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NUTRIENT AND MYCORRHIZAL EFFECTS ON THE ROOT-SHOOT RATIO
OF CONTAINERIZED PONDEROSA PINE SEEDLINGS

The University of Arizona

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NUTRIENT AND MYCORRHIZAL EFFECTS ON THE ROOT-SHOOT
RATIO OF CONTAINERIZED PONDEROSA PINE SEEDLINGS

by

Zane J Cornett

A Dissertation Submitted to the Faculty of the

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In Partial Fulfillment of the Requirements
For the Degree of

DOCTOR OF PHILOSOPHY
WITH A MAJOR IN WATERSHED MANAGEMENT

In the Graduate College

THE UNIVERSITY OF ARIZONA

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THE UNIVERSITY OF ARIZONA
GRADUATE COLLEGE

As members of the Final Examination Committee, we certify that we have read
the dissertation prepared by Zane J Cornett

entitled NUTRIENT AND MYCORRHIZAL EFFECTS ON THE ROOT-SHOOT RATIO OF
CONTAINERIZED PONDEROSA PINE SEEDLINGS

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direction and recommend that it be accepted as fulfilling the dissertation
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SIGNED: _____

James J. Covert

This document and endeavor is dedicated

to my mother and father,

whose levels of talent and intelligence

have provided those unattainable goals

that are so important to strive towards,

and whose understanding and guidance

have strengthened my ability to do so.

-zjc

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TABLE OF CONTENTS

	Page
LIST OF ILLUSTRATIONS	viii
LIST OF TABLES	ix
ABSTRACT	x
INTRODUCTION	1
LITERATURE REVIEW	4
Drought Resistance vs. Root-Shoot Ratios	4
Manipulation of Root-Shoot Ratios	5
Background	5
Dry Matter Partitioning in Plants	7
Non-Nutritional Means of Root-Shoot Ratio Manipulation	9
Nutritional Manipulation of Root-Shoot Ratios	12
Mycorrhizae	17
Definitions and Historical Background	17
Types of Mycorrhizae	19
The Symbiotic Relationship	22
Cultural Effects on Mycorrhizal Formation	32
Mycorrhizal Effects on Root-Shoot Ratios	34
METHODS	36
RESULTS AND DISCUSSION	44
Preliminary Studies	44
1981 vs 1982	45
Treatment Interaction, Ranking, and Regressions	46
Peatmoss and Seedling Analyses	54
APPLICATIONS AND CONCLUSIONS	58
APPENDIX A: AMOUNTS AND ANALYSIS OF FERTILIZERS USED IN NUTRIENT TREATMENTS	64
APPENDIX B: MODIFIED MELIN-NORKRANS AGAR	66
APPENDIX C: RESULTS AND DISCUSSION OF SPRING 1980 ROTATION	67

TABLE OF CONTENTS--Continued

	Page
APPENDIX D: DATA LISTING FOR SPRING ROTATIONS OF 1981 AND 1982	70
LITERATURE CITED	76

LIST OF ILLUSTRATIONS

Figure	Page
1. Nitrogen level versus mean root-shoot ratio	51
2. Nitrogen level versus mean mycorrhizal infections	52
3. Mean nitrogen and phosphorus content of 26 week old seedlings	56

LIST OF TABLES

Table	Page
1. Nutrient treatments in parts-per-million nitrogen	38
2. Results of t-tests comparing means of the 60 ppm N level treatments from the 1981 and 1982 rotations	46
3. Results of two-way analysis of variance testing for mean differences due to treatment and treatment interactions . .	47
4. Ranked means of nitrogen level treatments	48
5. Ranked means of inoculum treatments	48
6. Nitrogen and phosphorus content of peatmoss used in substrate	54
7. Mean nitrogen and phosphorus content of 26 week old seedlings	56

ABSTRACT

Attempts at reforestation of many sites in the southwestern United States have repeatedly failed. Experience and research show that moisture stress is the primary cause of seedling mortality. Therefore, it is of utmost importance to produce planting stock for these areas that are as drought tolerant as possible. Seedlings with high ratios of root mass to shoot mass and adequate mycorrhizal infections should be more resistant to harsh conditions than most seedlings currently produced in nurseries and greenhouses. Inferences from other research indicated that the root-shoot ratios of seedlings could be increased solely by decreasing the amount of nitrogen supplied to them. Mycorrhizal formation would also be enhanced by minimal nitrogen levels.

Containerized ponderosa pine seedlings (*Pinus ponderosa* Lawson var. *scopulorum* Engelm.) were grown in commercial greenhouses at various levels of nitrogen fertilization and treated with several mycorrhizal inoculums. Mycorrhizal treatments significantly increased shoot height and diameter, but no other seedling parameters. The inoculums did not affect the root-shoot ratio or the percent of short roots that became infected. Nitrogen levels significantly affected all parameters measured. As nitrogen concentration increased, shoot height, diameter, and weight increased, while root weight, root-shoot ratios, and mycorrhizal infections decreased. The inverse relationship between fertilizer nitrogen concentration and the resulting root-shoot ratios of the seedlings was

linear and highly correlated. Nitrogen and percent mycorrhizal infection was nearly linear and also inversely correlated.

The results of this research are immediately applicable to current greenhouse and nursery operations. When stock is to be planted on sites where seedling survival may be compromised by harsh environmental conditions, production methods should be modified to yield seedlings with maximum root-shoot ratios and heavily infected with mycorrhizae.

INTRODUCTION

Reforestation is a critical component of forest management, important to insure both continued resource production and resource protection. In the southwestern United States natural regeneration of ponderosa pine (*Pinus ponderosa* Lawson var. *scopulorum* Engelm.) is frequently nonexistent, especially on volcanic derived soils. Soil moisture is a critical factor in reproducing ponderosa pine. Precipitation in the pine type is adequate for tree growth, but frequent summer drought conditions make seedling establishment precarious at best (Schubert 1974, Heidmann 1969). It has been calculated that the combination of a good seed crop coupled with the summer precipitation necessary to insure natural regeneration on most pine sites in the southwest occurs about once every forty-five years (Fowells 1965). However, recent progress in site preparation and management prescriptions designed to conserve soil moisture have led to successful natural reforestation on some limestone and sandstone derived soils in northern Arizona (Heidmann et al. 1982).

The planting of seedlings eliminates the uncertainty of sporadic seed crops. Nonetheless, attempts at establishing stands of commercially important trees have repeatedly failed on many sites. This results in lost resources, wasted monies, and understocked sites. Again, lack of summer moisture is the most often cited cause of plantation failure (Heidmann, Larsen and Rietveld 1977). To increase the probabilities of successful reforestation efforts, seedlings must be cultured in nurseries

or greenhouses that are more resistant to moisture stress than those currently produced.

Fertilization practices currently followed in most greenhouses and nurseries (refer to Tinus and McDonald 1979) result in seedlings with excellent (and sometimes phenomenal) top growth. However, little consideration is given to the size or quality of the root systems beyond minimum standards. Large tops can become a drastic and often fatal burden on inadequate root systems when the trees are removed from a controlled environment and outplanted on sites that are often harsh. The quantity of water needed by such tops is greater than the small, and initially inactive (Bowen 1973) root systems can supply. Therefore, nutrient regimes need to be designed to yield a maximum of root mass with a healthy, but minimal top. Seedlings could be produced that are suited to a variety of sites by manipulating their root-shoot ratios.

Mycorrhizae are organs that result from the symbiotic relationship of fungi and roots. They exist on most of the world's naturally established land plants. Many studies have shown mycorrhizal seedlings to be more resistant to water and nutrient stress than nonmycorrhizal seedlings (Kormanik, Bryan and Schultz 1977, Marx 1976a, 1975b, Bowen 1973, Mexal and Reid 1973, Harley 1970, Trappe and Strand 1969). Again, fertilization practices normally used in growing seedling stock inhibit or prevent the establishment of mycorrhizae (Ruehle and Marx 1977, Zak 1975, Marx and Barnett 1974, Harley 1965). Because of this, most seedlings used in plantations are nonmycorrhizal, and therefore less likely to survive than mycorrhizal seedlings.

This research was undertaken in an effort to produce ponderosa pine seedlings that would be better adapted to the harsh conditions usually encountered in the southwest. This could be achieved by increasing the root-shoot ratios and mycorrhizal infections of the seedlings produced. It was hypothesized that the root-shoot ratio of containerized ponderosa pine seedlings would respond in a near-linear manner to varying levels of nitrogen applied in fertilizers. Consequently, low nitrogen levels would result in seedlings with greater absorbing tissue relative to transpiring tissue than those produced at higher nitrogen levels. The percentage of short-roots that are mycorrhizal should also be increased by lowering nitrogen levels. On the basis of this nutritional concept, root-shoot ratios of containerized seedlings should be maximized if, 1) all nutrients except nitrogen are supplied at nonlimiting levels, and 2) nitrogen is supplied at the lowest level possible that still maintains a healthy, nonchlorotic plant. Swan (1960) termed this condition "hidden hunger"--the circumstances in which growth is depressed by a mineral deficiency which is not severe enough to induce visual symptoms.

It has been proposed that seedlings can be "tailored" to specific planting sites by inoculating them with appropriate mycorrhizal fungi (Marx 1977). This author would like to suggest that ponderosa pine seedlings can be "tailored" to planting sites by adjusting the root-shoot ratio to meet the degree of moisture stress the seedling is likely to encounter on that particular site. Ideally, then, the forest manager would be able to place an order for planting stock, specifying the seed-source, average root-shoot ratio, and species of mycorrhizal inocula for each plantation.

LITERATURE REVIEW

Drought Resistance vs. Root-Shoot Ratios

Drought can be defined as soil conditions in which little or no moisture is available to plants. Drought resistance, therefore, is the capacity to survive drought with little or no injury. Drought resistance in plants can be roughly divided into the areas of tolerance and avoidance. Tolerance involves the plant's ability to withstand high internal moisture stress and still function. The feasibility of breeding plants to physiologically withstand increasing levels of tissue dessication is questionable. Drought avoidance involves increased abilities to absorb moisture and/or the ability to conserve available moisture. Breeding is probably not necessary to instill these attributes because of the inherent plasticity of plants. Manipulation of the plant's environment during initial growth and development can greatly affect one or both processes (Sutton 1980, Kramer and Kozlowski 1979, Bilan 1971, Luckwill 1960).

The root-shoot ratio is an important factor in the development of internal water stress under any particular circumstance. The sizes of the root and shoot systems influence the relative uptake and loss of moisture (Lopushinsky and Beebe 1976). If, due to optimized growing conditions, a tree is produced that has a large top relative to its root system, that tree may transpire in amounts greater than the roots are capable of absorbing under field conditions (Edgren 1975). Wagg and Hermann (1962) found that high air temperature and strong winds may cause

an unfavorable water balance in pine seedlings and kill them even though the soil moisture may still be available. However, if the root-shoot ratio is high, the absorbing capabilities of the roots are more likely to be comparable with the transpiration requirements of the shoot. Shirley and Meuli (1939) found some correlation between increasing root-shoot ratios and increased drought resistance. They also noted that smaller plants were more resistant to drought than the larger ones. Under any given conditions, a smaller plant would tend to absorb and transpire less water than a larger one, thus conserving the available moisture. Ledig, Borman and Wenger (1970) pointed out that under natural conditions, a plant maintains a balance between absorbing and transpiring surfaces as a normal pattern of growth. This maintains a resistance to drought. Work with herbs (Atkinson and Davison 1973) also showed greater drought resistance with increasing root-shoot ratios. Hauxwell (1966) found that ponderosa pine with the highest average root-shoot ratios also had the highest average index of drought resistance and the highest percentage of drought survival. Yet, Stone and Jenkinson (1971) complained that "Grading of ponderosa pine nursery stock as now practiced has little, if any, bearing on whether seedlings will survive in the field." Seedlings must have a balance between roots and shoots, and have roots capable of functioning after transplanting occurs.

Manipulation of Root-Shoot Ratios

Background

The relative growth rate of root systems and the aerial parts of plants has received widely fluctuating attention in the past century.

This relative growth rate has been variously described as shoot-to-top ratio, top-root ratio, root-shoot ratio, etc. Due to the perceived importance of relatively large root growth, this author will use "root-shoot ratio"--defining it as the ratio of root systems to tops (stems, branches, and leaves) in oven-dry weight. While some of the literature covered uses the other terms, they have all been converted to the "root-shoot ratio" pattern to avoid confusion.

As early as 1930, writers were stressing the importance of balance between tops and roots as "of the utmost importance to the survival of trees" (Toumey and Korstian 1930). Baker (1934) stressed the importance of high root-shoot ratios for seedling survival under severe climatic conditions, noting that "under favorable planting conditions, top-root ratio is much less important, as high survival is normally expected with almost any kind of stock." In 1932, Aldrich-Blake found that progressive increases in nitrogen supplies significantly decreased the relative root weight of several conifers and at least one broad-leaved tree.

Until recently, the subject of root-shoot ratios and their importance to plant survival had not been explored much further, often being ignored completely in the literature. Jones (1968) concurred that the effects of nutrient supply on the ratio of shoot to root had been appreciated for many years, yet he was quick to point out that "Despite these facts, ...the subject seems to have received remarkably little systematic study, and it is treated very briefly in textbooks of silviculture and silvics" (e.g.: Daniel, Helms and Baker 1979). There has been little,

if any, research conducted in which the primary objective was increasing the root-shoot ratio of plants. Most often, mention of root-shoot ratios in the literature, if it is mentioned, comes from observations made during the course of other studies.

The increasing importance of artificial regeneration has led to much research on the most effective way of producing planting stock. This is especially true in the area of containerized seedling production. Unfortunately, seemingly all the research has dealt with optimizing the growth of the plants with little consideration to the root systems (refer to Tinus 1974, Hahn 1978, Tinus and McDonald 1979, Wood and Hanover 1981). The root-shoot ratio of any planted seedling, whether bare-root or containerized, is of utmost importance to its survival, and should be considered accordingly.

Dry Matter Partitioning in Plants

The mechanism by which root-shoot ratios change is unclear, but most explanations rely on competitive sink-source relationships between shoots and roots. This theory is supported by the fact that high growth rates of both roots and shoots rarely occur simultaneously (Brouwer 1962, 1966, Brouwer and DeWit 1969, Stone and Jenkinson 1970, 1971, Cannell and Willett 1976, Kramer and Kozlowski 1979). Shoots are dependent upon the roots for water, nutrients, organic nitrogen compounds (mostly amides and amino acids), and hormones, while the roots are dependent upon the shoots for photosynthates, vitamins, and other organic compounds and hormones. These various physiological ties between the root and shoot systems

together form a complex and highly sensitive control system by which the plant is able to adjust its root-shoot ratio according to the environment in which it is growing, such that overall performance of the plant is optimized (Chapin 1980, Cannell and Willett 1976, Luckwill 1960).

