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Ricardo S. Silberman for the degree of Master of Science

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Harry B. Lagerstedt

Lime was applied at different rates to filbert trees grown in containers in an acid soil. As lime application rate increased, the leaf Mn and extractable soil Mn were significantly reduced. In control trees leaf Mn was over 1300 ppm, but no growth reduction or Mn toxicity symptoms were found. Filbert seedlings grown in a nutrient solution at two different pH levels and at different Mn rates did not show toxicity symptoms when leaf Mn ranged from 190 to 1500 ppm. A slight Mn-induced chlorosis and a reduction in growth were apparent at Mn levels of about 1800 ppm. Severe toxicity symptoms, accompanied by a sharp reduction in growth appeared at a Mn leaf concentration of 3700 ppm. As Mn in the leaves increased, Fe decreased. However, Fe/Mn ratios did not correspond with toxicity symptoms or normal growth. Filberts appear to be extremely tolerant to high Mn in their tissues.

Aspects of Manganese Nutrition in Filbert Trees

by

Ricardo S. Silberman

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ASPECTS OF MANGANESE NUTRITION IN FILBERT TREES

INTRODUCTION

Filberts are commercially produced in Turkey, Italy, Spain, and the U.S. in order of importance. Turkey accounts for approximately 70% of the world's supply, Italy about 22%, Spain about 5%, and the U.S. almost 2.6%. About 98% of the filberts in the U.S. are produced in the Pacific Northwest, primarily in the Willamette Valley in Oregon. The area under cultivation is about 28000 acres (about 13000 hectares) with an estimated inshell production of 13500 metric tons. This production supplies almost 50% of the U.S. consumption, the rest being imported. Filberts add about $11,300,000 annually to Oregon's economy.

In the filbert growing area west of Eugene, the soils are acidic with a pH that is normally below 6.0. Analysis of soil samples from several orchards in the Eugene area indicated a range of soil pH from 4.8 to 5.2. Chemical analysis of filbert leaf samples from the mentioned orchards showed a high level of manganese. The concentration of manganese was in the range of 1000 to 2000 ppm as compared to a normal range of 180-800 ppm. Also, low nut yields and poor tree vigor were observed in these orchards.

The application of liming materials in acid soils supplies Ca^{+2} and increases the soil pH (3, 82, 97). Another benefit of liming an acid soil is the reduction in the solubility of manganese, and its subsequent depletion from the soil solution. Manganese, unless found in very low concentrations, is toxic to most plants, and thus

reduces growth. It is well known that the application of lime to acid soils in the Willamette Valley has increased the yield of filberts and tree performance (6). Thus, it is a recommended practice to apply lime in filbert orchards with a soil pH below 6.0 before the orchard is established. It has been reported that the concentration of manganese in filbert leaves was reduced slightly by liming acid soils (6, 52). The purpose of this study was to determine the effect of liming on manganese leaf concentration in filbert trees.

Plant analysis has been demonstrated to be an important diagnostic tool to indicate the availability of mineral elements. Although all plants require the same minerals to complete their life cycles, the quantities and balances necessary for optimum growth and production vary greatly among species. In filbert trees, the optimum range of manganese concentration in leaves has not been fully determined, but preliminary studies indicate that it ranges from 180 to 800 ppm (19). Epstein and Lilleland (29) indicated that filberts are probably more tolerant to manganese toxicity than other fruit and nut trees. A solution culture experiment was designed to establish the values of normal and toxic ranges of manganese in filbert leaves, and to induce and describe manganese toxicity symptoms.

REVIEW OF LITERATURE

Soil Manganese

1. Introduction

Manganese (Mn) occurs in several kinds of primary rocks and particularly in ferromagnesian materials. The Mn released from these rocks by weathering, forms a number of secondary minerals, the most important being pyrolusite (MnO_2) and manganite (MnO(OH)). Total Mn levels may differ considerably between different soils which show a range from 20 ppm to 6000 ppm. Though the total analysis of Mn in the soil is not a measure of availability to plants, it is generally accepted that a certain portion of the total is potentially available (12, 92). In soil solutions, total dissolved Mn is generally less than 1 ppm (89).

The chemistry of Mn and its compounds in the soil is still largely unexplained, because Mn exists in several oxidation states and forms nonstoichiometric oxides with mixed valence states (53). Manganese in the soil can be divided into the bivalent ion, which is the predominant species in soil solution as the exchangeable or nonexchangeable ion, and the insoluble higher oxides. All forms are in dynamic equilibrium with one another in the soil solution. At pH values above 5.5, soil organisms can readily oxidize the bivalent form (56). This oxidation is rapid in well-aerated soils, especially in the higher pH ranges of 6.0 to 7.5. It has been reported that MnO_2 is autocatalytic in the sense that once a little of the oxide is formed, the oxidation of Mn^{+2} is greatly increased (59). The

reverse action also occurs; the higher oxides are reduced, whether by direct reaction with organic matter, or by biological processes. Reduction by organic matter is more likely at low pH values, since the oxidizing power of the higher oxides increases rapidly with acidity. Biological reduction can take place at any pH value (if the oxygen tension is low) when the anaerobic bacteria use the higher oxides as a source of oxygen (56). A long period of waterlogging at a high temperature can liberate large amounts of soluble Mn from the soil (34). The bivalent form of Mn is more common in strongly acid soils, since bacterial oxidation is very slow or absent, whereas organic matter can reduce the higher oxides. In neutral or alkaline soils the bivalent form of Mn is almost completely excluded, since bacterial oxidation is rapid, and reduction by organic matter is very slow. In moderately acid soils the bivalent form diminishes with rising pH, since bacterial oxidation rises to a maximum while reduction by organic matter decreases in importance (35, 56, 72).

2. Factors Affecting the Availability of Manganese in the Soil

The degree of availability of micronutrients in soils is a function of their partition among different forms. This is influenced by many factors. Each form is related directly or indirectly to the soil solution through a dynamic equilibrium.

Viets (95) views these micronutrient forms in terms of pools. The chemical pool is the amount of an element in a given state that can be estimated by extraction and isotropic dilution. Successive pools represent varying degrees of availability from ions in the

soil solution to those remaining in primary minerals. According to this view, increases or decreases in availability are represented by shifts in the element from one pool to another. Organization in these terms is of limited value, but aids in visualizing the manner in which various factors contribute to the availability of micronutrients (in this case, manganese) to plants.

2.1 pH

Hale et al. (42) reported that acid soils contained between 13% and 41% of their total reducible Mn in the exchangeable form. They also found a direct relationship between exchangeable Mn in the soil and leaf Mn in the plants.

Several authors have reported that the level of exchangeable Mn in the soil, and also plant absorption of Mn were decreased by the application of lime, dolomite, calcium hydroxide, and potassium hydroxide to the soil (2, 3, 6, 31, 55, 61, 82, 97, 100). Lime and dolomite, when added to the soil, raise the pH and bring about conditions that favor oxidation of Mn. Lime and dolomite will increase the hydroxil ion concentration to a point where the solubility product of manganous hydroxide is exceeded. Thus, manganese hydroxide precipitates in a finely divided state, which will favor its rapid oxidation.

Christensen et al. (21) found that liming a soil from pH 4.6 to 6.5 decreased exchangeable Mn 20 to 50 times. Fujimoto and Sherman (35) also observed a great variation in exchangeable Mn upon the additionof 4 tons of lime to Hawaiian soils. White (100) reports

that soil Mn extracted with water and with neutral 1 N ammonium acetate was markedly reduced by liming. Lime applications increased yields of beans and peas and decreased tissue Mn levels.

Several reports state that the addition of fertilizers to the soil, particularly with materials containing chlorides, nitrates, or sulfates, is responsible for large pH reductions and an increase in extractable Mn (35, 55, 99, 100). Labanauskas et al. (55) indicated that applications of ammonium nitrate and treble superphosphate increased Mn and iron (Fe) content in avocado leaves. Williams et al. (103) showed that fertilizers increased Mn concentrations of plants in the order $(NH_4)_2SO_4 > NH_4NO_3 > Ca(NO_3)_2$, which coincided with the order of soil acidification by the different fertilizers. Painter and Hammar (78) found that applications of ammonium nitrate and muriate of potash greatly increased leaf Mn in filbert leaves. The effects of the applications of nitrogen and potassium were largely additive in that the highest application rates resulted in the highest leaf Mn concentrations. However, Westermann et al. (99) found that the effect of muriate of potash on soil Mn availability could not be explained on the basis of changes in soil pH. They found that chloride gives up electrons in an oxidation-reduction reaction and thus reduces Mn to a soluble form. Other workers (19, 52) have indicated that reductions in soil pH were proportional to nitrogen applications which brought about an increased leaf Mn concentration. Fujimoto and Sherman (35) showed that when sulfur was added to the soil, the exchangeable Mn content was increased. The sulfur is rapidly oxidized to sulfuric acid mainly by biological

processes. This oxidation lowers the pH of the soil, and thus, further increases the reduction of the oxides of Mn, making Mn more available in the soil. Lohnis (65) found that in an acid soil injury caused by excess Mn could be diminished by fertilizing with magnesium sulfate.

Sims et al. (85) found that soil Mn extracted by DTPA, was significantly related to Mn uptake by plants under a wide range of soil conditions. They showed that soils with lower pH values had the highest amounts of water-soluble, exchangeable, and organic Mn; whereas soils with higher pH values contained larger amounts of reducible Mn. Chelation of native Mn or the addition of ^{54}Mn to DTPA sites was variable among soils, and was related to soil pH. In soils with lower pH values, Mn chelated by DTPA was derived primarily from exchangeable, organic, and reducible fractions. In soils of higher pH values the reducible fraction was the primary source of Mn for chelation to DTPA sites. Since DTPA-extractable Mn and Mn absorbed by plants have been shown to be closely related, Sims et al. speculate that plants would accumulate Mn from the same fractions as DTPA in a given soil.

Browman et al. (17) showed that EDTA, $Mg(NO_3)_2$ and CH_3COONH_4-extractable soil Mn are good predictors of Mn availability to plants. Manganese uptake was closely related to soil pH. A leveling-off in Mn uptake by sweet corn occurred above pH 5.7 which was also correlated to the amounts of soil Mn extracted by the different chemicals.

2.2 Organic Matter

The presence of organic matter may promote the availability of certain elements, presumably by supplying soluble complexing agents that interfere with their fixation.

The effect of organic matter on Mn in soils is particularly pronounced. The addition of organic matter has been found to increase exchangeable Mn in acid soils (21). Leeper (56) reported that the availability of active Mn oxides in soils is due to their reduction by soil organic matter; this reduction is enhanced at low pH values since the oxidizing power of the higher oxides increases with acidity. In soils limed to approach near neutrality, the effects of organic matter additions on the Mn status are short-lived because of more rapid decomposition of organic matter and fixation of released Mn.

