee 1972) and availability of phosphorus in phosphorus fertilizer is generally found to decrease with an increase in temperature from 5 to 35 degrees C (Beaton et al. 1965). High temperature may result in greater growth occurring on ammonium sources of nitrogen than on nitrate (McFee and Stone 1968). Watering, especially, should be watched since most of the nutrients are held in solution in the rooting media commonly used. Frequent and heavy irrigation could lead to excessive leaching of nutrients and, conversely, sparse irrigation to salt build-up.

MYCORRHIZAL INFECTION

Seedlings raised in artificial cultures may develop mycorrhizal associations (Purnell 1958), but they may not if the nitrogen and phosphorus supply level is high (Fowells and Krauss 1959; Addoms 1937). Attention to inoculation and development of suitable mycorrhizae is worth considering since it is generally acknowledged that such associations are important in nutrient uptake after outplanting. Research on inoculation and the relative efficiencies of various mycorrhizal fungi is, however, still at an early stage (Trappe 1967; Mejstrik and Krause 1973).

SEEDLING QUALITY

In the beginning of the production period, the fertilizer regime is designed to promote rapid growth. Toward the end of this period, the object is to improve the quality of seedlings so that they will withstand frost and winter drying and have an increased potential for growth and survival after outplanting. The importance of the nursery fertilizer regime for subsequent growth has been demonstrated (Anderson and Gessel 1966; Krueger 1967; Smith et al. 1966; Radwan et al. 1971).

Total plant size is an important quality, but the distribution of dry matter must also be considered; e.g. root/shoot ratio, stem diameter and leaf quantity. Within limits, an increase in mineral supply increases shoot growth relative to root growth (Brouwer 1962). Stem diameter growth often continues after

height growth has stopped and 'sturdiness' of the seedling can, therefore, be improved by fertilization in late summer and fall. A common practice, as indicated previously, is to deprive the plants of nitrogen for a few weeks toward the end of summer while maintaining or increasing phosphorus and potassium supply. After bud set, the nitrogen supply is increased.

Fertilization in the fall, after shoot growth has ceased, could become an important tool in increasing plant quality, but more research is needed. Root growth of many woody plants continues during the dormant season as long as the soil remains unfrozen (Tukey and Meyer 1966). Fertilization of *Taxus* and *Forsythia* with N, P and K in the fall increased root growth and concentration of these elements in the plants while the shoots remained dormant (Meyer and Tukey 1965). Subsequent shoot growth in the spring doubled as a result of fall nitrogen application. The effect of phosphorus was smaller and potassium had no effect on growth but reduced winter injury. Benzian and Freeman (1967) also found that late-season fertilization with N and K increased concentration of these elements in several conifer seedlings and subsequent growth in height and diameter. The nitrogen status affects leaf initiation of Douglas-fir and, therefore, the growth potential for the following year (Brix and Ebell 1969). For Douglas-fir, leaf initiation continues into November (Owens 1968) and, for this reason, it could be important to maintain a high nitrogen level in the fall.

Seedling survival and growth after out-planting depends on a rapid root extension. This is especially critical following growth in containers with a small rooting volume relative to the size of the seedling top produced. The container system is designed to protect the roots during transplanting, but proper nutrition is required to produce roots with good growth potential. More research on this important aspect is needed. Fertilization with 10-52-10 in the fall and winter in British Columbia, and with similar compounds elsewhere, is done primarily to increase root mass and its potential for growth following planting.

Survival during drought is, in addition to root extension, also affected by the ability of the plants to reduce water loss and to tolerate plant water deficit. Several studies have shown that mineral nutrition affects drought resistance, although the mechanism involved is not well known. Loblolly pine seedlings, grown under normal moisture conditions with an optimal nitrogen supply for growth, were also the most drought resistant (Pharis and Kramer 1964). Phosphorus and nitrogen fertilization increased drought resistance of red pine seedlings

(Shirley and Meuli 1939), and a balanced N, P, K fertilization, but not N alone, improved drought resistance of longleaf pine (Allen and Maki 1955). Mineral nutrition also affects transpiration rates. Potassium plays an important role in stomatal movement (Fischer 1963) and deficiency in this element has resulted in a high transpiration rate in *Pinus sylvestris* (Zech et al. 1969; Christersson 1973). Christersson (1973) found no effect of calcium or magnesium on transpiration rate.