Water, nitrogen, and carbohydrates are by far the most important components of this sink-source competition (Luckwill 1960, Jones 1968). Relative sink strength is as follows: reproductive growth > shoot growth > root growth \approx diameter growth (Kramer and Kozlowski 1979). This is supported by Ledig et al. (1970), who point out that "An individual [plant] would be at an advantage if it distributed more of its photosynthates to the production of leaves, provided that the roots were of sufficient extent to supply water to the top."

If, for instance, the mineral and moisture supply is abundant, shoot growth will be limited by carbohydrate production and/or translocation from storage. The carbohydrates produced will be utilized in the shoots for the production of proteins and other growth substances, with very little being translocated to the roots. Root growth is then limited by the carbohydrate supply. In such a case, the amount of nutrients and moisture absorbed will not increase since their uptake largely depends on the extent of the root system. The supply of materials necessary for growth in the shoot will gradually decrease. Thus, a decreasing portion of the carbohydrates produced can be utilized in the shoot, allowing increased translocation to the roots. Root growth will increase as its carbohydrate supply increases. This will allow the resumption of mineral and water uptake in quantities sufficient for shoot

growth, and the cycle is repeated. The general principle involved is that the plant adapts its growth to its environment by maintaining a ratio of nutrient uptake to carbohydrate synthesis, and by doing so manipulates its root-shoot ratio (Luckwill 1960, Jones 1968).

Brouwer (1962, 1966), and Brouwer and DeWit (1969) substantiate the change in sink strengths by the proximity of the particular meristems to the most limiting factor. When nutrients and water are abundant, carbohydrates are limiting and the shoot is the strongest sink. When nutrients or water become limiting, the root system becomes the strongest sink.

These ideas also apply to seasonal periodic growth of roots and shoots. In the spring, while shoot growth is still inhibited by factors such as air temperature and photoperiod, root growth is active. As shoot growth increases, root growth decreases. As long as internal stresses do not limit shoot growth during the plant's normal growing season, root growth will not again increase until photoperiods and temperatures stimulate bud formation in the shoot. Root growth (and diameter growth) will then be active until external conditions inhibit further growth (Stone and Jenkinson 1970, 1971, Cannell and Willett 1976, Kramer and Kozlowski 1979).

Non-Nutritional Means of Root-Shoot Ratio Manipulation

One strong assumption can be inferred from known physiological concepts and the results of various studies: root-shoot ratios can only be increased by limiting the top growth of the seedlings. There is no

known combination of nutrients or treatments that will stimulate the growth of root systems without causing significant increases in top growth (Philipson and Coutts 1977).

Nutrients and water as limiting factors should not be a concern in greenhouse seedling production. With adequate carbon dioxide, water, nutrients, photoperiod, and proper temperature, growth will be limited only by the plant's capability of producing tissue. The partitioning of growth between the various plant organs is affected by genetics, physiological status of the plant, and the environment in which it grows.

Namkoong and Conkle (1976) found that different provenances of ponderosa pine responded to microsite conditions in several ways. Some families developed unusually large root systems during early growing periods at the expense of height growth and crown position. These larger root systems were better adapted when tree-to-tree competition for soil moisture took place. At this point in stand growth, effective competition for soil moisture can reverse early advantages of favored crown positions. Age too can have an effect on the root-shoot ratio of trees. While it has been found that mature plants will tend to maintain a relatively constant ratio over time (Brouwer 1962, Ledig et al. 1970, Cannell and Willett 1976), it is quite dynamic during the first few years. Jones (1968) and France (1982) found that root-shoot ratios decreased in young seedlings, while Ledig et al. (1970) found the opposite. Comparison of seedling ages on which the conclusions were based, however, indicates that the root-shoot ratio increases for four to six months as the plant produces an adequate complement of lateral and short roots and then

declines for several years. This concept is supported by the seeming discrepant findings cited above and those of the author (unpublished data).

Increasing light intensity causes an increase in relative root growth, while extending photoperiods favors shoot growth. Increasing light intensity stimulates higher photosynthate productivity allowing a greater portion to be translocated to the roots, increasing relative root growth (Luckwill 1960, Brouwer 1962, Ledig et al. 1970). Conversely, increasing the photoperiod allows the shoot to grow for longer periods of time (when conditions are such that it is still the dominant sink) resulting in taller, heavier seedlings with lower root-shoot ratios (Owston and Kozlowski 1976). This was confirmed by McCreary, Tanaka, and Lavender (1978) who found that not only did extending photoperiods decrease root-shoot ratios, but that the amount of decrease could be varied by the intensity of the supplemental lighting. Higher light intensities during supplemental periods caused more growth and lower root-shoot ratios than lower intensities.

Temperature variations, carbon dioxide concentration, and exogenous gibberellic acids may all cause changes in relative shoot and root growth. Research has shown that optimum temperatures for shoot growth are higher than those for roots (Sheppard 1981, Brouwer 1966). Thus, when temperature conditions are "optimized" for seedling production, it generally leads to a decrease in the resulting root-shoot ratios. Similarly, applications of exogenous gibberellins (Heidmann 1982, Wood and Hanover 1981) and increased CO₂ concentrations (Wood and Hanover

1981, Funsch, Mattson, and Mowry 1970) both significantly increase height growth of seedlings without corresponding root growth.

Shoots being more susceptible to moisture stress than roots are likely to grow relatively less under dry conditions than moist conditions (Brouwer 1962, Ledig et al. 1970). Stone and Jenkinson (1970) concluded that the relationship between available water and root growth was controlled by top growth through its absence or presence. As available water increased, top growth increased with root growth remaining constant in greenhouse studies and actually decreasing in growth chamber experiments. McDonald and Running (1979) found that root-shoot ratios significantly affect the development of plant water stress, and indicate that water stress can be used to stimulate relative root growth. The use of induced water stress as a treatment in culturing seedlings with high root-shoot ratios and other desirable features holds much promise, and should be researched further.

Nutritional Manipulation of Root-Shoot Ratios

The key element to top growth, and therefore root-shoot ratios, is nitrogen (Fowells and Krauss 1959). Except in those areas where moisture is the limiting factor, the deficiency of nitrogen in forest soils is usually considered the factor most limiting to forest production (Daniel et al. 1979, Kramer and Kozlowski 1979, DeBell 1979, Pritchett 1979). Specific localities may have deficiencies in the other primary plant nutrients--phosphorus and potassium. The other nutrients essential for plant growth are infrequently deficient or limiting in forest soils (Pritchett 1979).

Nitrogen is utilized in the plant for production of many compounds; proteins, hormones, enzymes, amino and nucleic acids, vitamins, and chlorophyll comprising the majority of the nitrogenous substances. The element is essential for all aspects of growth and is important in carbohydrate production as a component of the chlorophyll molecule. Kramer and Kozlowski (1979) provide a good discussion of the general role of nitrogen in the physiology of woody plants. There are striking differences in the availability and utilization of nitrogen between natural systems (i.e., forest soils) and the relatively axenic systems of nurseries, and especially greenhouses. The competition and interactions of a natural soil system render much of the nitrogen present unavailable. DeBell (1979) estimates that at least 90% of soil nitrogen exists in forms or conditions unavailable for tree growth. Inorganic nitrogen reserves existing as ammonium, nitrate, or nitrite are available for plant absorption, but are continually depleted by leaching, microbial competition, and immobilization through soil particle surface phenomena (Slankis 1974). Consequently, only a small portion of nitrogen applied to forest soils is actually taken up by the forest tree crop (DeBell 1979). Conditions found in nurseries and greenhouses severely limit those phenomena allowing a more direct relationship between the amount of nitrogen applied and that actually utilized by the trees.

The form in which nitrogen is applied to seedlings can alter its response. Studies have consistently shown that greater height and shoot growth, and lower root-shoot ratios, result from nitrogen fertilizer applied as ammonium rather than nitrate (Swan 1960, van de Driessche

1978, France, Cline and Barry 1981, France and Reid 1981). While plants can absorb either ammonium or nitrate, nitrate must undergo reduction to ammonium before it can be utilized within the plant. This reduction is an energy expending procedure, which would reduce the amount of carbohydrates available for other plant processes. Middleton and Smith (1979) calculated that nitrate assimilation requires 8% more energy than ammonium nitrogen.

Phosphorus is extremely important in the production and transfer of energy within plants through various metabolic pathways (Bidwell 1979, Kramer and Kozlowski 1979). Phosphorus is also incorporated into phospholipids and nucleic acids. Much of the phosphorus taken up by a plant is "recycled," not only within individual metabolic processes, but also within the plant as a whole (Barrow 1977). Because of this, more phosphorus does not necessarily mean more growth (Menge, Grand and Haines 1977). The energy pathways within the plant are easily saturated with phosphorus when it is supplied in abundance. Swan (1960) found that higher levels of phosphorus readily inhibited total growth.

While potassium is required in relatively large amounts by plants (second to nitrogen), it apparently is not incorporated into plant structural components. Its function appears to be catalytic in nature and is very important in enzymatic reactions (Tisdale and Nelson 1975) and plant water relations (Hsiao 1973). Due to its extensive role mediating metabolic processes throughout the plant, it is very important in the overall functioning and health of a plant.

Nutritional culturing of conifers has been studied for at least half a century. The quality and conditions of those studies have varied tremendously, as have the conclusions derived from them. Invariably, the experiments were undertaken for one of three reasons: 1) basic knowledge of conifer nutrition, 2) promoting increased growth (productivity) of forest trees, or 3) determine causes and solutions of growth limitations or health problems. While it was often observed which conditions limited growth and those that promoted growth, this author is not aware of research intended to limit growth of healthy seedlings. Careful analysis of the nutritional studies that have been done allow the conclusion to be drawn that nitrogen is the only element that significantly affects the partitioning of dry matter between roots and shoots. A review of some of those nutritional studies follows.

In 1939, two studies were published concerning pine nutrition as affected by nitrogen, phosphorus, potassium (Shirley and Meuli 1939) and calcium (Mitchell 1939). In both studies, it was found that the root-shoot ratio varied inversely with nitrogen concentrations. While increasing levels of the other nutrients (up to toxic levels) consistently produced larger trees, there was no significant effect on the root-shoot ratio of the seedlings. At very low levels of phosphorus, nitrogen uptake was somewhat inhibited. Mitchell (1939) concluded that when adequate supplies of all other essential elements were present, shoot growth was more limited by nitrogen deficiency than was root development.

Fowells and Krauss (1959) stated that root-shoot ratios appeared to be controlled by the supply of nitrogen, though there was less

consistency in the relation of height and nitrogen. Height differences were not significant at the lower levels of nitrogen, though dry weight of the shoot was. This phenomenon was caused by the increasing size and number of needles with increasing nitrogen. These authors also found inhibition of nitrogen absorption under very low levels of phosphorus. Two studies with ponderosa pine seedlings (Potter 1964, Hauxwell 1966) found responses similar to those above. Both authors found significant increases in shoot growth and decreases in root-shoot ratios with increased levels of nitrogen. Phosphorus stimulated root and shoot growth equally, without significant effects on the root-shoot ratios. Hauxwell (1966) had interesting results with high levels of potassium, though. Very high potassium levels decreased relative shoot growth. It is unknown whether this was due to a selective toxic inhibition or a result of disturbed water relations within the plant. The maximum root-shoot ratios found in Hauxwell's study were with the lowest nitrogen and highest potassium levels. Recent research supports the above studies, confirming increased growth with unchanging root-shoot ratios with increasing phosphorus levels, and increased growth with decreasing ratios as nitrogen is increased (van den Driessche 1978, 1980, France et al. 1981, France and Reid 1981). Van Eerden (1974) showed that top growth of containerized seedlings can be reduced or stopped by withholding nitrogen.

A series of experiments on the mineral nutrition and root development of trees provided interesting information not only on the partitioning of growth between roots and shoots, but also between portions of the root system exposed to various nutrient levels (Coutts and Philipson 1976,

1977, Philipson and Coutts 1977). The authors found that when root systems were divided with one portion in a nutrient solution and the other portion in a nutrient-free solution, root growth was heavily partitioned to those roots exposed to nutrients. If the solutions were reversed, there was rapid cessation of growth in those roots removed from nutrient exposure and resumption of growth for those roots placed in the nutrient solution. They also found, like other researchers, that total root dry weight showed no clear relationship with nutrient levels, while shoot growth was significantly stimulated as applied nutrients increased.

Mycorrhizae

Definitions and Historical Background

In 1885, Frank (as cited in Harley 1969) described associations between fungal hyphae and tree roots and gave the name mycorrhiza (a compound Greek term meaning, literally, "fungus root") to the composite fungus-root organs. These root organs were termed ectotrophic because of the presence of mycelium on the outside of the organ. In 1887, Frank (as cited in Hatch 1937) also described roots with exclusively intracellular infections and designated them endotrophic mycorrhiza. Since then, the terms have been shortened to ectomycorrhizae and endomycorrhizae, respectively (Peyronel et al. 1969).

Harley (1969) maintains that most forest trees are normally dual organisms, analogous to lichens, because they absorb materials from the soil through organs covered with fungal tissue. Marks and Kozlowski

(1973) defined mycorrhizae as prolonged symbiotic associations between nonpathogenic or weakly pathogenic fungi and the living cells of roots.

Mycorrhizae have been found in various fossils as far back as the Lower Devonian, some 325 million years ago (Harley 1970). Hatch, in his landmark publication "The Physical Basis of Mycotrophy in *Pinus*" (1937), covered early literature extensively and pointed out that Frank was not the first person to describe mycorrhizae. "For more than a century the most common type of root encountered by investigators of trees growing in natural habitats seem to have been mycorrhizal. Indeed, although they described typical mycorrhizae in every respect, few investigators recognized that the roots which they regarded as the normal absorbing organs of trees were infected by fungi." A book by Schacht (1860, as cited in Hatch 1937), printed in both German and French, contained extensive drawings of the roots of *Abies pectinata* D.C. (*A. alba* Mill.) that showed white swollen tips and racemose branching of the short roots, which typify the mycorrhizae of this fir. Without recognizing their true nature, a number of excellent drawings and descriptions of mycorrhizal roots of beech were published by Muller in 1878 (as cited in Hatch 1937). In Italy, Ibelli (1883, as cited in Hatch 1937) described and illustrated both the mantle and the intercellular net very accurately, yet failed to realize the significance of the structures.