Addition of organic matter with a high carbon-nitrogen ratio increased the availability of manganese in the soil (35). This organic matter contains large amounts of easily oxidizable substances such as starch and sugar. Under these circumstances, oxidation of the organic matter takes place with the formation of carbon dioxide. When the biological oxidation of the organic matter proceeds at a rate too rapid for the air to supply adequate oxygen, the reduction of the higher oxides of manganese takes place to supply the needed oxygen. These processes lead to an increase in available manganese.

Sanchez and Kamprath (81) also found that peatmoss added to acid soil increased exchangeable Mn, but they further noted that it

decreased acid-extractable Mn when the soil was limed. Page (77) showed that an increase in pH is accompanied by a fast reduction in the level of water-soluble Mn, thus excluding the possibility that biological oxidation of Mn is the cause of reduced availability. Page concludes that Mn becomes unavailable with increasing pH by the formation of Mn^{+2} complexes with soil organic matter, the capacity of which is increased as soil pH is increased.

The effect of organic matter on manganese transformations in the soil causes three reactions:

1. Complexing agents which are produced effectively reduce the activity of the free ion in solution.
2. There is a decrease in the oxidation potential of the soil, either directly or indirectly, through increased microbial activity.
3. There is a stimulation in microbial activity that results in incorporation of manganese into biological tissue.

2.3 Microbiological Factors

The primary ways in which microorganisms may affect the availability of nutrient elements and Mn in the soil are the following:

1. Release of inorganic ions during the decomposition of organic materials.
2. Immobilization of ions by incorporation to a less available form.

3. Oxidation of an element, generally to a less available form.
4. Reduction of an oxidized form of an element under limiting oxygen conditions.

Probably the most important microbiological effects on the availability of micronutrients involve the oxidation and reduction of iron (Fe) and Mn. There are indications that microorganisms control the oxidation state of Mn and that changes in oxidation potential and pH have their effect only through microbiological activity. Cell poisons such as toluene and azide inhibit the oxidation of Mn^{+2} . Soil sterilization is known to increase available Mn (33, 34, 91).

In 1913, Beijerinck (8) first observed that soil organisms could oxidize Mn. When soil was added to an agar medium containing manganese carbonate ($MnCO_3$), he found that concretions of MnO_2 were produced. Beijerinck and later Bromfield and Skerman (16) identified a number of soil bacteria and fungi that are effective in oxidizing Mn^{+2} .

Of special interest is the role of bacteria in gray speck disease of oats. It was first found that if oats were supplied with less than 14 ppm Mn, gray speck symptoms developed. If oats were grown in a sterile system, the Mn level could drop to 5 ppm without Mn deficiency being observed. However, if the solutions were inoculated with fresh soil, gray speck appeared, but if the soil was sterilized first, it did not (80). The conclusion was that organisms attracted to the rhizosphere, oxidized and precipitated

Mn. Timonin (90) showed that oat varieties particularly susceptible to gray speck had a higher proportion of Mn-oxidizing bacteria in their rhizosphere than did nonsusceptible varieties.

The microbial decomposition of organic complexing agents that serve to stabilize reduced forms of Mn, provides indirect means of promoting the oxidation of it.

Oxidation of Mn in soils is, of course, a reversible process. When the soil is waterlogged and the oxidation potential approaches 0.2 volts, higher oxides of Mn can be reduced. Reduction is an energy-requiring process and the importance of microbiological activity can be demonstrated by the addition of easily decomposable organic matter (38, 51, 81).

2.4 Oxidation and Reduction

There is a close relationship between the state of oxidation of the element and the oxidation potential of the soil. If the oxygen supply in the soil is insufficient, soil microorganisms are forced to utilize progressively weaker electron acceptors. After oxygen and nitrate have been exhausted, manganese hydroxydes are reduced and Mn^{+2} concentrations in the soil solution become appreciable. When rice paddies are drained before harvest, redox potentials rise, and Mn^{+2} concentrations decrease (12).

2.5 Seasonal Variation

The availability of many elements in the soil varies considerably from one part of the year to another. However, there

is considerable divergence of conclusions as to the effect of season on soil availability of micronutrients.

Manganese exhibits the most pronounced seasonal variation in availability, probably due to microbially induced oxidation and reduction (5, 16). In 1934, McCool (67) first noted that water-soluble Mn was high during the summer months. Grasmanis and Leeper (40) reported that Mn toxicity was related to the rate at which Mn is reduced in dry soils, and the rate at which it is biologically oxidized in moist soils. Others found 5 to 10 times as much exchangeable soil Mn in summer as compared to winter. The increased availability in the summer is commonly reflected in plant response. Chlorosis from Mn toxicity has been associated with hot, and dry, summer months. High Mn uptake was associated with high soil temperature and low moisture (68).

DeLong et al. (23) could not find any seasonal trends, but they noted that the Mn extracted with 0.2 N acetic acid increased following each rainfall. It was also observed that exchangeable Mn increased following rainy periods, and easily reducible Mn underwent a corresponding decrease. Fujimoto and Sherman (34) observed that when soils were moistened to field capacity, the level of exchangeable Mn was decreased gradually. On the other hand, when the soil was waterlogged, Mn was released. In the winter and spring under condition of precipitation and low temperatures the chlorosis associated with Mn toxicity diminished or disappeared.

2.6 Rhizosphere

Variations in nutrient content of different plant species growing in the same media are commonly associated with the absorption and transport system of the particular plant. Plant roots are known to exude a great variety of compounds in quantities enough to alter the availability of nutrients in their environment. The effect of these compounds on microbial activity is very marked.

Rhizosphere bacteria appear to reduce the availability of Mn to oats. Jones (50) showed that when a soil was sterilized the uptake of Mn was greatly increased. Timonin (90) found that plants grown in soils treated with chloropicrin, cyanogas-$Ca(CN)_2$, or formaldehyde were free from symptoms of Mn deficiency. Applications of straw mulch resulted in an increase in the population of Mn oxidizing bacteria and thus in severe deficiency symptoms. Timonin also observed that oats susceptible to Mn deficiency had a particularly high density of Mn-oxidizing bacteria around their roots. This suggests that the root exudate pattern of the different varieties of oats, can influence the rhizosphere organisms which in turn, can lead to a Mn deficiency in one species, while a second remains healthy. It has also been shown that the oxidizing properties of some rhizosphere organisms can help to reduce Mn toxicity by inoculating with rhizosphere bacteria.

Beckwith (7) suggested that organic substances given off by the root might form complex ions with Mn^{+2} and Mn^{+3}. Bromfield (14, 15) studied the availability of biologically formed manganese oxide to oats. The oxide was completely available to oats grown in sand

culture but only slightly available in a manganese deficient soil. This difference in availability was probably due to the decomposition by soil microorganisms of MnO_2 reducing substances released by roots. He also found that root washings contained substances capable of dissolving manganese oxides and the activity of these substances increased with increasing acidity.

Godo and Reisenauer (39) measured the solubility of soil Mn and of MnO_2 in root exudates and in rhizosphere and bulk soils over the pH range of 4.5 to 6.5. The relationships between pH and MnO_2 solubility of root exudates closely resembled those between plant uptake of Mn and soil pH. Similarly, the relationship between $CaCl_2$-soluble Mn in the rhizosphere soil and soil pH resembled that between plant uptake of Mn and soil pH. The pattern of the bulk soil was that of the soil alone. They found that the amount of Mn dissolved from the rhizosphere was considerably greater than from the bulk soil. They verified that the relationship between soluble Mn and soil pH is linear in soil not influenced by the growing plant, but in soil influenced by the plant the relationship approximates the shape of the curve depicting plant uptake of the element with pH. It was concluded that root exudates make an important contribution to plant uptake of soil Mn, with the effect being particularly marked in systems more acidic than pH 5.5.

Jauregui and Reisenauer (49) studied the reactions of malic acid, an important constituent of root exudates, with the hydrous oxide of manganese. They found that the reaction of malic acid with δ-MnO_2, followed either of two pathways depending on the pH

controlled adsorption of carboxylates on the oxide surface. In acid systems, 6 mol of Mn^{+2} are released. Otherwise, only 2 mol of Mn^{+2} are released.

Physiological Aspects

1. Biochemical Functions of Manganese

Plants apparently absorb manganese primarily in the divalent state. The divalent manganese ion activates many enzyme reactions involved in carbohydrate breakdown and in the metabolism of organic acids, nitrogen, and phosphorus. It is also involved in photosynthesis.

In its biochemical functions Mn^{+2} resembles Mg^{+2}. Both ion species bridge ATP (adenosine triphosphate) to phosphokinases and phosphotransferases, but the bridge formed by Mn^{+2} differs slightly from that formed by Mg^{+2}. Decarboxylases and dehydrogenases of the TCA (Tricarboxylic acid) cycle are activated by Mn^{+2}, but Mn^{+2} is not specific for these enzymes, and can be substituted by Mg^{+2} (57).

Manganese activates IAA oxidase and thus brings about the oxidation of IAA. The activation mechanism is not clear, although it is possible that a valency change is involved (69). Morgan et al. (70) found that there was a direct correlation between a high (toxic) level of nutrient Mn and both tissue manganese and IAA-oxidase activity. There was an inverse correlation between high manganese and IAA-oxidase inhibitor activity. It seems that there was a high level of IAA-oxidase inhibitor(s), which allowed the enzyme present to function more actively. The degree of enzyme stimulation was directly related to the severity of the symptoms. The researchers advance an hypothesis that above a given threshold

concentration, tissue manganese causes an increase in activity of the IAA-oxidase system which, in turn, reduces the supply of auxin. The auxin deficiency produces abnormal growth as reflected by shortened internodes, restricted leaf expansion, abscission of leaves, loss of apical dominance, and death of apical buds.

Manganese is also in some way involved in the oxidation-reduction processes in photosynthetic electron transport. Manganese is essential in photosystem II where it participates in photolysis and can function as an electron donor. The evidence is that the Hill reaction is specifically inactivated due to Mn deficiency (11). Homann (47) reported that higher plants responded to Mn deficiency either by adjusting the number of chloroplasts per cell to the limited Mn supply, or by forming disorganized chloroplasts with low chlorophyll content. He showed that Mn is firmly bound to the lamellae of the chloroplast and that the normal arrangement of the grana in pokeweed (Phytolaca americana) and tobacco chloroplasts becomes severely disorganized as a result of Mn deficiency.

2. Uptake and Translocation

The rate of manganese uptake differs considerably between plant species. Generally, uptake rates are lower than for other divalent cation species (e.g., Ca^{+2}, Mg^{+2}). Manganese uptake is metabollically mediated (69).

Manganese uptake may be decreased by high pH or by high concentration of calcium, magnesium, ammonium ion, iron, or other competing cations in the growth medium. Lohnis (65) found that Ca

and Mg depressed Mn uptake in plants grown in nutrient solution. Maas et al. (66) working with excised barley roots found that calcium, up to a certain concentration, appeared to enhance the rate of Mn absorption, but at higher concentration exerted a depressing effect. Under the same conditions, Mg had a highly depressing effect. The combination of both Ca and Mg was even more inhibitory to Mn absorption than Mg alone. Manganese had no effect on Ca absorption, but effectively inhibited the absorption of Mg. On the other hand, Mn may also depress the uptake of other cation species. For example, increasing Mn supply reduced the iron content of tomato, oat, citrus, and soybean plants (86, 88, 93).