One of the most crucial problems in growing container plants is to harden the plants in late summer against frost damage. Temperature and photoperiod are important factors, but mineral nutrition also plays a role in cold hardiness (Alden and Hermann 1971; Levitt 1956). A continuing nitrogen application throughout the summer will prolong shoot extension and delay development of cold hardiness. However, nitrogen application in the fall after bud set appears to be beneficial. Benzian (1966a) found that a top dressing of nitrogen, applied in a nursery so late in the season that it increased seedling nitrogen concentration without increasing shoot growth, decreased frost damage in December in Sitka spruce and western hemlock, and a late potassium application was similarly effective in Sitka spruce. Correction of magnesium deficiency decreased incidence of frost damage in lodgepole pine and Sitka spruce (Atterson 1967). Christersson (1973) found no effect of potassium, calcium or magnesium on frost hardiness of Scots pine seedlings following growth under favorable growing conditions or subsequent to a 3-week acclimatization period under low temperature and short photoperiod. He felt that potassium would improve winter survival, not by increasing frost hardiness but by improving the water economy of seedlings, thus avoiding winter drying. The role of potassium in frost hardiness is supposedly to increase cell permeability to water and soluble carbohydrate content and to increase synthesis of amino acids (Levitt 1956). However, fertilizer experiments have not been conclusive in the general importance of potassium and other minerals in frost hardiness. More research, therefore, is needed to establish optimum nutrient levels and effective stages in hardiness development as well as the interaction among nutrients and with environmental conditions such as temperature, photoperiod and water stress. Also, more attention is needed on the frost hardiness of roots since they are exposed to lower temperatures when grown in containers than under ordinary conditions.

CONCLUSION

Plants are being successfully raised in large numbers in container systems and seedling nutrient requirements are largely satisfied. Conversely, deficiencies have been noted that may occur again unless a thorough understanding of the systems is obtained. Development of container systems is likely to continue and changes of temperature, light, moisture, CO₂ concentration, mycorrhizal associations or seasonal conditions associated with development could result in a previously satisfactory nutrient regime becoming inadequate. Similarly, it is evident that mineral nutrient regimes can be considerably improved. For instance, there is a need to shorten the time required to produce plantable stock for species such as western hemlock and white spruce. With outdoor container production in British Columbia, seedlings of these species have not reached a satisfactory size in one growing season. Greenhouses and shelterhouses are coming into use to prolong the growing season, but better mineral nutrition with the resultant increased growth rate may offer a cheaper alternative.

So far it has been usual to assess seedling quality in terms of height, stem diameter, total weight, root shoot ratio and color. Other factors, such as root growth potential, bud size, nutritional state of the seedlings and drought and frost hardiness are equally important in determining seedling performance after out-planting. These factors are controlled in part by the mineral nutrient regime used in seedling production. Container systems have an advantage over bars root nurseries in quality control in that virtually all macro-nutrients are supplied artificially.

At present, rooting media are prepared from naturally occurring substances, but synthetic compounds are now manufactured for the purpose of growing plants (e.g. White and Schneider 1972). Presumably it will be possible to tailor the cation exchange capacity of synthetic media to the requirements of the system and slow release nutrients can be incorporated to support growth for at least the first few weeks after germination. However, for growth over a longer period of time, we are still in search of slow release fertilizers for which the rate of nutrient release is governed by the need of the plants rather than some other conditions, such as temperature.

The cost of fertilizers is only a minor part (about 3%) of the total production cost of container-grown seedlings (Huseby 1973), and the potential for improving rate and quality of growth cheaply by means of better mineral nutrition is evidently large. More research is therefore warranted to improve timing, type

and quantity of fertilizer dosage and to relate the studies to advancements in other growing techniques.