As Sarauw indicated in 1893 (as cited in Hatch 1937), the very fact that these figures were included in the forestry publications of the period is excellent evidence that mycorrhizae (although not regarded as dual structures) were regarded as the normal and typical absorbing organs

of trees. Sarauw also noted that in the entire silvicultural literature of that time (1893), not a single illustration of roots from older trees is found that does not show evidence of a fungal mantle. Despite the literature showing the prevalence of mycorrhizae, some authors persisted in the belief that mycorrhizae were the exception, not the rule. One of the last and most adamant of these was W. B. McDougall. McDougall (1922) and McDougall and Jacobs (1927) repeatedly insisted that mycorrhizae, although produced in many plants, were infrequent, abnormal, and pathological structures. However, Pessin (1928) summarized the opinions of the majority of the scientists involved with mycorrhizae and tree-root research of the time: "Mycorrhizas were found in abundance on roots of *Pinus palustris*, *P. echinata*, *P. caribea* and *P. taeda*. It seems inconceivable, at least to this writer, that seedlings which appear to be literally covered with mycorrhizas and yet seem perfectly vigorous should harbor a parasitic fungus." (See following discussion on symbiosis.)

Types of Mycorrhizae

Endomycorrhizae are the most common type of mycorrhizae. Except for the plant species whose roots form ectomycorrhizae, and the few families that are not mycorrhizal, all plant groups have endomycorrhizae (Gerdemann 1971, 1968). Endomycorrhizae are so called because the fungal structures are almost entirely within the host root, and not on the root surface. The penetrating hyphae may be simple or profusely branched, and in both cases serve to increase the surface area over which exchanges of nutrients and water between fungus and host can occur (Robinson 1967, Trappe 1981).

Endomycorrhizal fungi do not normally cause color or physical changes in the infected root; because of this, the endomycorrhizal infections must be ascertained microscopically. The hyphae of the endomycorrhizal fungi grow into the cortical cells of the roots forming arbuscules (specialized absorbing hyphae or haustoria). Large vesicles, which are swollen hyphae, may also be seen in endomycorrhizal roots. If vesicles and arbuscules are present, the endomycorrhizae are called "vesicular-arbuscular" (VA) mycorrhizae (Marx 1975a).

Ectomycorrhizae occur normally on the roots of forest trees such as pine, spruce, fir, beech, birch, eucalyptus, alder, oak, hickory, and others. Most of the fungi that form ectomycorrhizae produce mushrooms and puffballs. These are epigeous fungi, those whose fruiting bodies occur above ground. However, some hypogeous fungi also form ectomycorrhizal associations (Webster 1970). In North America, there are over 2,400 species of fungus that are known to form ectomycorrhizae (Marx 1975a). This class of mycorrhizal fungi almost always modifies the color and shape of roots enough to be evident to the naked eye. In the genus *Pinus*, bifurcate roots are usually formed. The zone of mycorrhizal infection begins behind the apical meristem and ends where the primary cortex begins to deteriorate. Over this area a fungal sheath, or mantle, composed of tightly interwoven hyphae, is formed. The fungal sheath may be from several to as many as several dozen hyphal diameters in thickness (Slankis 1971, Marx and Bryan 1975a). Under microscopic examination, hyphae of ectomycorrhizal fungi can also be observed growing

intercellularly, forming the Hartig net, which appears to cement the cells together as it replaces the pectinate middle lamella (Marx 1975a).

Ectendomycorrhizae are a class that is apparently an intermediate of the other two classes, but more closely related to ectomycorrhizae. Wilcox (1971) suggested that ectendomycorrhizae may only be a step in ectomycorrhizal formation. This class of infection is typified by the growth of the fungal hyphae around the cortical cells of the root in a Hartig net arrangement, without forming a fungal sheath. This type of infection is not very common, nor considered to be very important. It is most often found occurring in nursery soils that have been previously fumigated.

Some species of mycorrhizae have very broad host ranges, while others have very narrow host ranges (Trappe 1962, Malloch, Pirozynski and Raven 1980). Even though some species of mycorrhizal fungi are more beneficial than others, a given individual tree may have associations with several different species of fungi at a single point in time (Marks and Foster 1973). Not all tree species require mycorrhizae in order to survive. However, some trees, particularly those of the genus *Pinus*, do have an obligate need for mycorrhizae (Marx and Barnett 1974, Harvey, Jurgensen and Larsen 1976). Reddy and Khan (1972) found that in India, there are instances where the very existence of a plant species depends on the availability of a suitable fungal partner.

There are indications that some plant species may be able to form both ectomycorrhizae and endomycorrhizae (Malajczuk et al. 1981). However, because ponderosa pine has not been found to form endomycorrhizal

associations, and rarely, ectendo- associations (Trappe 1962, Wright 1971), the remaining portions of this literature review will deal primarily with ectomycorrhizae.

The Symbiotic Relationship

Symbiosis may take the form of commensalism, mutualism, or parasitism. The distinctions among the types of symbiotic associations are not always clearly defined; furthermore, one type often intergrades into another (Whaley et al. 1964). Mutualism is the symbiotic term generally applied to mycorrhizal associations. Marks and Foster (1973) supported that definition: "Like lichens, mycorrhizae are truly symbiotic and produce new, consistent morphological entities in which both organisms benefit from the association." Hacskaylo (1972) described the mycorrhizal association as "the ultimate in reciprocal parasitism, an evolutionary development...an interdependency that requires an uninterrupted exchange of certain essential metabolites." The key point in mycorrhizal associations is that the root-inhabiting fungi are not pathogenic, but beneficial to their tree hosts. Pyrozynski and Malloch (1975) and Malloch et al. (1980) present strong cases that higher terrestrial plants could not have evolved without the benefits of the fungal symbiont.

There are many ways in which mycorrhizae are beneficial to their tree hosts. One of the basic benefits, and probably the most important in afforestation programs in arid areas (Meyer 1973), is in the uptake of water. The absorbing surface and volume of the root system is tremendously increased by the hyphae of the fungal sheath and those hyphae extending from mycorrhizae into the soil (Bilan 1971). Harley (1969)

estimated that, disregarding the increased soil volume occupied by hyphae extending into the soil, ectomycorrhizae possess surface areas as much as 1000 times greater than nonmycorrhizal short roots. The extensions of hyphae into the soil exploit a volume greater than nonmycorrhizal roots-- materials more than 4 cm distant from the nearest host root can be absorbed by hyphae and translocated to the root (Trappe 1981). Many studies have shown that the mycorrhizal association facilitates an increased capacity of the tree to draw moisture from the soil (Kormanik et al. 1977, Marx and Barnett 1974, Voigt 1971, Schmidt 1947, McComb 1938). Bowen (1973) found that mycorrhizae were much more resistant to water stress than uninfected pine roots. He also found that mycorrhizae sustained water uptake functions longer than nonmycorrhizal roots.

Nutrient absorption and translocation by mycorrhizal fungi has been the most extensively discussed topic in mycorrhizae literature. Stahl, in 1900 (as cited in Hatch 1937), noted that fungi, as evidenced by the high nitrogen and mineral salt content of their fruiting bodies, are extremely efficient in extracting nutrients from organic materials. This consideration, and observations that the abundance of mycorrhizae varies inversely with soil fertility, led Stahl eventually to the opinion that the basis of the habit, as he expressed it, is poverty of mineral salts.

Hatch (1937) concluded from his studies that it was not necessarily a poverty of mineral salts, but an unbalanced nutrient supply that was the basis for mycorrhizal associations. When he provided seedlings with complete nutrient supplies, mycorrhizal development was greatly

suppressed; but, "...mycorrhizae were profusely developed when the nutrient environment was unbalanced by omission of one of the three elements, phosphorous [sic], potassium, or calcium." These findings have been supported by more recent studies (Sihanonth and Todd 1977, Marx 1975b, Bowen 1973, Shoulders 1972, Went and Stark 1968, Rosendahl 1942).

As in the case of water, the potential for nutrient absorption is greatly increased if only from the absolute increase in absorptive surfaces. Nutrients do not move horizontally within soil solutions at a very rapid rate, but hyphae of fungi are known to grow towards areas of nutrient concentration (Webster 1970, Hacskeylo 1971). Thus, the mycelium connected with the fungal sheath provides a physical extension into potential sources of nutrients that uninfected roots could not tap (Bowen 1973).

Another factor in the increased ability of mycorrhizae to absorb and translocate nutrients is the longevity of feeder root functions. In nonmycorrhizal root systems, feeder roots have very high absorptive capacities for a few days. This occurs while the root is young; as the root ages, absorptive capacities decrease dramatically. Marx (1975a), Bowen (1973), and Wilcox (1971) found that mycorrhizae maintained high absorptive potential for longer periods of time than uninfected feeder roots. High absorptive potentials over a longer period of time could be very crucial to nursery or greenhouse stock during the critical first season after outplanting. It has also been found that mycorrhizal roots actually live longer than do nonmycorrhizal feeder roots (Marx 1975a, Bowen 1973, Wilcox 1971).

In 1934, Rayner concluded that mycorrhizae benefit trees if only by converting non-available soil materials into readily available nutrients. This is supported by a study by Bowen and Theodorou (1973) which found that seedling growth was stimulated by the presence of mycorrhizal fungi without infections occurring. Rosendahl (1942) found that mycorrhizal fungi liberated difficultly soluble potassium and phosphorus. The most dramatic increases in the absorption of difficultly soluble nutrients have been with phosphorus and phosphates (Kormanik et al. 1977, Marx 1975b, 1976a, Harley 1970, Trappe and Strand 1969). Barrow (1977) indicated that in some ecosystems mycorrhizal fungi may be more important in the uptake of phosphorus than the roots themselves. As early as 1949, it was known that mycorrhizal roots had a large capacity to absorb and store phosphorus (Kramer and Wilbur 1949). Recent research by Harley (1981) and Malajczuk et al. (1981) has shown that phosphorus accumulation in the fungal mantle of mycorrhizae takes the form of polyphosphates. This accumulation and storage is an adaptation for long-term survival in phosphate deficient soil. Voigt (1971) suggested that increased solubility and uptake in the presence of mycorrhizal fungi may result from higher metabolic activity of mycorrhizal over nonmycorrhizal roots. France (1980) and France and Reid (1981) found mycorrhizal fungi to be physiologically more efficient than roots for mineral absorption. This efficiency difference was more pronounced when nutrients were limiting. Thus, the "unbalanced nutrient supply" that encourages the development of mycorrhizae can actually be due to the unavailability of the limiting nutrient(s), rather than the total lack of it. Elements

known to be included in this category are: N, K, Ca, Mg, Fe, Cu, Mn, Na, Si, Zn, Al and B (Kormanik et al. 1977).

"The most striking result obtained in the study of the uptake of cations by mycorrhizal roots is the selectivity that the roots display in the absorption of cations from mixed solutions" (Harley 1969). Harley (1969, 1970) and Bowen (1973) found that mycorrhizae not only selectively absorb, but selectively accumulate nutrients. As indicated above, this is especially true of phosphorus and phosphates. Marx and Barnett (1974) included nitrogen, potassium, and calcium among those nutrients that are accumulated, and it is probably true for others. During periods of phosphate "flushes" through the soil, mycorrhizae absorb the ions at a very rapid rate. Bowen (1973) reported absorption rates by mycorrhizae that are two to nine times greater than for uninfected roots. These mycorrhizal concentrations of nutrients are not immediately passed on to the host, but are accumulated in the fungal sheath until the external supply of the ion is depleted. When the host develops a deficiency, the stored nutrient is translocated to the host over an extended period of time.

Recent research on the ability of mycorrhizae to selectively prohibit the absorption of ions has important implications in the revegetation of strip-mined land and other adverse sites (Ruehle 1980, Marx and Artman 1979, Marx 1976a, 1976b, 1975a, 1975b). While tree roots tend to absorb toxic as well as nontoxic ions, fungi have demonstrated the ability, or selectivity, to only absorb those nutrients that are beneficial. In 1966, Schramm found that six species of hardwoods and two species of pine

survived on anthracite wastes in Pennsylvania only when the trees were heavily mycorrhizal. Plants that were not mycorrhizal did not survive. Marx (1976b) found that only a few ectomycorrhizal fungi were adapted to the spoils resulting from strip mining. *Pisolithus tinctorius* (Pers.) Coker and Couch adapted very well to coal wastes, allowing revegetation of those soils in Alabama. While not all mycorrhizal fungi are adapted to adverse soil conditions, further experiments with soils of specific toxicities should uncover species of fungi that are adapted to those conditions. Adaptations are also indicated for the high soil temperatures that are associated with many adverse sites (Marx 1975b).

Another beneficial characteristic of mycorrhizal roots is their inherent resistance to pathogens. Young seedlings are highly susceptible to fungal and bacterial pathogens because of their limited root systems. On a mature tree with a large root system, a pathogen may attack and become parasitic on a relatively small portion of the roots and not have a significant effect on the tree's health or growth. Some pathogens, however, are virulent enough to be fatal even to healthy, mature trees. Ectomycorrhizae have been found resistant to feeder root infections caused by many pathogens, including *Mycelium*, *Pythium*, and *Fusarius* spp., which are present in many forest and nursery soils (Marx 1975a, Richard, Fortin and Fortin 1971). Some mycorrhizae are more resistant than others, indicating variation in adaptability to adverse biological as well as adverse chemical edaphic factors. Vaartaja and Salisbury (1965) found *Suillus granulatus* (Fr.) Kuntze, as well as other mycorrhizal fungi, to be strongly antagonistic to pathogenic fungi and bacteria.

In 1970, Catalfomo and Trappe concluded that no one factor is responsible for the protective role of mycorrhizal fungi. More recent studies (Zak 1975, Marx 1973, HacsKaylo 1972, Marx 1971) have indicated that some or all of the following factors may furnish protection against pathogenic invasion: 1) utilization of root carbohydrates and other chemicals which are attractive to pathogens, 2) provision of a physical barrier to pathogens in the form of the fungus mantle, 3) secretion of antibiotics which inhibit or kill the pathogen, and 4) stimulation of the host root cells during symbiosis to produce chemical inhibitors.