Manganese is relatively immobile in the plant and it is not clear if it can be translocated in the phloem to any extent. Manganese is preferentially translocated to meristematic tissues (89).

Manganese content is generally higher in leaves than in stems and petioles, and higher in mature leaves than in younger leaves. Manganese tends to accumulate in leaf margins, distal interveinal areas, leaf tips and localized spots in older leaves. Roots generally contain more Mn than do leaves (87).

Economic plant species differ widely in Mn uptake. In a study of eight fruit species growing in the same soil the average foliar Mn values ranged from 494 ppm (filbert, var. Barcelona) to 62 ppm (cherry, var. Bing) (29). Under optimal conditions of Mn availability in nutrient solutions, peas, lettuce, and sunflower accumulated Mn concentrations that were five to six times those of

tomato. Lockman (63) reported differential Mn uptake by three tobacco varieties. Such differences may or may not reflect actual differences in Mn requirement.

Anderson and Harrison (2) found that cotton varieties differed significantly in their ability to extract manganese and iron from a soil with a pH of 6.0. Manganese and iron uptakes were positively and significantly correlated.

It has been suggested that manganese deficiency could be largely overcome in cereals by the selection of varieties that are more efficient in extracting manganese from the soil (36, 74). Other factors reported to affect manganese uptake are temperature and light intensity. Several investigators have found that higher temperatures increased manganese uptake by plants (24, 27, 34). Epstein (27) suggested that the lack of severe manganese toxicity in potatoes grown in acid soils in Maine is due to reduced manganese uptake at low soil temperature. Seasonal effects on manganese uptake have been shown to coincide with temperature effects (73). Lohnis (64) found that plants grown in a warm greenhouse tolerated higher manganese concentrations in their tops than those grown in the field.

Manganese Toxicity

1. Plant Symptoms

Manganese excess generally affects plant tops more severely than roots. Manganese accumulates in the foliage somewhat in proportion to visible injury, but these symptoms of manganese toxicity are highly variable among plant species. Toxicity in plants is characterized by marginal chlorosis and necrosis of leaves, cupping of young leaves and a speckling of older leaves, which is associated with localized manganese accumulations (37, 48, 54, 86, 101). Specific plant physiological disorders associated with manganese toxicity are "crinkle leaf" of cotton (1) , "stem streak necrosis" of potato (10), and "internal bark necrosis" (IBN) of apple trees (26, 83, 104). In severe cases of manganese toxicity, plant roots turn brown, usually after the tops have been severely injured.

Hiatt and Ragland (45) observed toxic symptoms in tobacco when manganese was about 3000 ppm, however, concentrations of up to 5000 ppm did not materially reduce growth. Leaf-bronzing symptoms occurred when carrot tops contained 2600 ppm, and yields were reduced at internal concentrations of 7100 to 9100 ppm (41). Vlamis and Williams (96) found that rice has a high tolerance to excess manganese because its leaves accumulated 5 to 10 times as much manganese as those of oat, barley, wheat and ryegrass. Manganese concentrations in old rice leaves were 6000 to 7000 ppm. Toxic symptoms were observed in alfalfa tops containing more than 175 ppm

of manganese. The concentrations of manganese in the tops of manganese-sensitive plants, are generally well correlated with injury and soluble manganese content in the growth medium, (if other factors are relatively constant).

Plant symptoms of manganese toxicity are often at stress levels which produce little or no reduction in vegetative growth. By contrast, Al toxicity can greatly reduce yields (by root damage) without producing clearly identifiable symptoms in plant tops (45).

Hiatt and Ragland (45) found high concentrations of soluble Al and Mn on very acid Kentucky soils. They reported that Al was more injurious to growth than Mn at the same concentration, but that Al did not produce any of the characteristic symptoms of Mn toxicity. They concluded that it is difficult to know to what extent Al may stunt the growth of manganese toxic plants grown in the fields. Therefore, in acid soils containing high levels of both Al and Mn, the plant growth reduction observed may be erroneously attributed to Mn toxicity, when Al toxicity is the more important of the two factors.

2. Interaction of Manganese with Other Mineral Elements

Manganese toxicity can be reduced by increasing the concentrations of other cations that compete for absorption by plants. Additionally, some elements appear to interact with manganese inside the plant and thereby affect its toxicity.

Manganese toxicity has been associated with iron deficiency in several crops (37, 44, 64, 87, 94). The addition of iron salts or

iron chelates to the growth medium can reduce manganese toxicity in tobacco, rice, clover, bush beans, tomato, oats, peaches, and apples. Iron treatments reduced manganese toxicity in nutrient solutions but this is attributed to a reduction in manganese uptake, rather than to an increase in iron uptake. Wallace and Mueller (98) supplied manganese in the nutrient solution at or near the stress point and with a high and a low level of iron supplied as chelate. They found that manganese resulted in considerable stress at low iron level and in no stress at the high iron level. The high iron level suppressed manganese concentrations in leaves. According to Twyman (94) a decrease in manganese toxicity, when increasing the iron supply to tomato and oat plants grown in water culture, was due to a dilution factor and antagonism. The available manganese is diluted by the increasing quantity of tissue produced as the iron concentration is increased.

Several investigators have emphasized Fe/Mn ratios in relation to manganese toxicity and iron deficiency. In general, ratios between 1.5/1 and 2.5/1 have been considered optimal for normal plant growth (93, 94). A high Fe/Mn ratio is associated with manganese deficiency, a ratio of about 1 with mild toxicity, and smaller ratios are associated with severe toxicity.

Twyman (93) considered that excess Mn affected the action of Fe within plants, by controlling the Fe^{+2}/Fe^{+3} ratio in the cell, rather than Fe uptake. An excess in Mn causes Fe immobilization which brings about Mn toxicity or Fe deficiency symptoms. Epstein and Stout (30) suggested that Mn interfered with the transport of Fe

from the roots to the shoots.

Manganese absorption in tomatoes is affected by interactions between iron, manganese, and molybdenum (51). Manganese had a depressive effect on yield which was counteracted by added iron, but the amount of iron needed was increased as the molybdenum supply increased. Gerloff et al. (38) also reported that molybdenum accentuated manganese-induced iron chlorosis, decreased iron uptake, and decreased growth in tomatoes.

In filberts, Painter and Hammar (78) found that nitrogen and potassium applications increased manganese leaf content. The effects were largely additive and the highest N and K ratios resulted in the highest leaf Mn. It has been suggested that K ions could bring about changes in root permeability, which would affect Mn uptake and accumulation. Bortner (13) suggested that a high internal phosphorus concentration in plants may decrease the toxicity of excess Mn by rendering it inactive within the plant. Domoto and Thompson (25) also suggested that the incidence of internal bark necrosis in apples increased with low phosphorus concentrations. Increased Ca levels in the growth medium often decrease Mn uptake and toxicity (22, 25, 37, 43, 65, 97).

Finally, there is evidence that a soluble source of silica (Si) in the growth medium can protect plants against Mn toxicity (102). Lewin and Reimann (58) found that plants grown in nutrient solution in the absence of Si developed brown necrotic spots characteristic of manganese toxicity. In all species tested Si prevented the development of necrotic spots and decreased the Mn content of the

tissues. Williams and Vlamis (102) showed that barley plants were considerably less susceptible to Mn toxicity when Si was added to the culture medium. Okuda and Takahashi (75) reported that in Si-deficient rice plants manganese was transported to the aerial parts. However, in plants supplied with Si Mn^{+2} was readily oxidized by rice roots, rendered insoluble, and precipitated on the surface of the roots.

STUDY OF THE EFFECT OF LIMING AN ACID SOIL ON LEAF MANGANESE IN FILBERT TREES[1]

R. Silberman[2] and H. B. Lagerstedt[3]

Department of Horticulture, Oregon State University, Corvallis, OR 97331

Additional index words. Corylus avellana L., hazelnut, mineral nutrition, pH.

Abstract.

Lime was applied to filbert (Corylus avellana L.) trees grown in containers at the rates of 0, 6.0, 9.2, 13.8, and 15.8 MT/ha. Lime applications significantly reduced leaf Mn, and extractable soil Mn. Soil pH increased significantly as lime application rate was increased. Extractable soil Mn was well correlated with soil pH and with leaf Mn levels. Liming did not affect plant growth, and Mn toxicity symptoms were not visible. Leaf Mn levels in the control trees was over 1300 ppm.

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[2]Graduate Student.

[3]Research Horticulturist. U.S. Department of Agriculture, Agricultural Research Service.

Introduction

Most manganese (Mn) toxicity occurs on highly acid soils. It has been reported by several authors that liming an acid soil to pH 6.0 to 6.5 decreased the level of exchangeable Mn in the soil, and also plant absorption of Mn (17, 21, 31, 61, 81). Liming highly acid soils usually corrects Mn toxicity (1, 10).

Leeper (56) suggested that Mn exists in the soil in the water-soluble form, exchangeable, available manganic oxides, and insoluble higher oxides of Mn all of which are in equilibrium. Mulder and Gerretsen (72) stated that soils with a pH lower than 5.5 may contain most of their Mn in the water-soluble and/or exchangeable form. As the pH of the soil is increased, bivalent Mn is converted to the less available manganic oxides. Page (77) suggested that the relation of soil pH to water-soluble Mn is incompatible with the theory that non-availability of Mn is the result of the formation of insoluble higher oxides at high pH values. He concluded that the formation of complexes of Mn with organic matter in the soil may account for the observed relationship of Mn and pH. Browman et al. (17) found that Mn uptake by sweet corn was closely related to soil pH, and that Mn extractability was markedly dependent on soil pH. Lindsay and Norvell (60) found that soil Mn extracted by DTPA (diethylene triamine pentacetic acid) was significantly related to Mn uptake by plants under a wide range of soil conditions. Sims et al. (85) showed that chelation of native Mn or added ^{54}Mn to DTPA sites was related to soil pH. In soils with lower pH values, Mn chelated by DTPA was derived primarily from exchangeable, organic,

and reducible fractions. In soils of higher pH values, the reducible fraction was the primary source of Mn. They speculate that since DTPA-extractable Mn and Mn absorbed by plants are closely related, plants would accumulate Mn from the same fractions as DTPA in a given soil. Other researchers have indicated that extractable Mn was markedly reduced by liming (81, 82, 100).