LITERATURE CITED

- Addoms, R.M.
1937. Nutritional studies on loblolly pine. *Plant Physiol.* 12:199-205.
- Alden, J. and R.K. Hermann.
1971. Aspects of the cold-hardiness mechanism in plants. *Bot. Rev.* 37:37-142.
- Allen, R.M. and T.E. Maki.
1955. Response of longleaf pine seedlings to soils and fertilizers. *Soil Sci.* 79: 359-362.
- Anderson, H.W. and S.P. Gessel.
1966. Effects of nursery fertilization on outplanted Douglas-fir. *J. For.* 64:109-112.
- Atterson, J.
1967. Slow-acting inorganic fertilizers. In: *G.B. For. Comm. Rep. For. Res. 1965/66*, pp. 21-23.
- Beaton, J.D., R.C. Speer, and G. Brown.
1965. Effect of soil temperature and length of reaction period on water solubility of phosphorus in soil fertilizer reaction zones. *Soil Sci. Soc. Amer. Proc.* 29:194-198.
- Benzian, B.
1965. Experiments on nutrition problems in forest nurseries. Vol. I. H.M.S.O. London. *G.B. For. Comm. Bull.* 37, 251 pp.
- Benzian, B.
1966a. Effects of nitrogen and potassium concentrations in conifer seedlings on frost damage. In: *Rep. Rothamst. Exp. Sta. for 1965*, Harpenden 1966, 58-59.
- Benzian, B.
1966b. Nutrition experiments in forest nurseries. *Quart. J. For.* 60:94-100.
- Benzian, B. and S.C.R. Freeman.
1967. Effect of "late-season" N and K top-dressings applied to conifer seedlings and transplants, on nutrient concentrations in the whole plant and on growth after transplanting. *G.B. For. Comm. Rep. For. Res.* pp. 135-140.
- Brix, H.
1971. Effects of nitrogen fertilization on photosynthesis and respiration in Douglas-fir. *For. Sci.* 17:407-414.
- Brix, H. and L.F. Ebell.
1969. Effects of nitrogen fertilization on growth, leaf area, and photosynthesis rate in Douglas-fir. *For. Sci.* 15:189-196.
- Brouwer, R.
1962. Nutritive influences on the distribution of dry matter in the plant. *Neth. J. Agric. Sci.* 10:399-408.
- Buckman, H.O. and N.C. Brady.
1969. *The nature and properties of soils.* 7th ed. MacMillan Co. N.Y., 653 pp.