Rovira (1965) and Melin (1963) found that exudates from roots may stimulate mycorrhizal growth, germination of microsclerotia, zoospore activity, and virulence of various pathogens. If mycorrhizae are developed on the roots, they normally will absorb the majority of the root exudates before they become available to potential pathogens. A fascinating series of experiments by Ratnayake, Leonard and Menge (1978) may have further elucidated the protective role of mycorrhizal fungi, through the indirect means of phosphorus nutrition. Their data show that variations in the amount of sugars and amino nitrogen compounds exuded from roots were more dependent on the permeability properties of the root membranes than the concentration of these compounds in the roots. Permeability of the membranes decreased with increasing phospholipid content, which increased with improved phosphorus nutrition. Thus, the improved phosphorus nutrition that normally occurs with the onset of mycorrhizal infection (Barrow 1977) could result in decreased exudation of those metabolites necessary for pathogen stimulation. The effects of

plant nutrition on mycorrhizal susceptibility will be discussed in more detail later.

Theoretically, a physical barrier to pathogens is formed in mature ectomycorrhizae by the tightly interwoven hyphae of the fungal mantle. This hyphal network usually is complete, i.e., relatively free of voids which would expose root tissue to direct contact with the soil. Therefore, to establish infections in the cortical tissue of a mycorrhizal root, a pathogen would have to be able to physically or enzymatically penetrate the fungus, as well as the plant's cortical tissues. The suggestion that mycorrhizae form a physical barrier to pathogens is supported by studies that highly correlate percentage of mycorrhizal roots with the degree of root infection control (Marx 1973).

Many fungi are known to secrete antifungal and antibacterial chemicals (Webster 1970), so it would not be unreasonable to assume that mycorrhizal fungi wage "chemical warfare" on pathogens. Along with experiments by Vaartaja and Salisbury (1965), Krywolap (1971), and others, Marx, in an exhaustive 1969 study, found that several mycorrhizal fungi common to the southeastern United States inhibited the growth of nearly half of 48 different fungal root pathogens and some pathogenic soil bacteria. One fungus, *Leucopaxillus cerealis* (Lasch.) Singer inhibited 92% of the test pathogens.

The specific effects of the growth hormones, or auxins, secreted by mycorrhizal fungi upon the host are little understood. Preliminary studies indicate that they may be significant. The characteristic morphology of mycorrhizal roots is one indication. These structural

deviations are caused by profound physiological and metabolic changes which the nonmycorrhizal shootroots undergo during their conversion to ectomycorrhizae. This is due to interactions between fungal auxins and host metabolites (Slankis 1971, 1961). The fungal auxins are not retained within the mycorrhizae, but are translocated into the mother root. Experiments with labeled auxins have shown that growth hormones from mycorrhizal fungi are translocated even into the shoots of seedlings (Slankis 1973). Wullschleger and Reid (1981) found that while some fungi may liberate cytokinins in pure culture, they may not transport them to a host plant. Other fungi that do not synthesize cytokinins in pure culture, may enhance host cytokinin levels by as much as 44% after forming mycorrhizae.

Along with auxins and cytokinins, fungal symbionts provide the host with gibberellins, and growth-regulating B vitamins (Kormanik et al. 1977, Miller 1971). These hormones are homologous to those formed by the plant itself, providing quantities of the growth regulators that are in excess of "normal" amounts. Yet these fungal exudates are important for "normal" growth; studies undertaken where nutrients and water were not limiting factors still resulted in abnormal development in the absence of mycorrhizal fungi (Kormanik et al. 1977). Melin (1963) concluded that mycorrhizal fungi exuded a substance, which he designated the M-factor, that acted as a growth regulator. However, its identity and specific function is not known. Bowen and Theodorou (1973) have isolated the substance, but have not been able to identify it. They also found that high concentrations of the M-factor were inhibitory to fungal growth. Mycorrhizal exudates do influence, and probably benefit the host plant's

development and growth. Linderman and Call (1977) conducted an experiment that had profound results in terms of exudate significance. They found that the addition of extract from ectomycorrhizal fungi to the rooting medium applied to woody cuttings of *Arctostaphylos* and *Vaccinium* resulted in significantly greater numbers and volumes of rootings than medium without the addition of extracts. This enhanced rooting was in the absence of any mycorrhizal infections. Gay (1981) recently had similar results rooting *Pinus halapensis* Mill..

Mycorrhizal fungi exhibit a remarkably low energy requirement for physiological maintenance (France and Reid 1981). Consequently, the benefits that they receive from the phytosymbiont are meager compared to the host benefits covered above. The major requirement of the fungal symbiont is carbohydrates, though some organic nitrogen compounds may be translocated from host to fungus (Björkman 1970). Optimal growth of fungal species is attained in the presence of specific hexoses (i.e., glucose, mannose, fructose), homogeneous disaccharides (cellobiose, sucrose, trehalose), and certain glycans (starch, pectin, dextrin) (Lamb 1974, Palmer and Hacskaylo 1970). The ability of ectomycorrhizal fungi to utilize more complicated carbon forms may actually reflect their potential for inducing specific degradative enzymes. Thus, fungal growth attained on complex carbon structures may reflect the action of celluloses, glycosidases, etc., in the conversion of these compounds into simple carbon forms which can more readily be utilized by the fungus (Lamb 1974, Palmer and Hacskaylo 1970).

Cultural Effects on Mycorrhizal Formation

It has frequently been stated by mycorrhizal researchers that many of the cultural practices used in raising planting stock severely limit mycorrhizal formation (Molina 1977, Marx 1975a, Zak 1975). Yet, as indicated previously, emphasis has remained on optimizing growing conditions; this is especially true of containerized systems. "Although the tops of seedlings grown in containers often grow luxuriantly, most root systems we have examined lack normal ectomycorrhizal development" (Molina 1980). "Most of the seedlings we have examined...routinely lack mycorrhizae. ...very little change in routine nursery practice is needed except in fertilizer management" (Molina 1979).

The mycorrhizal association, like shoot growth, is apparently quite sensitive to nitrogen concentrations. A considerable number of observations over many years indicate that high fertility levels (especially high nitrogen) repress or totally inhibit mycorrhizal formation. Fowells and Krauss (1959) noted that mycorrhizae formed readily on seedlings treated with low amounts of nitrogen, while the roots of seedlings treated with high levels of nitrogen were devoid of mycorrhizae and covered with root hairs. Similar results of high available nitrogen levels suppressing mycorrhizal formation were obtained by Marx et al. (1982), Menge et al. (1977), Sinclair (1974), Wright (1971), and Theodorou and Bowen (1969).

One of the most prominent attempts to explain the relationship between mycorrhizal formation and nutrient availability has been that of Björkman (1970). In essence, Björkman proposed that mycorrhizal formation is dependent on a surplus of soluble sugars in the roots, and these levels

are, in turn, determined by nitrogen and phosphorus availability and light intensity. High levels of available N and P stimulate metabolism and result in a depletion of soluble carbohydrates while low light intensities restrict the amount of carbohydrates produced. Thus, either condition can inhibit mycorrhizal formation. Extreme deficiencies of mineral nutrients are also detrimental to mycorrhizal formation due to the overall reduction in metabolism. Marx, Hatch and Mendicino (1977) provided supporting evidence for this theory with correlations between the sucrose contents of short roots and the percentage of short roots that were mycorrhizal. Simultaneously, sucrose levels varied inversely with levels of soil fertility. Björkman's theory is also supported by the findings of Ratnayake et al. (1978) relating phosphorus nutrition and root exudation which were discussed previously.

Some aggressive species of mycorrhizal fungi are somewhat suited for the high levels of nutrients and moisture found in greenhouses, though they may not be adapted to all outplanting sites. Some examples of these fungi are: *Thelephora terrestris* (Ehrh.) Fr. (Ruehle 1980, Marx et al. 1982); *Laccaria laccata* (Scop. ex Fr.) Berk. & Br. (Molina 1977, Sinclair, Sylvia and Larsen 1982); and *Pisolithus tinctorius* (Pers.) Coker and Couch (Cordell and Marx 1980). *Pisolithus tinctorius* is virulent enough, that under some conditions, increased nutrients may have no significant effect on mycorrhizal formations (France et al. 1981).

Though response to nitrogen fertilization is highly dependent upon rhizosphere and edaphic conditions, increased nitrogen levels may inhibit mycorrhizal formation in field conditions also. Menge and Grand

(1978) found greater numbers of mycorrhizal root tips and fruiting bodies in unfertilized plots, or plots fertilized with phosphorus only, than on plots fertilized with nitrogen. In 1965, Richards found that mycorrhizal development on 21 week old seedlings varied inversely with total N content. Yet at 45 weeks, when the nitrogen content of the seedlings had become uniform throughout treatments, mycorrhizal development was no longer significantly different.

As a general rule, high nitrogen concentrations appear to simultaneously increase shoot growth and decrease mycorrhizal formation to the point of significant negative correlation (Menge et al. 1977). Therefore, seedlings grown under nutrient regimes that enhance maximum root-shoot ratios are very susceptible to mycorrhizal infections (Munson, Trappe and Zak 1981).

Mycorrhizal Effects on Root-Shoot Ratios

The mycorrhizal association does not have a consistent effect upon the root-shoot ratio of the phytosymbiont. Molina reported in 1979 that inoculation of containerized seedlings had no significant effect on seedling height, stem diameter, top and root dry weights, and root-shoot ratios. In 1980 he reported that associations with *Laccaria laccata* may significantly decrease the root weight and stem diameters of seedlings. This was confirmed by Sinclair et al. (1982). France and Reid (1981) found that mycorrhizal infections often, but not always, reduce the root-shoot ratio of seedlings. Marx et al. (1982), in a series of experiments involving a wide range of conditions and many different species, found that more often than not, inoculation did not significantly alter

the root-shoot ratios. Some situations, however, resulted in lower root-shoot ratios, while others resulted in higher root-shoot ratios. Recent studies by Cline and Reid (1982) found rough correlations between increased mycorrhizal infections and decreased root-shoot ratios.

It is known that some species of mycorrhizal fungi may be more advantageous under a given set of circumstances than other species (Trappe 1977, Molina 1977). Therefore, one plausible explanation for the inconsistent effect of inoculations on the root-shoot ratios of planting stock would pertain to the variety of circumstances (cultural conditions) involved and the combinations of plants and fungi studied. If the mycorrhizal association is highly beneficial to the host plant, its growth will be improved. As discussed previously, improved growth generally translates to relatively greater top growth and reduced root-shoot ratios. If the association is not exceptionally beneficial to the host, growth differences are likely to be insignificant.

METHODS

All seedlings for this research were grown in containers at the Bureau of Indian Affairs greenhouse complex in McNary, Arizona. Conditions within the greenhouse followed the guidelines developed by Tinus and McDonald (1979) with adaptations for the production of ponderosa pine. Some deviation from their recommended procedures are listed below, particularly the absence of carbon dioxide generation during 1981 and 1982 and lower nutrient levels.

The containers used were Tinus Root-trainers (30 in³; 492 cc) manufactured by Spencer Lemaire Industries LTD of Canada. They are book type plastic containers, each with four cavities. Ten books are placed in metal baskets to keep the books closed and to facilitate handling, thus each basket contains forty seedlings. Seedling substrate was composed of equal parts peatmoss and vermiculite. After filling the baskets with substrate, three or four seeds were placed in each cavity and covered with moist perlite. Seedlings were thinned to one per cavity after germination. Thinned seedlings were transplanted into any empty cavities, if necessary, but only within baskets. This assured full utilization of greenhouse space, without transferring seedlings between treatments. Seeds used in this study were collected in 1979 from the "west end" of the White Mountain Apache Indian Reservation (seed lots FAW 79-3 and FAW 79-17). The area is moderately xeric and typical of most ponderosa pine sites in the southwest.

Treatments for this study fall into two categories: fertilizer regimes and mycorrhizal inoculums. Manipulation of nutrients is the main focus of the research due to their effect on root-shoot ratios. It appears from the literature and preliminary studies that reducing levels of nitrogen will be the most successful means of increasing root-shoot ratios. Nutrient levels are sought that will yield a healthy seedling with a minimum top and fully developed root systems. Mycorrhizal treatments are included to test their effect on root-shoot ratios and their interactions with nutrients. It is important to include mycorrhizal treatments since current trends indicate that inoculation of planting stock will soon become standard procedure in nurseries and greenhouses.

This research was conducted with the intent of arriving at conclusions that would produce prescriptions that could be immediately applied to public and private greenhouses. Consequently, the commercial fertilizers that are currently in use at the BIA greenhouses were used to manipulate the fertilization regimes. All treatments utilized various amounts of Peters 15-30-15 fertilizer with constant levels of Peters STEM (micro nutrients) and Ciba-Giegy Iron chelate. (Nutrient analysis and amounts of fertilizers used are given in Appendix A.) Concentrations of NPK needed to achieve specific ppm levels applied to the seedlings were derived from tables produced by Peters Fertilizer Products of Allentown, Pennsylvania and head specifications of the pumping system.

Fertilization began after germination and thinning were completed (four weeks after planting). During 1981 and 1982, nutrients were applied as a foliar spray thrice weekly for six weeks and twice weekly

the remaining five weeks. They were applied thrice weekly all eleven weeks in 1980. After fertilizers were applied, the seedlings were flushed with acid water (H_3PO_4 in water to pH 5.5-6.0) until water dripped from the bottom of the containers. Fertilization treatment levels were established from the literature and preliminary studies, and applied at rates indicated in Table 1.

Table 1. Nutrient treatments in parts-per-million nitrogen.

1980		1981		1982
Spring Rotation	Fall Rotation	Spring Rotation	Fall Rotation	Spring Rotation
35	40	60	30	30
52	60	100	45	45
71	71	140	60	60
		180	75	75

In 1980, each fertilization level was applied in a separate greenhouse. For the 1981 and 1982 rotations, blocks of baskets (treatments) were spaced apart so that the fertilization system could be flushed and drained between treatments. This allowed all the trees to be grown in the same greenhouse, allowing more uniform growing conditions than occurred when treatments were applied in separate greenhouses.

Mycorrhizal treatments were developed with the assistance of Drs. James Trappe and Randy Molina of the Pacific Northwest Forest and Range Experiment Station at Corvallis, Oregon. Treatments included: 1) control, no inoculum added; 2) duff; 3) *Pisolithus tinctorius* basidiospores; and 4) *Cenococcum geophilum* vegetative mycelium (1981 only). These treatments were applied across the nutrient treatments resulting in 16 total

treatments (4 nutrient levels x 4 mycorrhizal inoculums) in 1981, 12 treatments (4x3) in 1982, while there were 9 treatments (3x3) in 1980.