A few Willamette Valley filbert orchards with a soil pH less than 6.0 receive lime applications in an effort to improve nut size, and yields. Liming these soils increased nitrogen, potassium, and calcium uptake (6). The effect of soil liming on Mn uptake by filberts has received little attention. Baron and Gardner (6) found that Mn in filbert leaves was slightly reduced by liming. A knowledge of the relationships between soil Mn levels and plant uptake over the soil pH range usually encountered in filbert orchards would be of value for identifying and predicting potentially toxic conditions. A study was initiated to determine the effect of liming on the pH of an acid soil, on the concentration of Mn and on the concentration of other mineral elements in filbert trees.

Materials and Methods

Veneta loam soil (18) was obtained from an orchard where filbert trees exhibited a high concentration of manganese in their leaves. The soil had a pH of 4.9 $\pm$ 0.2. The soil was broken down and thoroughly mixed in a cement mixer with four different rates of calcium carbonate (6.0, 9.2, 13.8, and 15.8 MT/ha) to raise the pH

of the soil to 5.6, 6.0, 6.4, and 6.8 respectively. Unlimed soil was used as a control. The lime requirement was calculated using the SMP buffer test currently used by the Oregon State University Soil Testing Laboratory (9). The pH of all samples was determined at the beginning and end of the experiment using a glass electrode in a 1:2 soil:water mixture (9).

Nine-month-old self rooted 'Barcelona' filbert trees propagated by simple layerage, were planted in March, 1981 in one gallon plastic containers. Twelve trees were randomly assigned to the control and each lime level. The trees were grown in a greenhouse from March through September when they were moved out to a lathhouse. Each year approximately 10 g of Osmocote 14-14-14 was added per container. The experiment was continued until March, 1983. A completely randomized design was used.

At the time of planting and at the beginning of each growing season the trunk diameter was determined. Also, leaf samples for chemical analysis were obtained yearly in August from mid-shoot leaves. Each sample consisted of 10 to 15 fully developed filbert leaves per tree. Tissue samples were washed in a detergent solution and rinsed in distilled water; were dried at 60 C, ground in a stainless steel Wiley Mill to pass a 40-mesh sieve, ashed at 500 C for 8 hr, dissolved in 5 ml of a 1.8 N HCl solution containing 0.50% Li and 0.10% Co as an internal standard, and the different mineral elements determined by direct reading emission spectrophotometry. Tissue standards were calibrated against an internal standard of 0.50% Li and 0.10% Co in 1.8 N HCl. Nitrogen was analyzed by an

automated micro-Kjeldahl method.

At the end of the experiment, trunk and bud tissue samples were collected for chemical analysis. The analysis methods described above were used. Also soil samples were taken and extractable Mn was determined (9). Data were analyzed by ANOVA, and where significant differences existed, means were separated by Tukey's test at the 5% level.

Results

Lime applications increased the pH values of the soil close to the target values. However, by the end of the experiment in March, 1983, pH values had risen substantially (Table 1).

The amount of manganese extracted from the soil by DTPA was significantly higher in the unlimed check than in the limed treatments. As lime rate was increased there was a further reduction in extractable manganese. Nevertheless, there were no significant differences between the two highest lime rates. There was a strong correlation between extractable Mn and soil pH (Fig. 1). Also, DTPA-extractable soil Mn was well correlated with tissue Mn levels (Table 2, Fig. 2).

Lime applications resulted in markedly reduced concentrations of manganese in the leaves in 1981 and 1982 (Table 3). In the unlimed control soil, the average Mn leaf concentration was significantly higher than that of the limed treatments. Among the lime treatments there were significant differences only between the lowest lime rate and all the other rates. Manganese concentrations

Table 1. Effect of liming on average soil pH.

Lime Rate (MT/ha)	1981	1982
0	5.0	4.9
6.0	5.4	5.6
9.2	5.9	6.1
13.8	6.2	6.5
15.8	6.6	6.9

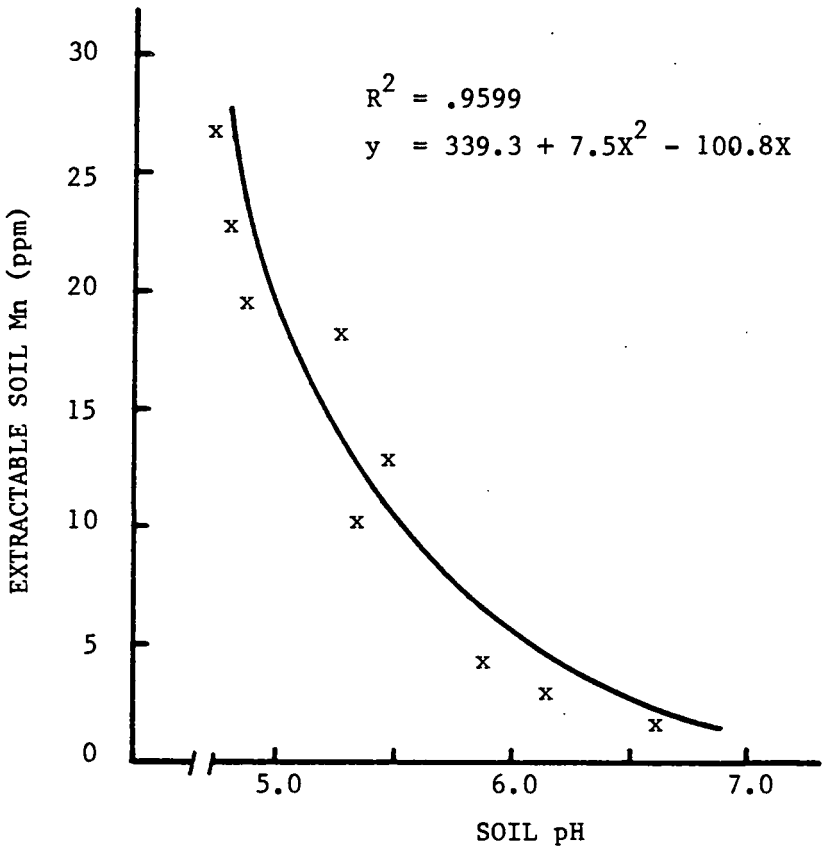

Fig. 1. Relationship between soil Mn extracted by DTPA and soil pH.

Table 2. Effect of liming on Mn leaf concentration (dry wt basis) in filberts and extractability of soil Mn by DTPA.

Lime rate (MT/ha)	Soil pH	Leaf Mn (ppm)	DTPA-Extracted Mn (ppm)
0	4.9	1336a[z]	26.4a
6.0	5.6	292b	9.5b
9.2	6.1	221c	5.6c
13.8	6.5	174c	2.2d
15.8	6.9	180c	1.7d

[z]Mean separation in columns by Tukey,s method, 5% level.

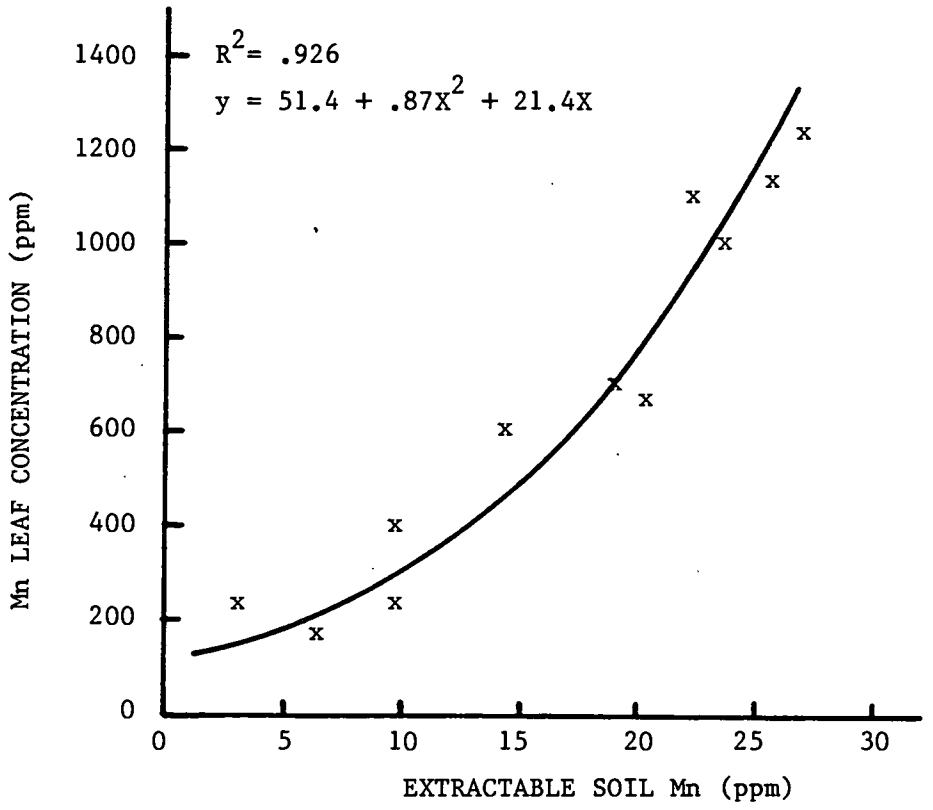

Fig. 2. Relationship between Mn leaf concentration and soil Mn extracted by DTPA.

in the leaves ranged from 135 ppm to over 1300 ppm. In the bud tissue, and trunk tissue manganese concentrations followed a similar pattern.

Nitrogen levels in the leaves were increased by the application of lime, and were above normal in 1981 and in the normal range in 1982 (Table 4). Potassium concentrations in the leaves of the limed treatments were significantly higher than those of the control soil. The Ca concentration was markedly increased as the lime rate was increased. Moreover this trend was more apparent and the differences much noticeable in 1982 than in 1981.

Iron, aluminum, and boron concentrations decreased as lime applications were increased and the differences were statistically significant between the unlimed check and the lime treatments. The differences were not significant among the lime treatments. Al and B concentrations followed this trend in both 1981 and 1982, but Al levels increased substantially in all treatments from 1981 to 1982. On the other hand, B levels between these years decreased markedly in the control, and increased somewhat in the lime treatments (Table 4). The other mineral elements, not shown, were not affected.

In the bud tissue there was a significant increase in the level of calcium with liming. However, there were no differences in the other mineral elements among the different treatments. In the trunk tissue Ca values did not appear to be correlated to the lime treatments and followed a rather erratic pattern (Table 5).

Tree growth was not affected by liming. The percent change in diameter for the 1981 and 1982 growing season did not indicate

Table 3. Effect of liming on Mn concentration (dry wt basis) in filbert leaves, trunk tissue, and bud tissue.

Lime Rate (MT/ha)	Leaf Mn (ppm) 1981	1982	Trunk Mn (ppm)	Bud Mn (ppm)
0	1315a[z]	1336a	259a	499a
6.0	223b	292b	105b	159b
9.2	154c	221c	111b	189b
13.8	140c	174c	64b	108bc
15.8	135c	180c	70b	73c

[z]Mean separation in columns by Tukey,s method, 5% level.

Table 4. Effect of liming on the mineral composition (dry wt basis) of filbert leaves.