- Chapman, H.D.
1966. Diagnostic criteria for plants and soils. University of California, Division of Agricultural Sciences, Berkeley, Calif. 793 pp.
- Cheung, K.W.
1973. Induction of dormancy in container-grown western hemlock (*Tsuga heterophylla* (Raf.) Sarg.). B.C. For. Serv. Res. Note 59, 5 pp.
- Christersson, L.
1972. The influence of urea and other nitrogen sources on growth rate of Scots pine seedlings. *Physiol. Plant.* 27:83-88.
- Christersson, L.
1973. The effect of inorganic nutrients on water economy and hardiness of conifers. I. *Stud. For. Suec.* 103:1-26.
- Etter, H.M.
1969. Growth, metabolic components and drought survival of lodgepole pine seedlings at three nitrate levels. *Can. Jour. Plant Sci.* 49:393-402.
- Evers, F.H.
1964. Die Bedeutung der Stickstoffform für Wachstum und Ernährung der Pflanzen, insbesondere der Waldbäume. *Mitt. Ver. Forstl. Standortsk. Forstpfl.zücht.* 14:19-37.
- Fischer, R.A.
1968. Stomatal opening: Role of potassium uptake by guard cells. *Science* 160:784-785.
- Fowells, H.A. and R.W. Krauss.
1959. The inorganic nutrition of loblolly pine and Virginia pine with special reference to nitrogen and phosphorus. *For. Sci.* 5:95-112.
- Giertych, M.M. and J.L. Farrar.
1961. The effect of photoperiod and nitrogen on the growth and development of seedlings of jack pine. *Can. Jour. Bot.* 39:1247-1254.
- Hacskeylo, J., R.F. Finn, and J.P. Vimmerstedt.
1969. Deficiency symptoms of some forest trees. *Ohio Agric. Res. Dev. Cent. Res. Bull.* 1015, 68 pp.
- Hewitt, E.J.
1966. Sand and water culture methods used in the study of plant nutrition. *Commonw. Bur. Hort. Plant. Crops. Tech. Comm.* 22 (2nd Rev. Ed.) Commonwealth Agricultural Bureaux, Farnham Royal, Bucks, England. 547 pp.
- Hoeking, D.
1971. Preparation and use of a nutrient solution for culturing seedlings of lodgepole pine and white spruce, with selected bibliography. Northern Forest Research Centre, Edmonton. *Can. Dep. Environ., Can. For. Serv., Inf. Rep. NOR-X-1.*
- Huseby, K.
1973. A tree seedling greenhouse: Design and cost. *Agric. Engineering Dept. Montana State Univ., Missoula, Montana.* 77 pp.
- Ingestad, T. and N. Molin.
1960. Soil disinfection and nutrient status of spruce seedlings. *Physiol. Plant.* 13:90-103.
- Ingestad, T.
1971. A definition of optimum nutrient requirements in birch seedlings. II. *Physiol. Plant.* 24:118-125.
- Klougart, A. and O. Bagge Olsen.
1969a. Substratum for container grown plants. *Acta Hortic.* 15:21-26.
- Klougart, A. and O. Bagge Olsen.
1969b. Nutrition of container plants. *Acta Hortic.* 15:34-36.
- Krajina, V.J., S. Madoc-Jones and G. Mellor.
1973. Ammonium and nitrate in the nitrogen economy of some conifers growing in Douglas-fir communities of the Pacific North-West of America. *Soil Biol. Biochem.* 5:143-147.
- Krueger, K.W.
1967. Nitrogen, phosphorus, and carbohydrate in expanding and year-old Douglas-fir shoots. *Forest Sci.* 13:352-356.
- Levitt, J.
1956. The hardiness of plants. Academic Press, New York, 278 pp.
- Leyton, L.
1952. The effect of pH and form of nitrogen on the growth of Sitka spruce seedlings. *Forestry* 25:32-40.
- Leyton, L.
1967. The mineral nutrient relations of conifer seedlings with special reference to the phosphate relations of *Pinus radiata* D. Don. *Anales Edaf. Agrobiol.* 26:635-651.
- Loustalot, A.J., S.G. Gilbert and M. Drosdoff.
1950. The effect of nitrogen and potassium levels in tung seedlings on growth, apparent photosynthesis, and carbohydrate composition. *Plant Physiol.* 25:394-412.
- Matkin, O.A. and P.A. Chandler.
1957. The U.C.-type soil mixes. pp. 68-85. *In* The U.C. system for producing healthy container-grown plants (K.F. Baker, ed.). Univ. Calif., Agric. Exp. Sta. Manual 23, 332 pp.
- Matkin, O.A., P.A. Chandler, and K.F. Baker.
1957. Components and development of mixes. pp. 86-107. *In* The U.C. system for producing healthy container-grown plants (K.F. Baker, ed.). Univ. Calif., Agric. Exp. Sta. Manual 23, 332 pp.
- McFee, W.W., and E.L. Stone, Jr.
1968. Ammonium and nitrate as nitrogen sources for *Pinus radiata* and *Picea glauca*. *Soil Sci. Soc. Amer. Proc.* 32: 879-884.
- McKee, W.H., Jr.
1972. Light and temperature influence phosphorus absorption by slash pine. *Comm. Soil Sci. Plant Analysis.* 3:223-229.