Duff was collected by scraping off the recent litterfall layers and shoveling all humus layers (down to mineral soil) into plastic garbage cans. The material was collected from beneath an 85 year old stand of ponderosa pine on a 6-8% slope with a southwest aspect. The material was prepared as inoculum by working it through a half inch mesh (1.27 cm) screen and adding it to the substrate at approximately 8% by volume. All inoculums were mixed with the substrate immediately prior to filling and seeding of the baskets.

Basidiospores of *Pisolithus tinctorius* (*P.t.*) were acquired from Randy Molina and James Trappe, as were cultures of *Cenococcum geophilum* (*C.g.*). The spores were collected in September 1979 from a dry site in Starr gulch (elevation ca. 600 m), Jackson County, Oregon, and kept dry at 2-4°C until used as inoculum. At that time, 100 mg of *P.t.* spores were suspended in a two liter solution of distilled water and the surfactant Tween 80 (.75 ml), then returned to 2-4°C. Spores were applied at a rate equivalent to .1 mg/ft² of substrate exposed when the baskets were filled. This was achieved by mixing the appropriate amount of suspension in several liters of water, pouring the water over a similar amount of vermiculite, mixing well, and then including the treated vermiculite with the rest of the substrate as it was mixed before basket filling.

Vegetative cultures of *C.g.* were produced by generally following the procedures developed by Marx and Bryan (1975b). Four isolates of *C.g.* were cultured in liquid modified Melin-Norkrans (MMN) medium

(Appendix B) for possible use as inoculum. Colonies were grown in 200 ml of liquid MMN in 500 ml Erlenmeyer flasks with cotton plugs. These cultures were kept at room temperature ($\approx 25^{\circ}\text{C}$) in the dark for 2 months. At that time, it was discovered that *C.g.* grew better at 20°C and were transferred to a dark growth chamber. When the cultures were four months old, one of the isolates (A-181) was chosen for culturing of inoculum.

Thirty-two large glass jars were filled with approximately 2800 cc of vermiculite, 200 cc of peatmoss, and 1500 ml of liquid MMN solution. This was thoroughly mixed, and jar and substrate sterilized in an autoclave. A slurry was made of the *C.g.* colonies by placing them in a sterilized Waring blender and blending for approximately 3 seconds. Twenty-five ml of the slurry were transferred to each of the sterile jars, which were then returned to the growth chamber maintained at 20°C . After two months, the cultures were removed from the growth chambers and transported to the greenhouse for inoculating the seedlings. The inoculum was prepared by rinsing the contents of the jars into a burlap grass seed bag and flushing with large amounts of tapwater to remove the MMN medium. All of the inoculum was placed in a large plastic container and thoroughly chopped and mixed to evenly distribute the mycelium. The inoculum was added to the seedling substrate as it was being mixed for basket filling at approximately seven percent by volume. *Cenococcium geophilum* inoculum was not used in the 1980 rotation because it was unavailable, and eliminated from the 1982 rotations due to the complete lack of results in 1981.

Photoperiods were extended by incandescent lighting at approximately 406 lux intensity. Extended photoperiods were utilized throughout

the 1980 rotations, though frequency of dark interruptions was not equal in all three greenhouses. During 1981 and 1982, equipment was standardized such that the dark period was illuminated for a total of 6% of the time with no continuous darkness longer than thirty minutes. Due to the difficulty of maintaining constant concentrations, carbon dioxide enrichment was abandoned during 1981 and 1982. Temperature regimes followed the recommendations of Tinus and McDonald (1979). The initial ten weeks of each rotation were as follows: day temperature, 22°C (72°F) optimum, 18-26°C (65-79°F) range; night temperature 24°C (75°F) optimum, 18-25°C (65-77°F) range. At ten, eleven, and twelve weeks, night temperatures were dropped to 21°C (70°F), 18°C (65°F), and 16°C (60°F), respectively, with day temperatures unchanged.

The spring 1980 rotation was sampled at eleven and fifteen weeks in the greenhouse, and again at nineteen weeks after having been in the lathhouse without fertilization for four weeks. The other rotations were sampled at ten and fifteen weeks only. Twenty trees were randomly sampled from each treatment, with four trees being selected from each of five baskets. Data gathered at the ten week period was not subjected to statistical analysis. The information was used as a subjective check on the progress of the treatments to prevent unnecessary losses of seedlings. At the time of sampling, the root systems were carefully cleaned and mycorrhizal infections rated on a scale of 0 to 5 (mycorrhizae data not collected at fifteen weeks in 1980). Ratings were assigned based on the percentage of short roots that were mycorrhizal according to the following scale:

5. 80 - 100% of short roots with mycorrhizal infections
4. 60 - 79% of short roots with mycorrhizal infections
3. 40 - 59% of short roots with mycorrhizal infections
2. 20 - 39% of short roots with mycorrhizal infections
1. 1 - 19% of short roots with mycorrhizal infections
0. None of short roots with mycorrhizal infections.

After mycorrhizal rating, seedlings from the 1982 rotation were measured for height (root collar to bud tip) and diameter (immediately above the cotyledons). Height and diameter data were not collected for the 1980 and 1981 rotations. When the greenhouse measurements were completed, the seedlings were placed individually into brown paper bags, sealed in plastic bags by treatment groups, and transported to the University of Arizona campus. The seedlings were dried for 24 hours at 104°C (220°F) in 1980 and at 85°C (185°F) in 1981 and 1982. The roots were then separated from the shoots at the root collar and weighed on a Mettler PC-440 scale, to the nearest .001 grams. Root-shoot ratios were determined by dividing the appropriate weights.

Peatmoss analyses for total nitrogen (Kjeldahl), total phosphorus (Vando-molybdate yellow color development), available nitrogen (N as water soluble NO_3), and available phosphorus (P as CO_2 soluble PO_4) were conducted in several University of Arizona College of Agriculture analytical laboratories. Seedlings from the 30, 45, 60, and 75 ppm N treatments (1982) that were uninoculated with mycorrhizae were analyzed for total nitrogen and total phosphorus at Northern Arizona University's School of

Forestry analytical laboratory. Roots and shoots were digested separately following the procedures outlined by Parkinson and Allen (1975) and analyzed on a Technicon Auto Analyzer II.

Data from the spring rotations of 1981 and 1982 were statistically analyzed on the SPSS program of the Sigma computer at Northern Arizona University, Flagstaff, Arizona, courtesy of the Rocky Mountain Forest and Range Experiment Station. A series of paired t-tests was run comparing the means of the 1981 and 1982 60 ppm nitrogen treatments. The 1981 data for that treatment were subsequently deleted from the data base for the remainder of the analyses. Two-way ANOVA's were run to determine if there were significant differences between treatment means and/or interactions between treatment types (mycorrhizal vs. nutritional). One-way ANOVA's and Student-Newman-Keuls multiple range tests were conducted to rank those treatments that were significantly different from each other. Finally, regressions relating ppm nitrogen to resulting root-shoot ratios and mycorrhizal infections were determined.

RESULTS AND DISCUSSION

The results of this research confirm the hypothesis that the root-shoot ratio of containerized ponderosa pine seedlings can be directly manipulated by varying nitrogen levels. All measured parameters significantly differed through the levels of applied nitrogen. Conversely, inoculum treatments had only minor effects on the morphology of the seedlings.

Preliminary Studies

The early portions of this research were conducted under conditions that were less than ideal. The 1980 fertilizer treatments were applied in three separate greenhouses, each with separate CO₂ generators, fertilization equipment, and slightly different lighting patterns. The 1981 and 1982 rotations were all grown in the same greenhouse, CO₂ generation was not attempted, and the lighting patterns had been standardized as described previously. In addition, two rotations were abandoned due to extenuating circumstances. The fall 1980 rotation was terminated at ten weeks when the fertilization equipment in two of the greenhouses became inoperable. At that time, the seedlings were moved into the lath-house, and no data were collected. The peatmoss utilized in the substrate for the fall 1981 rotation was from a different company than the peatmoss used in all other rotations. Those trees were extremely large considering the relatively low amounts of fertilizer being applied. A variety of

causes were considered, but no definite conclusions were drawn. The most plausible explanation would center on diverse nutritive characteristics of the two sources of peatmoss used. Due to the abnormal growth, seedlings were not measured. Peatmoss from the original lot was used in the spring 1982 rotation.

Due to greenhouse conditions and laboratory procedures that were not standardized, valid statistical analysis of data gathered prior to 1981 is not possible. Therefore, the information derived from the spring 1980 rotation was considered a "preliminary study" on which future research could be based. The results and a discussion of these data are presented in Appendix C. A complete data listing on which statistical analyses were conducted (spring rotations of 1981 and 1982) is presented in Appendix D. Further discussions pertain only to the statistically analyzed data, unless specified otherwise.

1981 vs 1982

Sixty parts per million nitrogen level treatments were included in both the 1981 and 1982 rotations to serve as an indicator of differences between the rotations. Results of t-tests on treatment means are presented in Table 2.

While inoculum and duff inoculum results did not significantly differ for shoot weight, root weight, and root-shoot ratio, the *Pisolithus tinctorius* (*P.t.*) spore inoculum treatments did vary for shoot weight and root-shoot ratio. Both the duff and *P.t.* treatments differed between 1981 and 1982 in percent mycorrhizal infections. Because the major emphasis of this research concerned nutritional effects on root-shoot

Table 2. Results of t-tests comparing means of the 60 ppm N level treatments from the 1981 and 1982 rotations.

Inoculum	Shoot Weight (g)	Root Weight (g)	Root-Shoot Ratio (g/g)	Mycorrhizal Infections (%)
Control	NS [†]	NS	NS	NS
Duff	NS	NS	NS	**
<i>Pisolithus tinctorius</i>	**	NS	*	**
All trees	*	NS	NS	**

[†] * = significant difference P=.05
 ** = significant difference P=.01
 NS = no significant difference P=.05

ratios, and that overall, there were no significant differences between 1981 and 1982 results for the root-shoot ratios, the data from one of the rotations were deleted from further statistical analysis. The 1981 data were deleted because they did not include shoot height and diameter parameters.

Treatment Interaction, Ranking, and Regressions

Results of the two-way analysis of variance indicated that there would be significant differences between nitrogen levels for all parameters. Inoculum treatments were significant only on shoot height and diameter. Treatment interactions occurred for both root weights and percent mycorrhizal infections (see Table 3).

Table 3. Results of two-way analysis of variance testing for mean differences due to treatment and treatment interactions.

Variation due to:	Shoot Height (mm) [†]	Shoot Diameter (mm)	Shoot Weight (g)	Root Weight (g)	Root-Shoot Ratio (g/g)	Mycorrhizal Infections (%)
Nitrogen levels	* ^{††}	**	**	**	**	**
Inoculum	**	*	NS	NS	NS	NS
Treatment Interaction	NS	NS	NS	*	NS	*

[†] Shoot height and diameter results do not include data from the 1981 rotation (100, 140, and 180 ppm N fertilization levels).

^{††} * = significant difference P=.05
 ** = significant difference P=.01
 NS = no significant difference P=.05

Increasing nitrogen levels (Table 4) and intentional mycorrhizal inoculation (versus no inoculum) (Table 5) both caused increases in shoot height. These increases were additive, as no treatment interaction occurred. Increased shoot height, diameter, and shoot weight as a response to increasing levels of nitrogen have been reported frequently (i.e., Swan 1960, Hauxwell 1966, Harrington and Kelsey 1979). Duff and *P.t.* inoculated seedlings were significantly taller than those which did not receive inoculum. However, only *P.t.* inoculated seedlings had increased diameters. Shoot weight increased with duff inoculum and more so with

Table 4. Ranked[†] means of nitrogen level treatments.

PPM N	Shoot Height (mm)	Shoot Diameter (mm)	Shoot Weight (g)	Root Weight (g)	Root-Shoot Ratio (g/g)	Mycorrhizal Infections (%)
30	113a	2.9a	0.937a	0.838ab	0.916a	40a
45	120ab	3.0ab	1.040a	0.919a	0.926a	26b
60	118ab	3.1b	1.080a	0.808bc	0.770b	20b
75	122b	3.1b	1.259b	0.924a	0.758b	22b
100	- ^{††}	-	1.096a	0.721c	0.678c	20b
140	-	-	1.456c	0.775bc	0.539d	1c
180	-	-	1.267b	0.602d	0.481d	0c

[†] Means within columns not followed by the same letter(s) are significantly different P=.05. Means were derived from all trees receiving a particular nitrogen level, regardless of inoculum. The 30, 45, 60, and 75 ppm N treatments were applied in 1982; 100, 140, and 180 ppm N treatments were applied in 1981.

^{††} Shoot height and diameter were not collected for 100, 140, and 180 ppm N treatments.

Table 5. Ranked[†] means of inoculum treatments.

Inoculum Type	Shoot Height (mm)	Shoot Diameter (mm)	Shoot Weight (g)	Root Weight (g)	Root-Shoot Ratio (g/g)	Mycorrhizal Infections (%)
No inoculum	113a	3.0a	1.117a	0.757a	0.725a	14a
Duff	121b	3.0a	1.167a	0.812a	0.741a	16a
<i>Pisolithus tinctorius</i>	121b	3.1b	1.202a	0.798a	0.707a	16a

[†] Means within columns not followed by the same letter(s) are significantly different P=.05. Means were derived from all trees receiving a particular inoculum treatment, regardless of nitrogen level. Means for shoot height and diameter do not include data from 100, 140, and 180 ppm nitrogen levels.

P.t. inoculum, but neither reached significance. Thus, the trend found in this study was that inoculated seedlings had larger shoots than those that were not inoculated. Marx (1976b) and Cline and Reid (1982) found similar results, while Molina (1980), Sinclair et al. (1982), and France (1982) found that heavy mycorrhizal formation may actually inhibit the growth of the seedlings. These conflicting results may be explained by several factors involved: the species of phytosymbiont, the species of mycosymbiont, the degree of infection, and the age of the seedling when measured. The combination of a less virulent tree species with a highly virulent fungus might cause a metabolite strain on the seedling that could inhibit growth to some degree. This is probably a temporary situation, with the mycorrhizal association undoubtedly resulting in a net benefit to the seedling. If the infections are not heavy, or the initial association is more balanced, the net benefit to the seedling (reflected in improved growth) would be evident at an earlier age. In the case of this study, the mycorrhizal infections at the time of sampling were not heavy enough to be a growth-inhibiting drain on the seedlings.

The treatment interactions that occurred in root weight and root-shoot ratio parameters were to be expected. Nitrogen levels roughly correlated with increased shoot weights and inversely correlated with decreased root weights. Consequently, as nitrogen increased, root-shoot ratios decreased. Meanwhile, inoculum treatments had no significant effect on shoot weight, root weight, or root-shoot ratios--thus the interaction. The insignificant increase of shoot weight for inoculum treated seedlings was evidently enough to prevent treatment interaction for that parameter.