Lime rate (MT/ha)	Year	Mineral Element[y]					
		N	K	Ca	Fe	B	Al
0	1981	2.43a[z]	.71a	1.23a	143a	24.5a	74a
6.0		2.63b	.88b	1.32a	111b	3.0b	45b
9.2		2.63b	.98b	1.58a	110b	3.5b	48b
13.8		2.52b	.82a	1.66b	105b	3.1b	46b
15.8		2.54b	.85a	1.61b	101b	3.5b	49b
0	1982	2.23a	.71a	.95a	137a	11.6a	109a
6.0		2.37b	.98b	1.67b	102b	5.0b	83b
9.2		2.44b	1.0b	1.67b	110b	4.9b	77b
13.8		2.41b	.96b	1.71b	113b	5.1b	71b
15.8		2.35b	.98b	1.96c	108b	5.1b	77b

[z]Mean separation in columns by Tukey's method, 5% level.

[y]N, K, and Ca in %. Fe, B, and Al in ppm.

Table 5. Effect of liming on Ca concentration in filbert bud tissue, and trunk tissue.

Lime Rate (MT/ha)	Bud Tissue (ppm)	Trunk Tissue (ppm)
0	0.50a[z]	0.67a
6.0	0.67b	0.93ab
9.2	0.71b	1.10b
13.8	0.72b	1.07a
15.8	0.66b	1.17b

[z]Mean separation in columns by Tukey's method, 5% level.

significant differences among the treatments. No visible symptoms of excess manganese were noted.

Discussion

As expected, lime applications increased soil pH (3, 31), and decreased tissue manganese levels (31, 41, 61). However, liming did not affect plant growth, and manganese toxicity symptoms were not apparent. Although in the control trees manganese leaf levels were extremely high (over 1300 ppm), tree performance was not affected. The possibility that filbert trees can tolerate high tissue manganese levels without showing toxic effects has been suggested (19,29).

The sharp reduction observed in Mn leaf concentration with liming was probably due to the fact that the root system was confined to a small soil volume (1 gallon pots), and that the soil and lime mixture was quite homogenous. Thus, the liming effect was enhanced by an intimate root-limed soil contact and a more complete liming reaction with the soil.

Several investigators have emphasized Fe/Mn ratios in relation to manganese toxicity and iron deficiency (93, 94). A ratio of about 1:1 has been associated with a mild manganese toxicity,and lower ratios with severe toxicity. Although the ratios were very small in the unlimed control (1:10) and in the limed treatments (about 1:2) neither manganese toxicity symptoms, nor any signs of iron chlorosis were observed. It seems that filberts are characterized by a strong tissue tolerance to high levels of manganese and, thus,

the Fe/Mn ratios cited in the literature for other crops would not seem to play a role in predicting Mn toxicity in filberts.

As lime additions increased soil pH, soil Mn levels were markedly decreased. A strong correlation between extractable-Mn and soil pH was found (Fig. 1). Fergus (31) noted a marked increase in exchangeable soil Mn at pH 5.0. Browman et al. (17) reported that soil pH is used most commonly as a variable in regression equations to predict soil Mn availability. However, predicting whether or not a soil will be Mn toxic is rather complicated. Seasonal fluctuations in pH (20) and Mn (40, 34), crop tolerance to manganese toxicity, the effects of fertilizers on soil pH, and therefore Mn availability (55, 100, 103) are some of the factors that require consideration.

DTPA-extractable soil Mn was well correlated with leaf Mn levels (Fig. 2). Sims et al. (85) reported that this correlation holds under a wide range of soil conditions and, therefore, DTPA-extractable soil manganese could serve as a reliable predictor of manganese availability to filberts.

Nitrogen levels in the leaves were adequate, although significantly higher in the limed treatments than in the unlimed check. This was probably due to an enhanced nitrification of N in the soil, as soil pH increased. Thus, the total uptake of N by limed trees would be substantially greater than by unlimed trees, and N applications could be reduced. Iron, Al, and B concentrations were significantly decreased by liming. Probably, this was the result of changes in soil ion availability due to the significant

increase in soil pH.

As suggested by other researchers, it can be concluded that filberts are extremely tolerant to Mn when compared with other fruit and nut trees (19, 29). Although liming significantly decreased Mn levels in filbert leaves no apparent differences in tree performance were observed. Liming increased nitrogen, potassium, and calcium uptake, which might improve tree vigor in the long term. Also, aluminum uptake was decreased, and there were no harmful effects on iron nutrition. However, there is no evidence that much would be gained by liming to pH levels higher than 5.6 to 5.8, because the benefits from each increment in lime diminish, but the cost for each increment remains the same. In filbert orchards with a low soil pH it seems reasonable to apply lime as a preventive measure against Mn toxicity.

MINERAL COMPOSITION OF FILBERT SEEDLINGS GROWING IN SOLUTION CULTURE WITH VARYING AMOUNTS OF MANGANESE AT TWO PH LEVELS[1]

R. Silberman and H.B. Lagerstedt[2]

Department of Horticulture, Oregon State University, Corvallis, OR 97331

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Abstract.

Filbert seedlings were grown in solution culture at two different pH levels and at Mn rates of 0.11, 1.1, 11, and 110 ppm. Normal ranges of Mn in leaves fluctuated between 190 to 1500 ppm. A slight Mn-induced chlorosis appeared at about 1800 ppm, with a reduction in growth. Severe toxicity symptoms were visible at 3700 ppm and produced a serious reduction in growth. Filberts are very tolerant to high Mn in their leaves, without showing harmful effects. As Mn in the leaves increased, Fe decreased. However, Fe/Mn ratios did not correspond with toxicity symptoms or normal growth.

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[2]Graduate Student and Research Horticulturist, respectively.

Introduction

It has been known for many years that the mineral nutrient requirements of all plants are not the same. Plants of different kinds differ greatly in composition although grown under identical conditions. There is also ample evidence of a marked variation in the susceptibility of plants to manganese toxicity.

Munns et al. (73) reported that oat plants grown in nutrient solution, developed consistent varietal differences in manganese concentration in the shoots. Heenan and Carter (43) indicated that there was a considerable variation in the tolerance of soybean cultivars to manganese toxicity. Ouelette and Dessureaux (76) reported that significant differences were noted in alfalfa clones in the rate of manganese translocation from the roots to the aerial portions of the plants. Plants which were the least affected contained smaller amounts of Mn in their stems and leaves and larger amounts in their roots. Gupta et al. (41) showed that Mn toxicity symptoms in carrots appeared when the Mn content of the tops was more than 2600 ppm. Hiatt and Ragland (45) found that tobacco plants began showing manganese toxicity symptoms when Mn was about 3000 ppm. However, concentrations up to 5000 ppm did not materially reduce growth. Fergus (31) showed that the Mn content of French beans ranges from 200 to 1000 ppm in healthy plants; concentrations of about 3000 ppm caused toxicity symptoms. Morris and Pierre (71) working with nutrient solutions found lespedeza and sweet clover to be much more sensitive to manganese toxicity than peanuts. Cowpeas and soybeans held intermediate positions. Epstein and Lilleland

(29) in a study of 8 fruit species growing in the same soil found that the manganese content of the leaves ranged from 495 ppm in filberts (var. Barcelona) to 62 ppm in cherry (var. Bing). Lohnis (64) suggested that in some plants the capacity to tolerate high levels of manganese is apparently associated with a weak absorption or selective exclusion of the element (oat, mustard, mangold), and in others, with a strong tissue tolerance to high levels of manganese (tobacco, flax, potato, strawberry).

Manganese toxicity symptoms in plants are characterized by marginal chlorosis and necrosis of leaves, cupping of young leaves and a speckling of older leaves (72) . Some specific physiological disorders associated with manganese toxicity are "crinkle leaf" of cotton (1), "stem streak necrosis" of potato (10), and "internal bark necrosis" of peaches and apples (22, 26). There is some evidence in the literature which suggests that filbert trees are tolerant to much higher concentrations of manganese in their leaves than most other fruit and nut trees (19, 29).

A solution culture experiment was initiated to determine the effect of manganese concentration and pH on the mineral composition of filbert leaves, buds, and roots; the manganese leaf concentration toxic to filberts; and to induce and describe manganese toxicity symptoms in filberts.

Materials and Methods

Filbert seeds were stratified in sand for 6 months at 8 C, and germinated in a mixture of equal parts of peat moss, perlite, and

vermiculite. A solution culture experiment was initiated in September, 1982, and conducted in the greenhouse for 5 months. The seedlings, 6 per treatment, were transplanted to 8-liter glazed crocks that contained the nutrient solutions. Before transplanting, the root system was rinsed extensively. The nutrient solution contained in each crock was aerated continuously and changed weekly.

The experiment consisted of four nutrient regimes and two pH levels (5.5 and 6.5). The manganese treatments in a modified Hoagland's (28) solution consisted of:

1. 0.11 ppm Mn
2. 1.1 ppm Mn
3. 11 ppm Mn
4. 110 ppm Mn

The seedlings were randomly assigned to each treatment and a completely randomized design was used.

Distilled water and reagent-grade salts were used. The pH of the nutrient solutions was checked twice weekly and adjusted when necessary. Because the volume of solution per container was large (6 liters) pH fluctuations were small ($\pm$ 0.3 pH units). As the average outdoor temperature fell and daylength decreased, the day-time maxima greenhouse temperature varied between 20 C and 28 C, growth was maintained with a 16-hour photoperiod provided by suplemental fluorescent light.

At the beginning and end of the experiment the trunk diameter and fresh weight of the seedlings was measured. Upon termination of the experiment in February, 1983, the seedlings were harvested and

the dry weight of roots, trunks, and leaves was determined. The leaf area from fully developed leaves was measured with a LI-COR (LI-3100) area meter. Leaf samples, trunk tissue, roots, and buds were collected for chemical analysis. Tissue samples were washed in a detergent solution, rinsed with distilled water, dried at 60 C, ground in a stainless steel Wiley Mill to pass a 40-mesh sieve, ashed at 500 C for 8 hr, and dissolved in 20 ml of a 20% nitric acid solution. The different mineral elements were determined by plasma spectroscopy (Jarrell-Ash ICAP 9000). Nitrogen was analyzed by an automated micro-Kjeldahl method. During the experiment the visual symptoms of Mn toxicity were recorded.

Results

In seedlings receiving 110 ppm of Mn the first symptoms of abnormality appeared 4 to 5 weeks after treatments were initiated. A slight interveinal chlorosis typical of the initial symptoms of Fe deficiency showed up on the terminal leaves. In time, these symptoms became more severe and were accompanied with signs of marginal necrosis. As leaves matured, and in older leaves the blade developed brownish specks which enlarge to became extensive necrotic spots with time. Also, some curling or cupping symptoms appeared. Manganese toxicity symptoms on filbert seedlings in the nutrient solution supplying 110 ppm of Mn exhibited restricted leaf expansion, abscission of older leaves, death of apical buds, and break of lateral buds. The lateral growth was chlorotic and the leaves were small. There was no visual evidence of depressed root

development among treatments, but the roots grown in the high-Mn solution were slightly darker brown than those grown in other solutions.