- Mejstrik, V.K. and H.H. Krause.
1973. Uptake of ^{32}P by Pinus radiata roots inoculated with Suillus luteus and Cenococcum graniforme from different sources of available phosphate. *New Phytol.* 72:137-140.
- Meyer, M.M., Jr. and H.B. Tukey, Jr.
1965. Nitrogen, phosphorus, and potassium plant reserves and the spring growth of Taxus [media] and Forsythia [Intermedia]. *Proc. Amer. Soc. Hort. Sci.* 87:537-544.
- Owens, J.N.
1968. Initiation and development of leaves in Douglas-fir. *Can. J. Bot.* 46:271-278.
- Owston, P.W.
1972. Cultural techniques for growing containerized seedlings. Proceedings of Joint Meeting, Western Forest Nursery Council, and Intermountain Forest Nurserymen's Assoc., Olympia, Wash. August 1972. pp. 32-41.
- Pharis, R.P., R.L. Barnes, and A.W. Naylor.
1964. Effects of nitrogen level, calcium level and nitrogen source upon growth and composition of Pinus taeda L. *Physiol. Plant.* 17:560-572.
- Pharis, R.P. and P.J. Kramer.
1964. The effects of nitrogen and drought on loblolly pine seedlings. 1. Growth and composition. *Forest Sci.* 10:143-150.
- Purnell, H.M.
1958. Nutritional studies of Pinus radiata Don. I. Symptoms due to deficiency of some major elements. *Aust. For.*, 22:82-87.
- Radwan, M.A., G.L. Crough, and H.S. Ward.
1971. Nursery fertilization of Douglas-fir seedlings with different forms of nitrogen. Pacific Northwest Forest and Range Experiment Station, Portland, U.S. For. Serv. Res. Pap. PNW-113.
- Rains, D.W.
1967. Light-enhanced potassium absorption by corn leaf tissue. *Science* 156:1382-1383.
- Shirley, H.L. and L.J. Meuli.
1939. The influence of soil nutrients on drought resistance of two-year-old red pine. *Amer. J. Bot.* 26:355-360.
- Smith, J.H.G., A. Kozak, O. Sziklai and J. Walters.
1966. Relative importance of seedbed fertilization, morphological grade, site, provenance, and parentage to juvenile growth and survival of Douglas fir. *For. Chron.* 42:83-86.
- Schomaker, C.E.
1969. Growth and foliar nutrition of white pine seedlings as influenced by simultaneous changes in moisture and nutrient supply. *Soil. Sci. Soc. Amer. Proc.* 33:614-618.
- Stone, E.L.
1968. Microelement nutrition of forest trees: A review. pp. 132-175, In Forest Fertilization, Theory and Practice. Symposium on Forest Fertilization, April 1967, Gainesville Florida. Tennessee Valley Authority National Fertilizer Development Center, Muscle Shoals Alabama.
- Swan, H.S.D.
1960. The mineral nutrition of Canadian pulpwood species. I. The influence of nitrogen, phosphorus, potassium, and magnesium deficiencies on the growth and development of white spruce, black spruce, jack pine, and western hemlock seedlings grown in a controlled environment. Pulp and Paper Research Institute of Canada, Pointe Claire, Quebec, PPRIC Tech. Rep. 168.
- Swan, H.S.D.
1971. Relationships between nutrient supply, growth and nutrient concentrations in the foliage of white and red spruce. Pulp and Paper Research Institute of Canada, Pointe Claire, Quebec, PPRIC W.P. 29.
- Tiffin, L.O.
1972. Translocation of micronutrients in plants, pp. 199-229, In Micronutrients in Agriculture. Mortvedt, J.J., Giordano, P.M., and W.L. Lindsay, eds. Soil Science Society of America, Inc., Madison, Wisconsin, U.S.A.
- Trappe, J.M.
1967. Pure culture synthesis of Douglas-fir mycorrhizae with species of Hebeloma, Suillus, Rhizopogon and Astreaus. *Forest Sci.* 13:121-130.
- Tukey, H.B., Jr., and M.M. Meyer, Jr.
1966. Nutrient applications during the dormant season. *Proc. Int. Plant Propag. Soc.* 16:306-310.
- van den Driessche, R.
1968. A comparison of growth responses of Douglas fir and Sitka spruce to different nitrogen, phosphorus, and potassium levels in sand culture. *Can. J. Bot.* 46:531-537.
- van den Driessche, R.
1971. Response of conifer seedlings to nitrate and ammonium sources of nitrogen. *Plant and Soil* 34:421-439.
- White, D.P. and G. Schneider.
1972. Soilless container system developed for growing conifer seedlings. *Tree Planters' Notes* 23(1):1-5.
- Wilde, S.A.
1958. Forest soils, their properties and relation to silviculture. Ronald Press, New York, 537 pp.
- Woodwell, G.M.
1958. Factors controlling growth of pond pine seedlings in organic soils of the Carolinas. *Ecol. Monogr.* 28:219-236.
- Zech, W., W. Koch, and F. Franz.
1969. Nettoassimilation und Transpiration von Kiefern zweigen in Abhängigkeit von Kaliumversorgung und Lichtintensität. *Forstw. Cbl.* 88:372-378.