The effect of increasing nitrogen concentration in the fertilizer on shoot and root weights, and the resulting root-shoot ratios was interesting. While the trends were for increased shoot weights and decreased root weights, the increments of change between the levels were inconsistent (Table 4). These inconsistencies disappeared, however, when the root-shoot ratios were calculated. The result was a linear relationship between fertilizer nitrogen levels and root-shoot ratios of the seedlings (Figure 1).

The contention of many mycorrhizal researchers that the "normal" greenhouse and nursery procedures commonly practiced result in an inhibition of mycorrhizal formation is strongly supported by the results of this study. As indicated in Table 5, inoculated seedlings did not form mycorrhizae more readily than the uninoculated seedlings. Inoculation from airborne spores or peatmoss material was equally effective. Nitrogen levels, however, had a very significant effect on the formation of mycorrhizae (Table 4). The percent of short roots that formed mycorrhizae was significantly higher at 30 ppm nitrogen. At 140 ppm and 180 ppm N, the percent of infections was drastically reduced. The range of 45 ppm to 100 ppm N had no significant differences in the percent of mycorrhizae formed. The results of the regression (Figure 2), however, indicate a near linear relation between nitrogen levels and mycorrhizal susceptibility.

It might be argued that phosphorus or potassium concentrations were responsible for the strong correlations with root-shoot ratios and mycorrhizal infections due to the use of NPK fertilizers. As discussed previously, however, past research indicates that only very low or very high levels of these nutrients affect changes in the relative growth rates

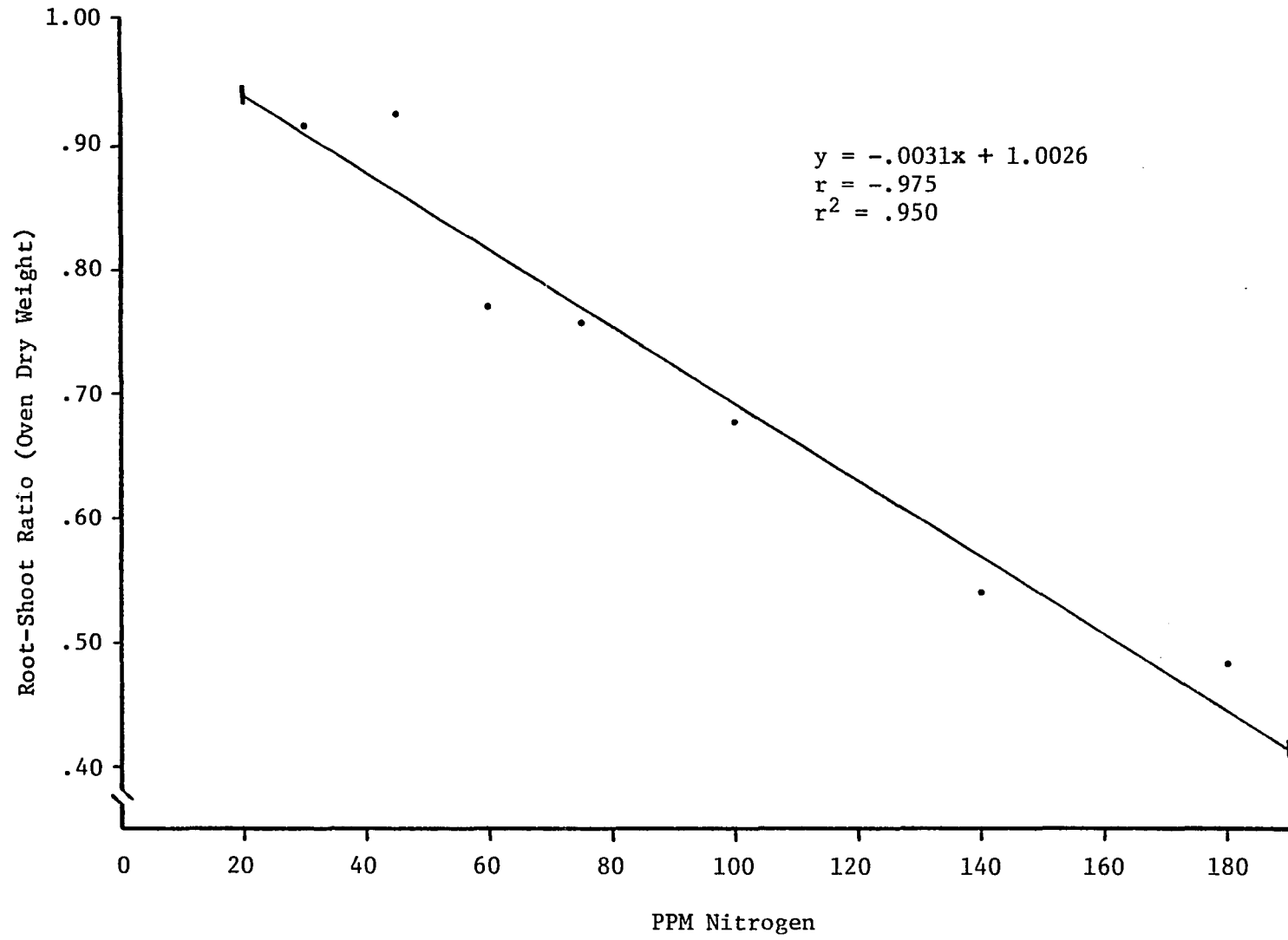


Figure 1. Nitrogen level versus mean root-shoot ratio.

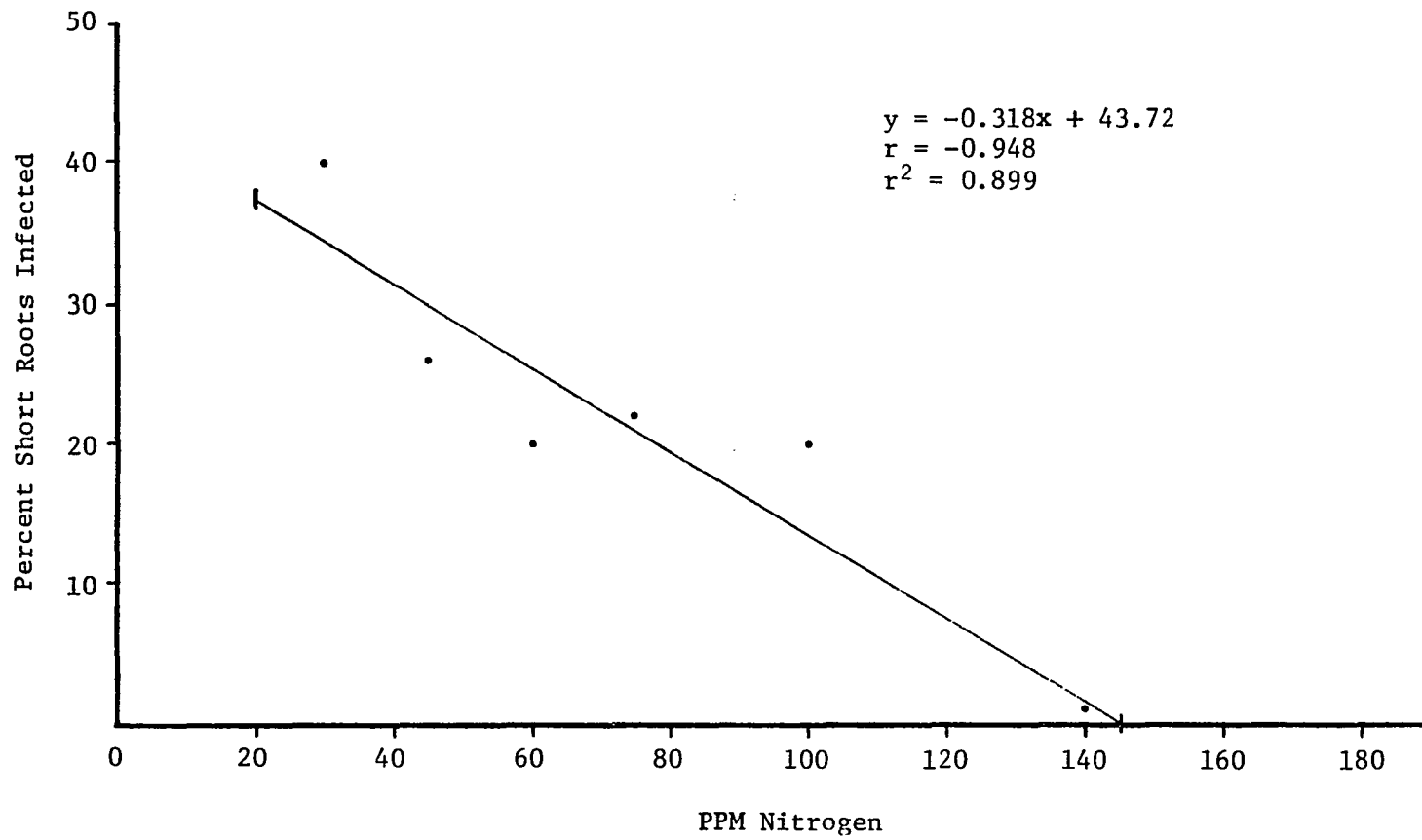


Figure 2. Nitrogen level versus mean mycorrhizal infections.

of roots and shoots (Potter 1964, Hauxwell 1966). The same is generally true for the relation between the degree of mycorrhizal infection and P and K. Much research has been done with mycorrhizae and phosphorus nutrition, particularly the host benefits from the mycorrhizal association. Fowells and Krauss (1959) found that mycorrhizae decreased as nitrogen increased from 1 to 400 ppm with phosphorus held constant at 100 ppm. When nitrogen was held constant at 100 ppm [which this author considers high], only .01 and .5 ppm phosphorus treatments had significant infections--mycorrhizae were "scarce or nonexistent" as phosphorus ranged from 1 to 400 ppm. Menge and Grand (1978) in a field study involving combinations of phosphorus and nitrogen fertilization found that nitrogen reduced the numbers of mycorrhizal tips on trees and the fruiting bodies occurring in the plantation. There were no significant differences for either parameter between unfertilized plots and those receiving only phosphorus. Beckjord, Adams, and Smith (1980) found that ammonium nitrogen at low, medium, and high levels caused progressive decreases in mycorrhizal infection of red oak.

There is no question that phosphorus plays an important role in the mycorrhizal association. That importance, however, appears to manifest itself primarily in improved phytosymbiont nutrition under conditions where phosphorus is limiting to plant growth. The mycosymbiont benefits indirectly from its association with a vigorous plant. Only extreme levels (low or high) of phosphorus appear to affect the formation of mycorrhizae. In contrast, many studies have indicated that nitrogen has a definite effect on mycorrhizal infections. Thus, it can be concluded

that the results of this research indicate an inverse relationship between the nitrogen concentration of the fertilizer applied to containerized ponderosa pine seedlings, and the resulting root-shoot ratios and mycorrhizal infections.

Peatmoss and Seedling Analyses

Results of the peatmoss analyses showed the material to be relatively free of immediately "available" nitrogen ($\text{NO}_3\text{-N}$) and phosphorus ($\text{PO}_4\text{-P}$) compared with the total nutrient levels (Table 6). Under greenhouse conditions, chemical and microbial activity would allow some mineralization, though the amounts of nutrients made available would be minimal compared to that applied as fertilizer. It is likely that the water soluble nitrates would be leached from the substrate very early in the rotation; thus the peatmoss as a source of nitrogen appears to be of minor importance.

Table 6. Nitrogen and phosphorus content of peatmoss used in substrate.

	Total (ppm)	Available (ppm)	Percent of Total Available
Nitrogen	7420	18.2	0.2
Phosphorus	530	12.1	2.3

Total nitrogen and total phosphorus analyses of the roots and shoots from 26 week old seedlings are summarized below (Table 7). Correlations between fertilizer levels and nitrogen or phosphorus concentrations in the top tissues were not evident. The relationship between nitrogen concentrations of the fertilizer and seedling roots was also insignificant. There was, however, a significant correlation between fertilizer levels and the phosphorus concentration of the roots (Figure 3).

The lack of significant change in most of the nutrient concentrations measured indicates growth was strongly related to nitrogen levels. While the mass of the seedlings increased (particularly the tops), the nitrogen concentration of the tissue remained relatively constant. Thus, there did not appear to be a dilution effect from rapid growth nor an indication of "luxury consumption." It is possible that there was some storage of phosphorus in the roots as shown by increasing concentrations at higher fertilizer levels. Since the seedlings did not show any visible symptoms of phosphorus deficiency, it may be concluded the phosphorus requirements of ponderosa pine seedlings are quite low. This also supports the theory that above deficiency levels, increasing phosphorus fertilization will not result in significant increases in growth.

Table 7. Mean nitrogen and phosphorus content of 26 week old seedlings.

Fertilizer (ppm N)	Nitrogen (mg/g)		Phosphorus (mg/g)	
	Tops	Roots	Tops	Roots
30	9.929a [†]	7.517a	3.515a	2.910a
45	10.076a	7.537a	3.336a	3.571ab
60	9.740a	8.009a	2.859a	4.261bc
75	9.918a	10.135b	3.596a	4.757c

[†]Means with columns not followed by the same letter(s) are significantly different P = .05.