Tissue Mn levels corresponded well with the intensity of the symptoms noted. Toxicity symptoms that consisted of chlorosis, marginal leaf necrosis, speckling, and death of apical buds were noted at Mn levels of about 3700 ppm. When the Mn concentration in the leaves reached 1800 ppm, filbert seedlings showed symptoms that varied from a slight to a severe interveinal chlorosis; and some speckling. No such symptoms occurred when leaf Mn concentrations ranged from 190 ppm to 1500 ppm.

For some of the parameters measured, there were differences between the two pH levels, but interaction of Mn treatments with pH was never significant. Therefore, only the main-effect means are presented below.

Increasing the Mn concentration in the nutrient solution caused a significant reduction in trunk diameter, the percent increase in fresh weight, and in leaf area of filbert seedlings (Table 6). A good correlation was found between Mn levels in the leaves and the parameters mentioned above (Fig. 3, Fig. 4). As the Mn concentration in the nutrient solution was increased, total dry weight of filbert seedlings was significantly reduced (Table 7). This reduction was particularly marked between the two lower and the two higher Mn rates. Leaf and trunk dry weight also decreased substantially as Mn was increased. Although root dry weight was reduced, it was not significantly affected. The leaves seemed to be

Table 6. Influence of Mn concentration in the nutrient solution on percent change in trunk diameter, percent change in fresh weight, and leaf area of filbert seedlings.

Mn conc. (ppm)	% change diameter	% change fresh weight	Leaf area (cm^2)
0.11	61ab[z]	114b	118a
1.1	74a	170a	128a
11	55b	112b	88b
110	39c	54c	60b

[z]Mean separation of Mn treatments by Duncan's multiple range test, at 5% level.

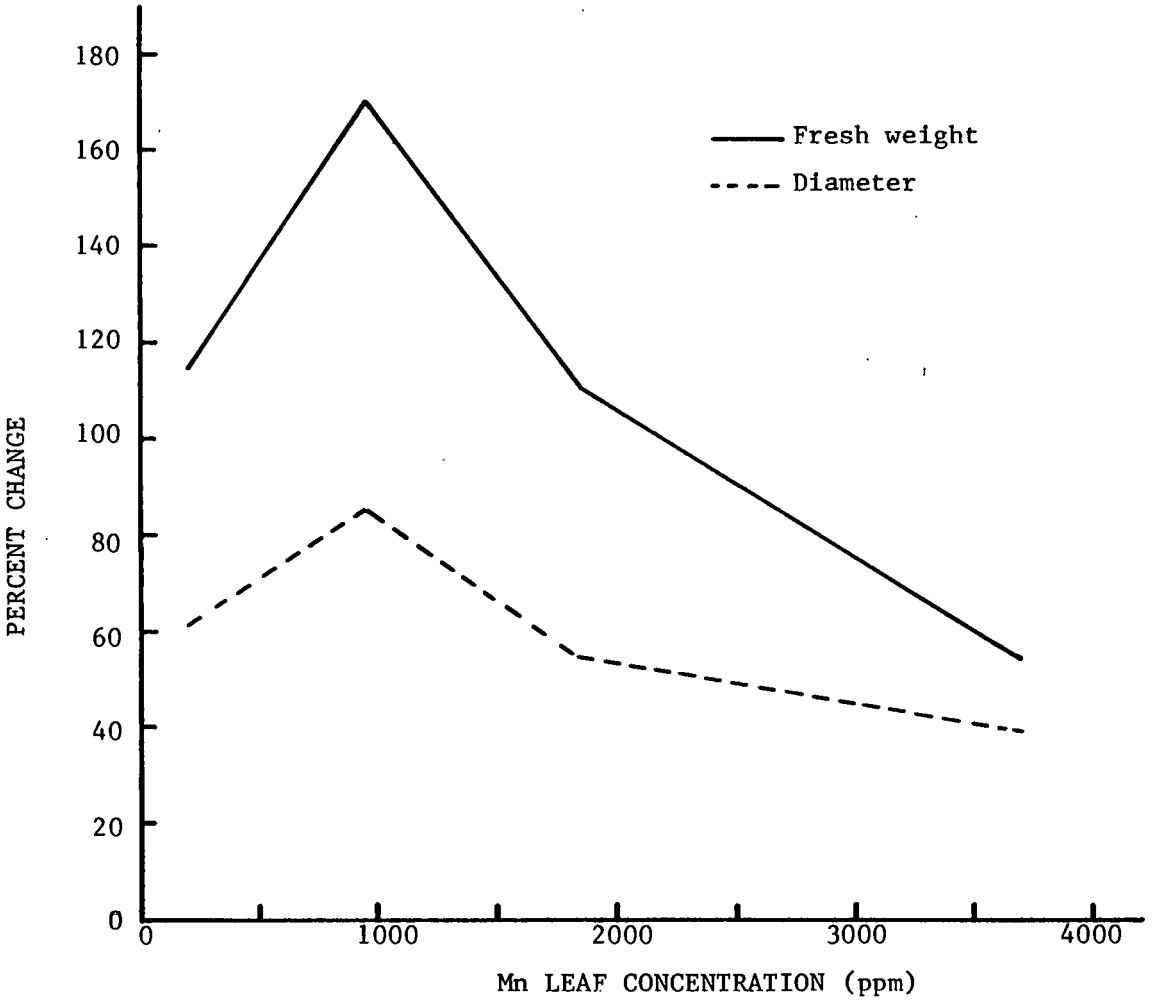

Fig. 3. Relationship between average Mn leaf concentration and percent change in trunk diameter, and percent change in fresh weight in filbert seedlings.

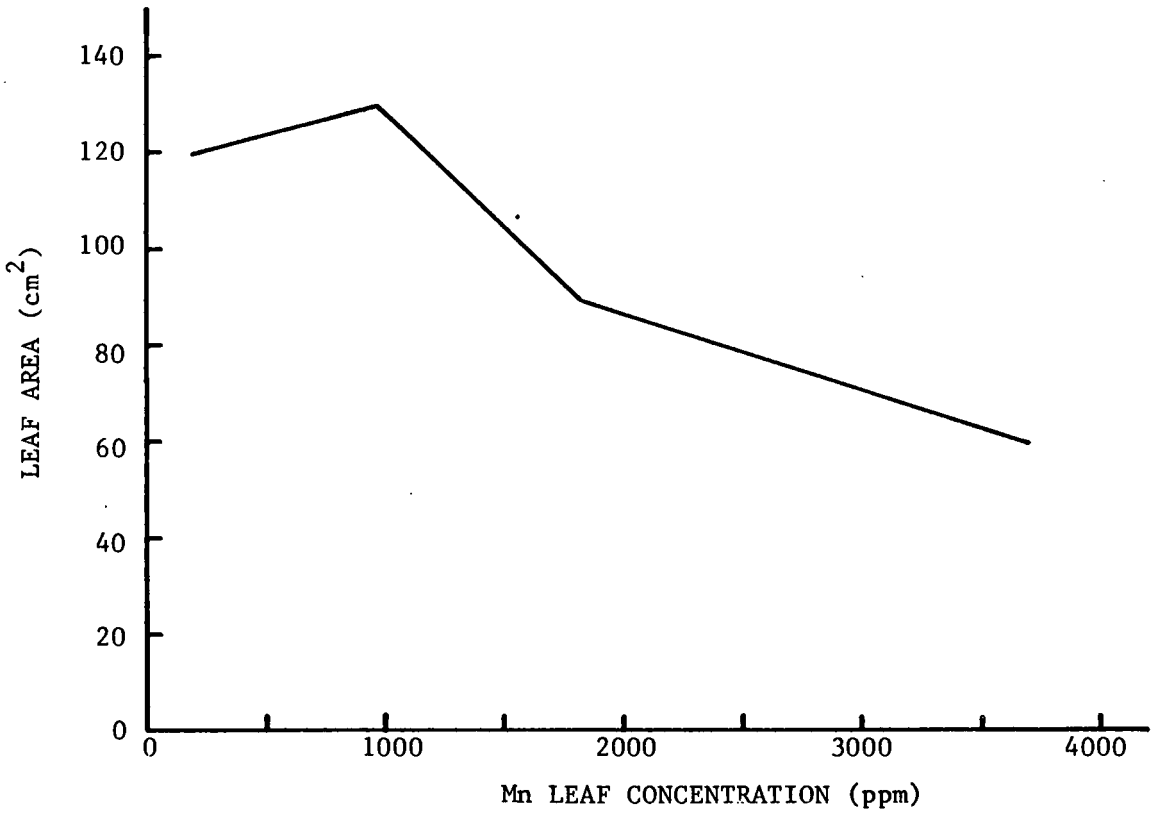

Fig. 4. Relationship between average Mn leaf concentration and leaf area in filbert seedlings.

Table 7. Effect of Mn treatment on leaf, root, trunk, and total dry weight of filbert seedlings grown in nutrient solution.

Mn conc. (ppm)	Dry Weight (g)			
	Leaves	Roots	Trunk	Total
0.11	11.2a[z]	4.2a	14.4a	29.8a
1.1	13.0a	4.3a	16.4a	33.7a
11	7.8b	3.4a	8.7b	19.9b
110	4.9c	2.8a	5.8b	13.5c

[z]Mean separation of Mm treatments by Duncan's multiple range test, at 5% level.

the most sensitive organs to the effects of Mn toxicity. It is obvious from the data in Fig. 5, that Mn leaf concentration and dry weight were well correlated.

The concentration of Mn in the leaves of filbert seedlings was significantly increased as Mn rate in the nutrient solution was increased (Table 8). The differences were significant among all treatments, and the Mn concentration ranged from 190 ppm to over 3700 ppm. The same pattern was repeated with roots, buds, and trunk tissue but the differences were not significant between the Mn solution rates of 0.11 and 1.1 ppm.

When considering the Fe concentration in the leaves, there seemed to be an antagonistic effect with Mn. There was a significant reduction in leaf Fe as substrate Mn increased (Table 9). Leaf Fe concentration was found to be inversely related to Mn leaf concentration (Fig. 6). Also, leaf Fe and leaf Mn plotted against Mn concentrations of the substrate shows clearly that low Mn in the substrate corresponds to low Mn and high Fe in the leaf tissue (Fig. 7). On the other hand, high Mn concentration in the substrate corresponds to high Mn and low Fe in the leaves. The ratios between Fe and Mn within tissues showed no definite relation to any particular toxicity symptoms or to normal plant growth. In buds and trunk tissue the Fe concentration was also significantly reduced, particularly at the higher rates of substrate Mn (Table 9). The Fe analyses for roots showed higher values than did those for other tissues. This was particularly true of the analyses of roots grown at the high Mn level, which shows very high values.

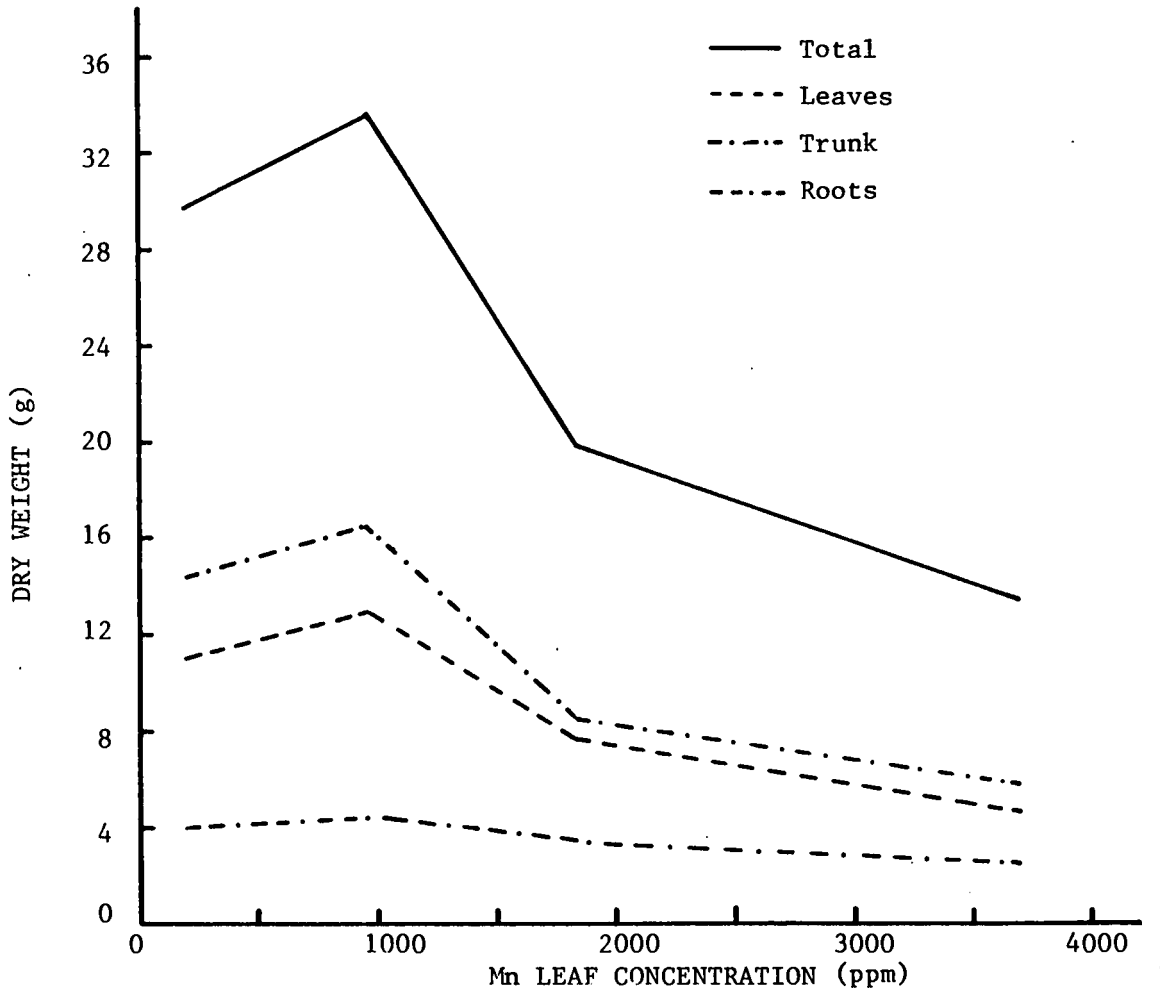

Fig. 5. Relationship between average Mn leaf concentration in filbert seedlings and root, trunk, leaves, and total dry weight.

Table 8. Effect of increasing levels of substrate Mn on the average concentration of Mn in leaves, roots, buds, and trunk tissue of filbert seedlings.

Solution Mn (ppm)	Mn concentration (ppm/g D.M.)			
	Leaves	Roots	Buds	Trunk
0.11	190d[z]	36c	155c	107c
1.1	968c	81c	457c	261c
11	1825b	417b	2017b	862b
110	3727a	1878a	3742a	1490a

[z]Mean separation of Mn treatments by Duncan's multiple range test, at 5% level.

Table 9. Effect of increasing levels of substrate Mn on the average concentration of Fe in leaves, roots, buds, and trunk tissue of filbert seedlings.

Solution Mn (ppm)	Fe concentration (ppm/g D.M.)			
	Leaves	Roots	Buds	Trunk
0.11	218a[z]	359c	134a	80ab
1.1	170b	337c	136a	92a
11	83c	485b	111b	69b
110	41d	760a	44c	50c

[z]Mean separation of Mn treatments by Duncan's multiple range test, at 5% level.

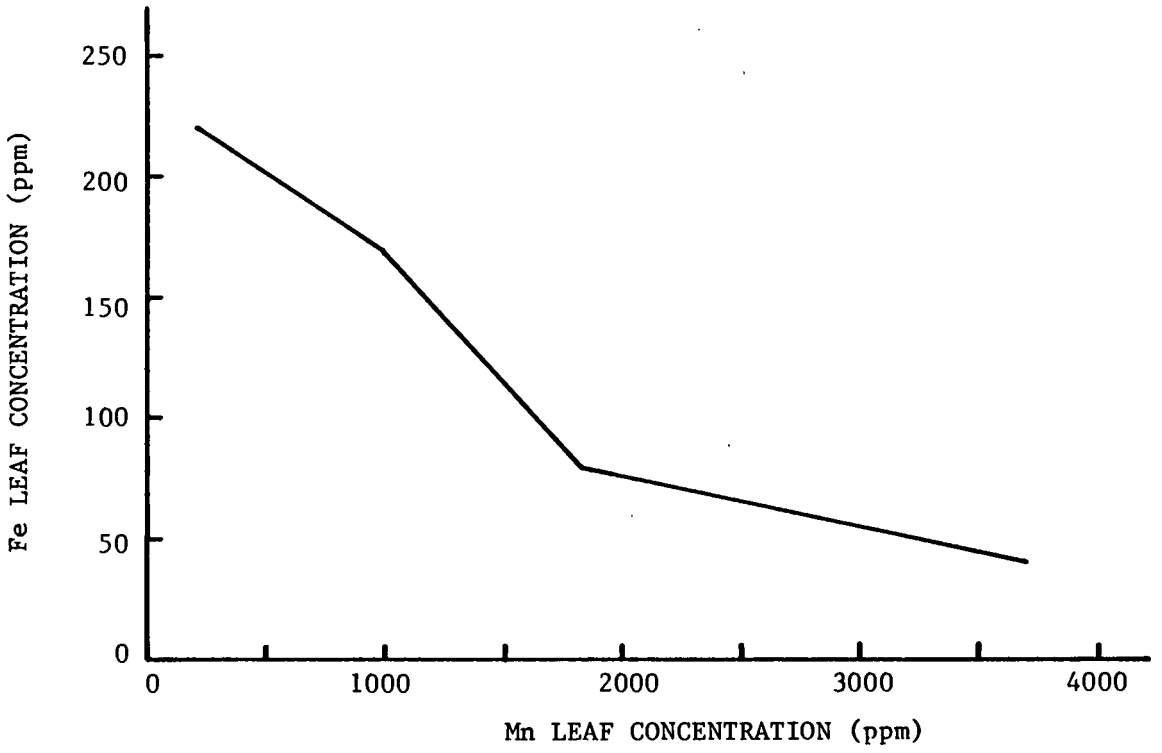

Fig. 6. Relationship between Mn leaf concentration and Fe leaf concentration in filbert seedlings grown in nutrient solution

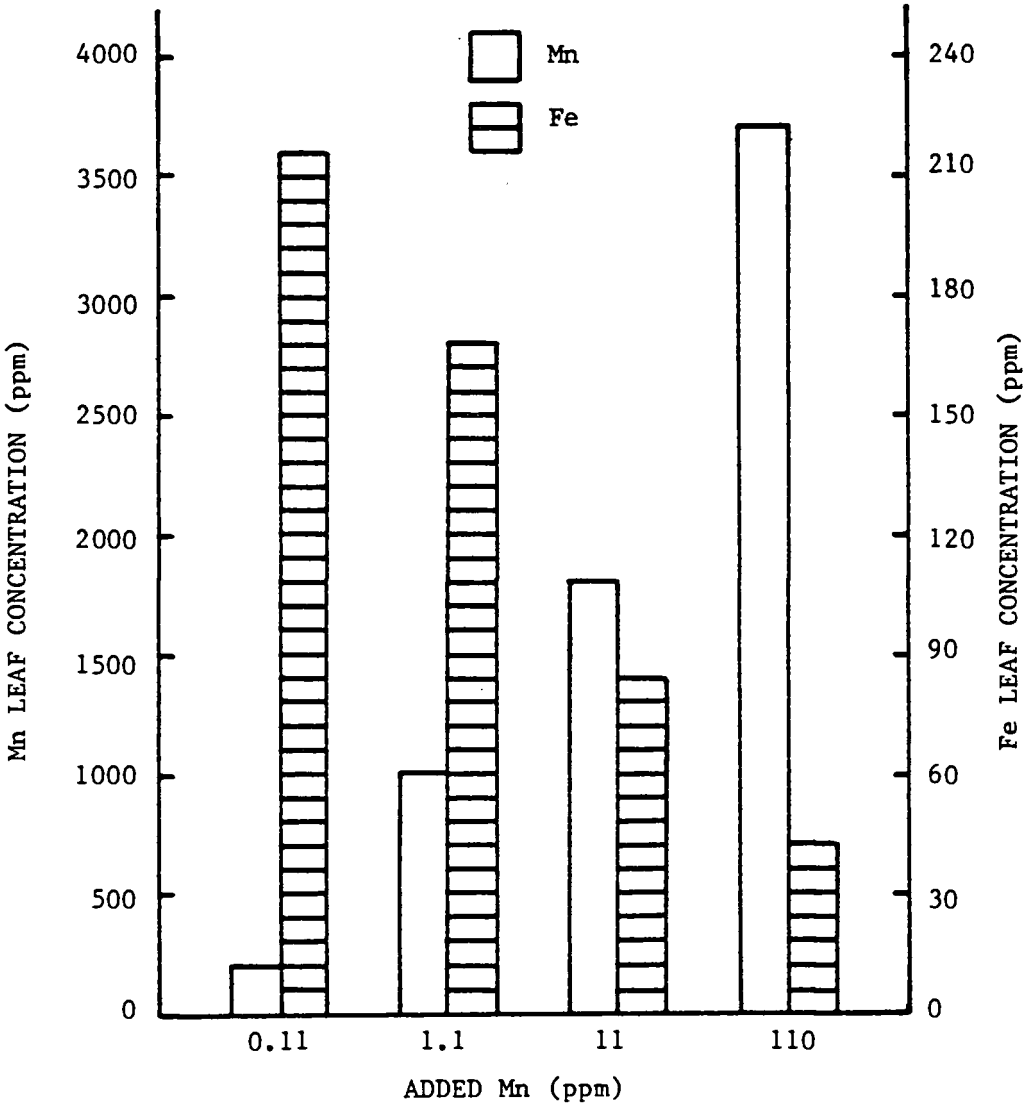

Fig. 7. Effect of increasing Mn concentration in the nutrient solution on the Mn and Fe content of leaves of filbert seedlings.