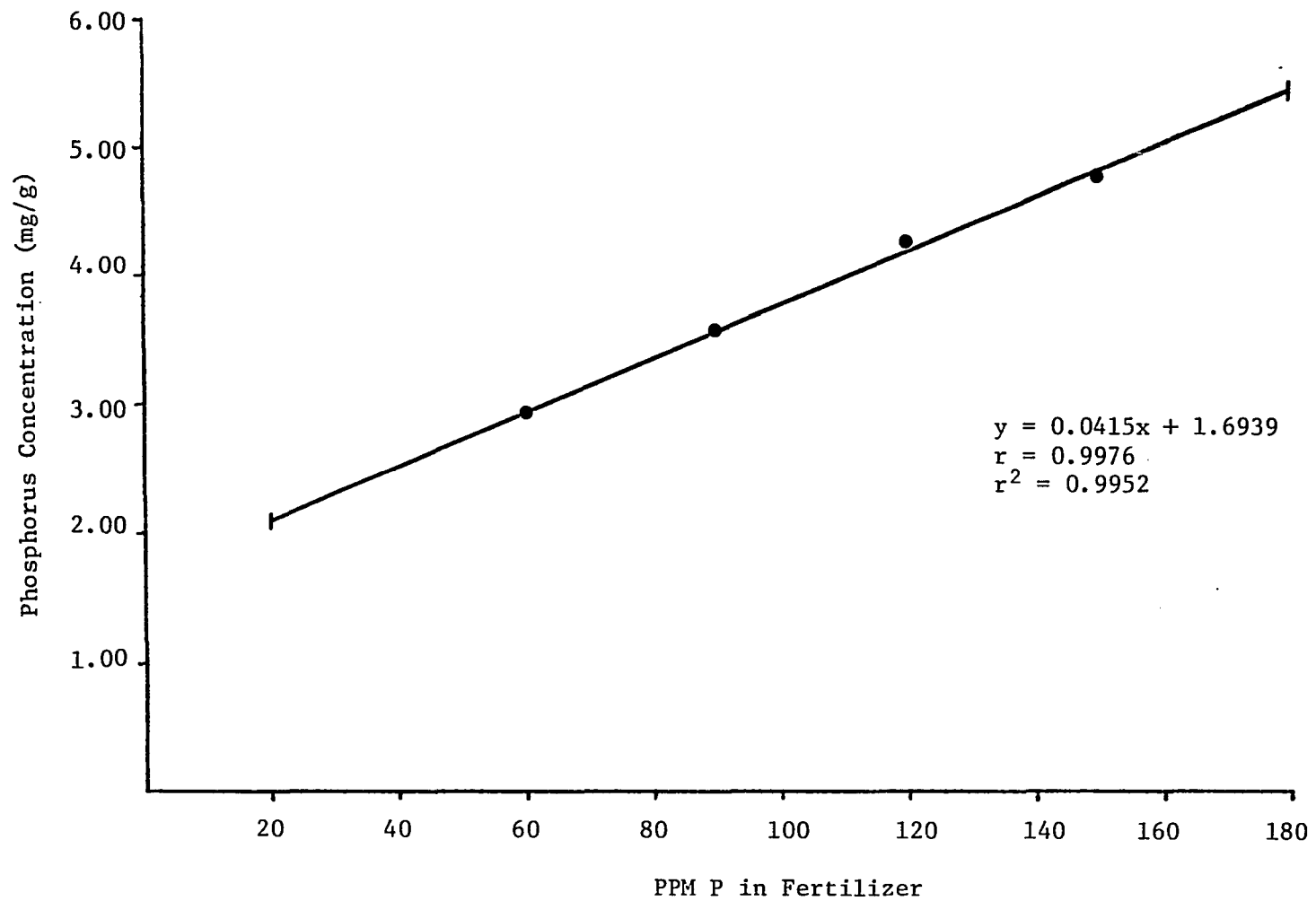


Figure 3. Fertilizer level versus phosphorus concentrations in roots of 26 week old seedlings.

APPLICATIONS AND CONCLUSIONS

When working with ponderosa pine, and probably most plant species, it is important to take into account the extreme variability between individuals. Therefore, statistics, discussions, and conclusions are commonly based, by necessity, solely on sample means. For example, in this study the standard deviations for each treatment averaged 15% of the mean for height, 13% for diameter, 34% for shoot weight, and 31% for root weight! These are standard deviations from the mean (standard error), not data ranges. Consequently, it is only practical to compare treatment means. Likewise, when a forest or greenhouse manager specifies a particular treatment, he (or she) must anticipate high variability between individuals while obtaining the desired average results. Thus, the results of this study can be used as a management tool to manipulate the root-shoot ratios of containerized ponderosa pine seedlings, when grown under the general conditions specified.

The importance of planting seedlings for reforestation and afforestation was stressed by Edgren (1975) and Molina (1977). Heidmann (1981) and Heidmann et al. (1982) confirm that natural regeneration of ponderosa pine is possible, but limited to specific soils and conditions. While successful forest management requires prompt regeneration, Harrington and Kelsey (1979) concluded that even obtaining adequate artificial regeneration of ponderosa pine was difficult. In a survey by Guldin (1982), it was found that an increasing number of firms and agencies are turning

to container-grown seedlings to regenerate difficult sites. While containerized seedlings are commonly more expensive to produce than bare-root planting stock, this increased cost may be offset by increased survival and growth, particularly on adverse or difficult to plant sites. Colby and Lewis (1973), basing relative costs on the survival rates of bare-root and containerized seedlings, found that the cost per surviving containerized seedling may be less than the cost per surviving bare-root seedling. Owston and Seidel (1978) found that overall growth of container-grown seedlings was greater than that of bare-root stock, even after three years. Guldin (1982) determined that transportation, handling, and planting costs of container-grown seedlings were no greater than for bare-root seedlings. While the cost of containerized seedlings depended heavily on the type of containers used, it frequently was no greater than the cost of bare-root stock. Williamson and Minore (1978) agreed that containerized seedlings provided more consistent positive results than conventional regeneration methods.

The use of containerized seedlings for reforestation of adverse sites not only provides more consistent planting success, it also allows the forest manager more accurate control for "tailoring" seedlings to specific plant sites than with bare-root stock. As discussed previously, the conditions in greenhouses allow a more direct relation between treatments applied and seedling response, than do nursery conditions. Complicating factors found in nursery situations, such as variable weather and soil interactions, are buffered in greenhouses.

Marx (1976b), Trappe (1977), and Molina (1980) all discuss the advantages of matching specific mycorrhizal fungi not only with the host, but with the planting site as well. Edgren (1975) maintained that reforestation sites should be classified (before harvesting, if possible) with the objective "of prescribing a particular size and shape of seedling for a site." He also advised the forest manager to always plan for the worst conditions an area could present. Even if extra costs are incurred, the success of such prescriptions often result in lower costs than those of the multiple outplanting attempts that are often required.

To secure plantation establishment quickly and consistently, foresters must understand the seedling responses to both nursery (or greenhouse) and planting site environments (Jenkinson 1980). If moisture is the most critical environmental factor on the plantation site (as is usually the case with ponderosa pine sites in the southwest), then seedlings that are to be planted should be physiologically and morphologically adapted to conditions of high transpiration and low soil moisture. "If moisture is going to be a problem, you must have a low top-root ratio" (Edgren 1975). This author would suggest that planting stock can be "tailored" to specific sites by adjusting the seedlings' root-shoot ratios to levels compatible with the anticipated moisture stress of the site. The results of this research indicate root-shoot ratios can be varied directly by changing the nitrogen content of the fertilizers. As the moisture stress for a site increases, less nitrogen should be applied to the seedlings. Seedlings with increased root-shoot ratios have been shown to be more drought tolerant than those with lower root-shoot

ratios (Hauxwell 1966, Shirley and Meuli 1939). Lopushinsky and Beebe (1976) found that when seedlings were outplanted on difficult-to-regenerate sites, those with the largest root-shoot ratios survived most frequently. When seedlings were planted on less harsh sites, where adequate survival is not difficult to attain, high root-shoot ratio seedlings grew significantly better than those with lower ratios (Strothmann 1980). Arnott and Beddows (1982) found similar results, with growth differences still increasing after five years.

The concept of "hidden hunger" discussed previously (Swan 1960) appeared applicable to the lowest nitrogen levels utilized in this study. The seedlings produced at these levels were vigorous and large enough to meet realistic planting requirements (Williams 1979), yet were slightly chlorotic at the end of the rotation. This should not be of concern, however, because the chlorosis is no longer evident after several weeks in the shadehouse (unpublished data). It is interesting to note that mycorrhizal infections also tend to increase during this period.

As pointed out by Molina (1979), mycorrhizae formation on containerized seedlings can be encouraged if only by changing the fertility management of the greenhouse (which also achieves the desired increases in root-shoot ratios). This was not so evident in this study. While mycorrhizae were significantly more abundant at the lowest level of nitrogen fertilization than the other levels, no treatment consistently produced heavy infections. Marx et al. (1982) indicated that while any mycorrhizae were better than none, significant seedling benefit did not seem to occur unless 40% or more of the short roots were mycorrhizal. At

the time of sampling, all treatments except the 35 ppm N were below that level.

There are indications, however, that southwestern ponderosa pine do not form heavy mycorrhizal infections. Cline and Reid (1982) and Riffle and Tinus (1982) both reported infection levels very similar to the results of this study. It is possible that even at low fertilization levels, that mycorrhizal formation on ponderosa pine is somewhat suppressed by frequent applications. As mentioned earlier, observations on seedlings grown in preliminary studies indicated mycorrhizal infections to be significantly heavier after several weeks in the shadehouse with no fertilization. Fruiting bodies of *Laccaria laccatta* and *Thelephora terrestris* were found growing in containers. Therefore, it is likely that mycorrhizal infections would be adequate by the time the seedlings were hardened off in the shadehouse and ready for outplanting.

The inoculum treatments (duff and *Pisolithus tinctorius* spores) did not significantly increase mycorrhizal formation. Marx, Bryan and Cordell (1976) indicated that artificial inoculation may be more successful if the substrate is fumigated. They also noted that basidiospore inoculum took longer than vegetative inoculum to colonize roots. Marx (1976b) had the same conclusions.

Molina (1980) and Malloch et al. (1980) stressed the importance of mycorrhizal root systems on planting stock destined for hard-to-regenerate or suboptimal sites, maintaining that mycorrhizal associations are particularly beneficial in extreme environments. Therefore, this author recommends that forest, nursery, and greenhouse managers should

insure inoculation of planting stock. This should be done even if only duff collected from or near the planting site, is used as inoculum. While the risk of introducing pathogens with this method does exist, it has rarely occurred (Trappe 1977). When tree-fungus combinations are found that are more beneficial than ambient associations, inoculation with specific mycosymbionts should be pursued.

Tailoring stock to planting sites should be practiced for seedling morphology as well as mycorrhizal associations. "The most important effect of the interaction of environmental factors is on the water economy of each individual site. Available moisture is the common denominator underlying a good many regeneration problems" (Edgren 1975). Past studies have shown that seedlings with high root-shoot ratios are more drought tolerant and have higher survival and growth rates than those seedlings with relatively large tops. This research shows that the root-shoot ratios of containerized ponderosa pine seedlings can be directly controlled by varying the nitrogen concentration of fertilizers. This trend is probably true of other species and bare-root seedlings, as well. Therefore, if the outplanting site is harsh, suboptimal, or otherwise difficult to regenerate--efforts should be made to maximize root-shoot ratios as much as is feasible. If the site will be easy to regenerate, then the capabilities of greenhouses to produce large seedlings quickly should be taken advantage of. As long as survival is not a problem, subsequent mycorrhizal infections will readily occur from ambient soil fungi.

APPENDIX A

AMOUNTS AND ANALYSIS OF FERTILIZERS USED

IN NUTRIENT TREATMENTS

Amount of fertilizers added to 100 liters of tapwater to achieve desired levels of nutrients. These concentrates are further diluted through the heads in the fertilizer system.

<u>Treatment Level</u> (ppm N)	<u>15-30-15</u> (Kg)	<u>STEM</u> (g)	<u>Iron Chelate</u> (g)
30	3.2	40.9	1220
45	4.8	40.9	1220
60	6.4	40.9	1220
75	8.0	40.9	1220
100	10.7	40.9	1220
140	14.9	40.9	1220
180	19.2	40.9	1220

15-30-15 NPK fertilizer analysis (Peters)

Nitrogen	as	NH ₃	-	10.57%
Nitrogen	as	NO ₃	-	4.43%
Phosphorus	as	P ₂ O ₅	-	30%
Potassium	as	K ₂ O	-	15%

S.T.E.M. Analysis (Peters)

Sulfur	as	S	-	15.00%
Boron	as	B	-	1.45%
Copper	as	Cu	-	3.20%
Iron	as	Fe	-	7.50%
Manganese	as	Mn	-	8.15%
Molybdenum	as	Mo	-	0.046%
Zinc	as	Zn	-	4.50%

Iron Chelate Analysis (Ciba-Geigy)

Sodium-ferric-diethylenetriamine pentacetate
10% Fe by weight

APPENDIX B

MODIFIED MELIN-NORKRANS AGAR

Salts amounts per 1000 ml of solution

CaCl	0.05 g
NaCl	0.025 g
KH_2PO_4	0.5 g
$(\text{NH}_4)_2\text{HPO}_4$	0.25 g
$\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$	0.15 g
Sequesterene 330 Fe2	1.21 ml of 24g/l solution, or 0.005 g

Organics amounts per 1000 ml of solution

Thiamine·HCl	100 mg
Malt Extract	3 g
Glucose	10 g
Bacto-agar	15 g

Add approximately 980 ml of distilled water to equal 1000 ml of solution.

For liquid solution, leave out sugar.

APPENDIX C

RESULTS AND DISCUSSION OF SPRING 1980 ROTATION

The results of the spring 1980 rotation indicated that seedling response to decreasing nutrient levels would be as hypothesized. Seedling size increased and root-shoot ratios decreased as nitrogen concentrations increased (Table C.1). Mycorrhizal infections also decreased as nitrogen increased. After four weeks in the lathhouse (without fertilization), the 19 week-old seedlings were heavier in both roots and shoots, the root-shoot ratios had increased, and mycorrhizal infections had increased.

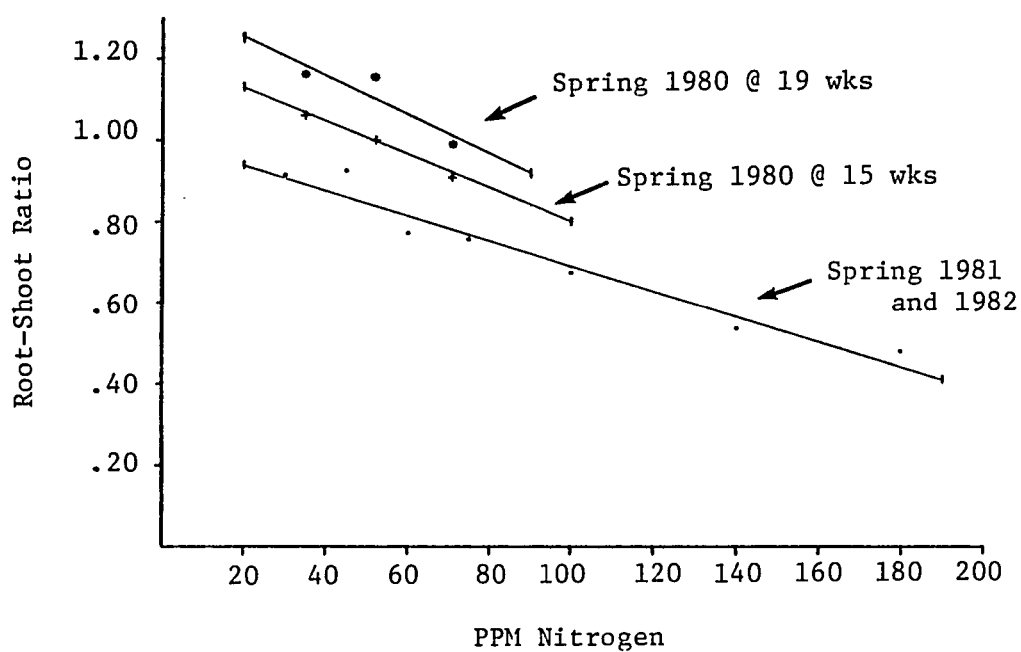
Table C.1. Data means from spring rotation 1980.