Other mineral elements in the leaves were affected, but not as severely as Mn and Fe (Table 10). Nitrogen and Ca concentrations were diminished significantly only at the highest rate of Mn in the solution. Phosphorus followed an erratic behavior, and the levels of K, Mg, and Cu were decreased at the higher rates of solution Mn. There also were significant differences in Zn concentration between treatments, except for the uppermost rates of Mn. Elements not shown were not affected, and their concentrations were in the normal range.

Discussion

It has been reported that plant uptake of manganese in solution grown plants is maximal at pH 6.5 and decreases as the pH changes in either direction (39). In this study, the interaction between manganese and pH was not statistically significant.

Mild Mn toxicity symptoms appeared when the Mn levels in the leaves was about 1800 ppm, and became progressively worse as the concentration of Mn increased. When the leaves contained about 3700 ppm Mn, the toxicity symptoms were very severe and were associated with a serious reduction in growth. Manganese toxicity values in filberts as indicated here are considerably higher than have been reported for many other crops. Labanauskas (54) found that, in general, most plants containing more than 400 to 500 ppm Mn exhibited toxicity symptoms. In potatoes, toxicity symptoms were visible at leaf concentrations from 400 to 900 ppm (76). Hiatt and Ragland (45) found that chlorosis and necrotic spotting of tobacco,

Table 10. Effect of substrate Mn on the average mineral leaf concentration of filbert seedlings.

Elements[y]	Solution Mn (ppm)			
	0.11	1.1	11	110
N	2.2a[z]	1.9a	2.0a	1.6b
P	0.35a	0.42b	0.37ab	0.34a
K	2.2a	2.2a	1.8b	1.9b
Ca	0.99a	0.95a	0.97a	0.81b
Mg	0.29a	0.28a	0.23b	0.22b
Cu	8.0a	6.8a	3.5b	2.6b
Zn	69a	44b	24c	19c

[z]Mean separation of Mn treatments by Duncan's multiple range test, at 5% level.

[y]N, P, K, Ca, and Mg in %. Cu, and Zn in ppm.

grown in nutrient solution, developed only when the Mn concentration in the tissues was more than 3000 ppm.

In this study, the normal range of Mn concentration in filbert leaves was from 190 to 1500 ppm without causing a reduction in growth. This indicates that filberts can accumulate larger amounts of Mn in their leaves than other fruit and nut trees, without harmful effects. Epstein and Lilleland (29) reported that the normal ranges of Mn in the leaves, were 72-127 ppm for almonds (var. Nonpareil), 55-125 ppm for apples (var. McIntosh), and 21-270 ppm for walnuts. Other researchers have indicated values of 55 to 145 ppm for pears (var. Anjou), and 180 to 260 ppm for cherries (46, 79).

Under a high Mn regime leaf area was markedly reduced, apical buds died, apical dominance was lost, and leaves abscissed. Morgan et al. (70) reported a direct correlation between high tissue Mn and IAA-oxidase activity, which brings about a reduction in auxin supply. The symptoms of auxin deficiency described by the authors are very similar to the Mn toxicity symptoms mentioned above. Thus, a severe Mn toxicity in plants could actually be the expression of an auxin deficiency. Further investigation would be needed to ascertain this assumption.

The Fe-Mn antagonism reported by several authors was also evident in the tissues analysed in this study (37, 44, 64, 94). As leaf Mn concentration increased, leaf Fe concentration decreased (Figs. 6, 7). According to Sommers and Shive (80) high concentrations of Mn in the tissues are invariably associated with

low concentration of Fe and vice versa. They suggested that when Fe is absorbed, it is retained in the active ferrous (Fe^{+2}) state under the influence of the strong reducing systems of the living cells. If, however, a strong oxidizing agent, such as Mn, with a high oxidation potential is present in adequate concentration, the active Fe may be oxidized to the ferric (Fe^{+3}) state, precipitated in the form of ferric organic complexes, and rendered biologically inactive. An Fe/Mn ratio of about 1 has been associated with a mild Mn toxicity, and smaller ratios with a severe toxicity (93). However, Fe/Mn ratios in the leaves (1.1, 0.17, 0.045, and 0.011 for each treatment respectively) did not correspond with toxicity symptoms or normal growth. It appears that filbert trees have a strong tolerance to Mn within the plant and thus, Fe-Mn ratios in filbert leaves do not seem to have a special relevance.

Roots contained a higher concentration of Fe than other tissues at all treatment Mn levels. This suggests a diminished ability of the roots to translocate Fe to the aerial organs. Epstein and Stout (30) suggested that Mn interfered with the transport of Fe from the roots to the shoots. Sideris (84) working with pineapples grown in solution culture found that the amount of Fe translocated from the roots was greatly reduced by Mn. He suggested that Mn induced chlorosis is brought about primarily by precipitation of Fe in the roots before it can be translocated to the leaves. However. it is difficult to determine by analysis of the roots whether the high Fe value was due to an Fe precipitate that adhered to the root surfaces and could not be removed by washing, or it was formed in the roots

following absorption. For this reason, the results of root analyses should not be overemphasized in consideration of the analytical data.

In summary,it can be concluded that filbert trees are extremely tolerant to a high Mn concentration in their leaves. Normal Mn ranges from 190 to 1500 ppm. A slight Mn-induced chlorosis appears at about 1800 ppm, accompanied by a reduction in vegetative growth. Severe toxicity symptoms were visible at leaf.concentration levels of about 3700 ppm, and this provoked a sharp reduction in growth. As Mn concentration in the tissues increased, Fe levels decreased. However, there was no relation between toxicity symptoms observed and Fe/Mn ratios.

DISCUSSION

Filbert trees can accumulate large amounts of manganese in their tissues without harmful effects. Liming an acid soil decreased tissue manganese levels but had no effect on plant growth. Trees grown in unlimed soil showed manganese leaf levels over 1300 ppm,but there was no reduction in growth, and manganese toxicity symptoms were not apparent. Filbert seedlings grown in a nutrient solution with different levels of manganese were not affected when the concentration of manganese in their leaves ranged from 190 to 1500 ppm. From this evidence, it can be concluded that the normal range of manganese concentration in leaves fluctuates between 190 to 1500 ppm. A reduction in growth, some speckling, and a slight manganese induced chlorosis appeared at manganese leaf levels of about 1800 ppm. Severe toxicity symptoms and a drastic reduction in growth were apparent at leaf concentrations of 3700 ppm. Thus, filbert trees are more tolerant to high manganese levels than other fruit and nut trees. However, it should be noted that manganese toxicity in filberts could often occur at stress levels which produce a reduction in growth and plant vigor, but without showing clearly identifiable toxicity symptoms in the plant foliage.

An Fe/Mn ratio of about 1 has been related to a mild Mn toxicity, and lower ratios with a severe toxicity. In both studies, ratios of 1 or below 1 (0.5 to 0.1) did not correspond with normal growth or toxicity symptoms. This evidence suggests that filberts are characterized by a strong tissue tolerance to high levels of Mn and thus, Fe/Mn ratios do not seem to be an helpful tool for

predicting Mn toxicity in filberts. Also, it is quite probable that different plants may require different Fe/Mn ratios, and extremely small ratios would be associated with toxicity symptoms in filberts. On the other hand, the data clearly demonstrates that Fe and Mn are intimately interdependent in their effects upon the plant. Under conditions of high Mn and adequate Fe supply the plants usually showed chlorosis, the intensity of which was correlated with the Fe and Mn levels in the leaves. The symptoms of Mn toxicity were quite distinct from those of Fe deficiency, but mild forms of the toxicity were identical with the Fe deficiency. This Mn toxicity chlorosis may be due to a competition between Fe and Mn for the active acceptors (62), to an antagonism between Fe and Mn whereby Mn in high concentration in the medium may retard the entry of Fe (93, 94), or to a direct toxic reaction of Mn on processes concerned in Fe metabolism (88).

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APPENDICES

APPENDIX A : Liming

Table 11. Effect of lime applications on leaf element content in filbert trees.

Lime rate (MT/ha)	Year	Leaf element content[y] (dry wt basis)										
		N	K	P	Ca	Mg	Mn	Fe	Cu	B	Zn	Al
0	1981	2.43	.71	.14	1.23	.31	1315	143	3.2	24.5	17	74
6.0		2.63	.88	.13	1.32	.30	223	111	3.1	3.0	15	45
9.2		2.63	.98	.14	1.58	.30	154	100	3.4	3.5	16	48
13.8		2.52	.82	.13	1.66	.31	140	105	3.0	3.1	14	46
15.8		2.54	.85	.13	1.61	.29	135	101	2.9	3.5	14	49
0	1982	2.23	.71	.12	0.95	.29	1336	137	5.0	11.6	23	109
6.0		2.37	.98	.13	1.67	.31	292	102	5.0	5.0	24	83
9.2		2.44	1.0	.13	1.67	.29	221	110	5.0	4.9	24	77
13.8		2.41	.96	.13	1.71	.30	174	113	5.0	5.1	24	71
15.8		2.35	.98	.15	1.96	.30	180	108	6.0	5.1	24	77

[y]N, K, P, Ca, and Mg in %. Mn, Fe, Cu, B, Zn, and Al in ppm.

APPENDIX B: Solution culture

Table 12. Effect of substrate Mn and pH on the average mineral leaf concentration of filbert seedlings.

Solution Mn (ppm)	pH	Leaf element content[y] (dry wt basis)										
		N	K	P	Ca	Mg	Mn	Fe	Cu	B	Zn	Al
0.11	5.5	2.6	2.3	.32	.92	.26	137	235	9.9	91	76	16
1.1		2.0	2.3	.36	.89	.28	906	164	7.3	91	43	18
11		2.1	1.7	.35	.93	.21	1673	76	3.3	86	19	18
110		1.6	1.9	.33	.78	.23	3402	41	2.6	90	16	15
0.11	6.5	1.8	2.1	.37	1.0	.31	243	202	5.6	93	61	20
1.1		1.9	2.2	.48	.99	.28	1030	175	6.3	95	45	18
11		1.9	1.9	.40	1.0	.25	1976	89	3.6	85	27	17
110		1.6	1.8	.37	.85	.26	4051	41	2.6	88	21	15

[y]N, K, P, Ca, and Mg in %. Mn, Fe, Cu, B, Zn, and Al in ppm.