PPM N	Mycorrhizal Inoculum	Shoot Wt. (g)		Root Wt. (g)		Root-Shoot (g/g)		Mycorrhizal Infections (%)	
		15	19 [†]	15	19	15	19	15	19
		wks	wks	wks	wks	wks	wks	wks	wks
71	none	.553	.776	.499	.847	.902	1.091	5	25
	duff	.649	.782	.609	.681	.938	.871	5	46
	<i>P. t.</i>	.593	.726	.528	.734	.890	1.011	32	49
71	\bar{x}	.598	.761	.545	.754	.910	.991	14	40
52	none	.422	.510	.452	.639	1.071	1.253	18	37
	duff	.543	.512	.514	.550	.947	1.074	40	54
	<i>P. t.</i>	.485	.524	.481	.587	.992	1.120	15	48
52	\bar{x}	.483	.515	.482	.592	1.003	1.149	24	46
35	none	.403	.441	.443	.528	1.099	1.197	40	63
	duff	.387	.477	.380	.583	.982	1.222	47	68
	<i>P. t.</i>	.389	.527	.422	.564	1.085	1.070	37	66
35	\bar{x}	.393	.482	.415	.558	1.055	1.163	41	66

[†]Seedlings grown 15 wks in greenhouse and 4 wks in lathhouse without fertilization.

The growing conditions in the three greenhouses used in 1980 were different from those of 1981 and 1982. However, the unstandardized conditions of 1980 did not alter the trend of increasing root-shoot ratios with decreasing nitrogen concentrations that was found under standardized conditions of 1981 and 1982. The conditions of 1980 resulted in a near-uniform shift of results towards higher root-shoot ratios (Figure C.1). Four weeks in the lathhouse without fertilization resulted in an additional shift.

The variety of unstandardized conditions (i.e., lighting, separate greenhouses, CO₂ generation) prevent determination of the causes of increased root-shoot ratios. It is even possible that the higher temperatures at which 1980 seedlings were dried (104°C vs 85°C) could have resulted in volatilization of some materials from the needles, lowering relative shoot weights and increasing root-shoot ratios. The importance of the results from this rotation is in the verification of the hypotheses and establishment of base fertilization levels from which to expand.



Spring 1980 @ 19 wks (15 wks in greenhouse plus 4 wks in lathhouse without fertilization)

$$y = -.0048x + 1.3525$$

$$r = -.905$$

$$r^2 = .819$$

Spring 1980 @ 15 wks

$$y = -.0041x + 1.2100$$

$$r = -.997$$

$$r^2 = .993$$

Spring 1981 and 1982

$$y = -.0031x + 1.0026$$

$$r = -.975$$

$$r^2 = .950$$

Figure C.1. Regressions of data means for spring rotations of 1980, 1981, and 1982.

APPENDIX D

DATA LISTING FOR SPRING ROTATIONS OF 1981 AND 1982

Explanation of printout information:

Columns:

1-5	sample number
7-8	fertilizer level
9	mycorrhizal treatment
10-11	seedling number from given treatment
13-15	seedling height in millimeters
16-18	seedling diameter in millimeters
20-24	shoot weight in grams
25-29	root weight in grams
31	mycorrhizal rating

Fertilizer levels:

30 = 30 ppm N (1982)
45 = 45 ppm N (1982)
62 = 60 ppm N (1982)
75 = 75 ppm N (1982)
61 = 60 ppm N (1981)
10 = 100 ppm N (1981)
14 = 140 ppm N (1981)
18 = 180 ppm N (1981)

Mycorrhizal treatment:

1 = no inoculum
2 = duff
3 = <i>Pisolithus tinctorius</i> basidiospores

1.000	30101	093	2.5	0.857	0.632	4	49.000	30309	136	3.0	1.388	0.996	1
2.000	30102	085	3.5	0.860	0.655	2	50.000	30310	129	3.0	1.044	0.837	3
3.000	30103	090	2.5	0.792	0.780	2	51.000	30311	102	2.5	0.861	0.806	2
4.000	30104	114	3.0	0.921	1.054	1	52.000	30312	101	3.0	1.056	0.932	1
5.000	30105	122	3.0	1.034	0.928	2	53.000	30313	120	2.5	1.056	0.932	1
6.000	30106	104	3.0	1.154	0.900	2	54.000	30314	094	3.0	0.949	0.776	2
7.000	30107	121	4.0	1.220	1.075	3	55.000	30315	102	2.5	0.804	0.667	5
8.000	30108	114	2.5	0.846	0.836	1	56.000	30316	086	2.5	0.827	0.731	4
9.000	30109	122	3.5	1.200	0.852	3	57.000	30317	121	3.0	0.980	0.737	1
10.000	30110	099	2.0	0.666	0.675	2	58.000	30318	141	3.5	1.365	0.852	2
11.000	30111	117	3.0	0.901	0.895	3	59.000	30319	137	3.5	1.325	0.837	1
12.000	30112	081	3.0	0.650	0.502	3	60.000	30320	113	2.5	1.033	0.767	2
13.000	30113	084	2.5	0.585	0.639	2	61.000	45101	098	2.5	0.805	0.710	1
14.000	30114	112	3.0	0.843	0.857	3	62.000	45102	113	3.0	0.661	0.610	1
15.000	30115	107	2.0	0.663	0.824	5	63.000	45103	114	2.5	0.978	1.093	1
16.000	30116	112	3.5	0.975	0.845	5	64.000	45104	126	2.5	0.978	1.093	1
17.000	30117	110	3.0	0.856	0.861	1	65.000	45105	138	3.5	1.497	1.253	2
18.000	30118	112	3.0	0.740	0.720	1	66.000	45106	102	3.0	0.986	0.806	2
19.000	30119	101	2.5	0.529	0.460	2	67.000	45107	091	3.0	0.830	0.819	4
20.000	30120	117	3.0	1.034	0.708	2	68.000	45108	122	3.0	0.966	0.806	2
21.000	30201	132	3.0	1.146	0.918	1	69.000	45109	096	2.5	0.653	0.707	3
22.000	30202	132	3.0	1.133	0.933	2	70.000	45110	078	3.0	0.702	0.926	1
23.000	30203	100	3.0	1.182	0.846	1	71.000	45111	116	3.0	1.035	0.780	2
24.000	30204	130	3.5	1.046	0.535	2	72.000	45112	104	3.0	1.035	0.780	2
25.000	30205	126	2.5	0.905	0.810	1	73.000	45113	103	3.5	0.954	0.717	1
26.000	30206	115	2.5	0.870	0.758	3	74.000	45114	157	3.0	1.331	1.038	2
27.000	30207	112	2.5	0.602	0.722	5	75.000	45115	068	2.0	0.257	0.555	1
28.000	30208	131	3.0	0.881	0.915	5	76.000	45116	139	3.0	0.940	0.697	1
29.000	30209	099	3.0	1.106	1.206	1	77.000	45117	105	3.0	0.940	0.697	1
30.000	30210	156	3.5	1.403	1.331	2	78.000	45118	117	2.5	0.573	0.563	1
31.000	30211	137	3.0	0.903	0.940	3	79.000	45119	121	3.0	0.855	0.957	1
32.000	30212	111	4.0	1.008	0.510	1	80.000	45120	102	3.0	0.930	1.153	2
33.000	30213	113	3.0	0.730	0.916	5	81.000	45201	096	2.5	0.800	0.718	2
34.000	30214	098	2.5	0.602	0.600	5	82.000	45202	141	3.0	1.252	1.411	2
35.000	30215	109	2.0	0.596	0.811	5	83.000	45203	138	3.0	1.221	1.028	1
36.000	30216	115	3.0	0.759	0.702	1	84.000	45204	125	3.0	1.063	0.850	1
37.000	30217	132	3.0	0.980	1.217	3	85.000	45205	116	2.5	0.907	0.626	1
38.000	30218	131	3.0	1.315	1.051	3	86.000	45206	136	3.0	1.070	0.891	3
39.000	30219	110	3.0	0.823	0.786	4	87.000	45207	133	2.5	0.794	0.737	2
40.000	30220	121	2.5	0.985	0.849	5	88.000	45208	139	3.5	1.678	1.185	2
41.000	30301	130	3.0	0.824	0.911	2	89.000	45209	126	3.0	0.890	0.951	1
42.000	30302	095	2.5	0.775	0.771	3	90.000	45210	087	4.0	0.948	1.037	1
43.000	30303	118	3.0	0.990	0.952	3	91.000	45211	109	3.0	0.665	0.792	1
44.000	30304	114	3.0	0.882	0.993	2	92.000	45212	165	3.5	1.471	0.993	3
45.000	30305	107	3.5	0.973	0.934	1	93.000	45213	106	3.0	1.172	1.098	2
46.000	30306	113	3.0	0.880	0.910	1	94.000	45214	132	3.0	1.330	1.186	3
47.000	30307	112	3.0	1.090	1.081	2	95.000	45215	095	2.5	0.787	0.875	4
48.000	30308	108	2.5	0.799	0.826	1	96.000	45216	100	2.0	0.576	0.581	1
							97.000	45217	140	4.0	1.768	1.379	3
							98.000	45218	126	3.0	1.124	0.700	1
							99.000	45219	098	3.0	0.674	0.739	1

100.000	45220	112	3.0	0.805	0.714	2	151.000	62211	090	3.0	0.694	0.624	1
101.000	45301	136	3.0	1.489	1.145	3	152.000	62212	098	3.0	0.780	0.735	2
102.000	45302	130	3.5	1.120	1.082	3	153.000	62213	132	3.0	1.079	0.995	1
103.000	45303	127	3.0	1.080	1.148	1	154.000	62214	106	2.5	0.675	0.574	1
104.000	45304	165	3.0	1.438	0.848	3	155.000	62215	118	3.0	1.144	0.948	2
105.000	45305	134	3.0	1.276	1.253	3	156.000	62216	111	3.0	0.990	0.860	1
106.000	45306	133	3.0	1.344	1.318	5	157.000	62217	114	3.0	1.036	0.625	2
107.000	45307	107	3.0	1.055	0.765	1	158.000	62218	132	3.5	1.085	0.680	1
108.000	45308	120	3.0	0.810	1.179	1	159.000	62219	125	4.0	1.138	1.115	1
109.000	45309	132	2.5	0.897	1.115	2	160.000	62220	098	3.0	0.768	0.544	3
110.000	45310	142	3.0	1.267	1.042	2	161.000	62301	115	3.0	0.978	0.771	1
111.000	45311	144	3.0	1.176	1.096	1	162.000	62302	114	4.0	1.621	0.850	2
112.000	45312	124	2.5	0.933	0.507	1	163.000	62303	108	3.0	0.948	1.056	1
113.000	45313	127	3.0	1.150	0.773	3	164.000	62304	117	3.0	1.478	1.040	1
114.000	45314	112	3.0	1.161	0.966	2	165.000	62305	128	4.0	1.955	1.207	1
115.000	45315	102	2.5	0.719	0.750	2	166.000	62306	097	3.0	1.063	0.651	1
116.000	45316	131	3.5	1.557	0.897	1	167.000	62307	157	4.0	1.955	1.207	1
117.000	45317	142	3.0	1.068	1.027	1	168.000	62308	108	4.0	1.398	0.818	1
118.000	45318	115	4.0	1.498	1.237	1	169.000	62309	121	3.0	1.008	0.706	2
119.000	45319	114	3.5	1.304	0.620	1	170.000	62310	125	3.0	0.993	0.621	1
120.000	45320	152	3.0	1.106	1.115	2	171.000	62311	107	3.0	0.875	0.776	3
121.000	62101	112	2.5	0.673	0.699	3	172.000	62312	112	3.0	1.218	0.820	2
122.000	62102	125	3.0	0.819	0.647	2	173.000	62313	145	3.5	1.542	0.745	1
123.000	62103	145	3.0	0.819	0.647	2	174.000	62314	100	3.0	0.765	0.367	1
124.000	62104	140	3.0	1.133	0.746	2	175.000	62315	136	3.0	1.634	0.920	2
125.000	62105	148	3.0	1.317	0.854	3	176.000	62316	067	3.0	0.550	0.592	1
126.000	62106	115	3.0	1.110	0.770	1	177.000	62317	115	3.0	1.022	0.844	2
127.000	62107	087	3.0	1.039	1.001	1	178.000	62318	116	3.5	1.109	1.141	1
128.000	62108	120	3.0	1.180	0.934	2	179.000	62319	107	3.0	0.957	0.719	1
129.000	62109	108	3.0	1.212	0.865	1	180.000	62320	127	3.5	1.669	1.152	1
130.000	62110	140	3.5	1.416	1.141	1	181.000	75101	112	3.0	1.268	0.886	1
131.000	62111	120	3.0	1.212	0.865	1	182.000	75102	114	3.0	1.093	0.734	1
132.000	62112	126	3.5	1.131	0.866	2	183.000	75103	132	3.5	1.303	0.960	1
133.000	62113	098	3.0	1.048	0.726	2	184.000	75104	075	2.5	0.744	0.566	1
134.000	62114	107	4.0	0.957	0.848	3	185.000	75105	127	3.0	1.188	0.834	1
135.000	62115	092	2.0	0.425	0.321	1	186.000	75106	136	3.0	1.476	0.900	1
136.000	62116	125	3.0	1.048	0.726	2	187.000	75107	130	3.0	1.193	1.029	2
137.000	62117	109	3.0	1.340	0.960	1	188.000	75108	118	3.5	1.739	0.984	2
138.000	62118	090	3.0	0.707	0.757	1	189.000	75109	128	3.0	1.171	0.674	1
139.000	62119	110	3.0	0.889	0.913	1	190.000	75110	130	3.0	1.210	0.694	1
140.000	62120	125	2.5	0.900	0.823	1	191.000	75111	100	3.0	0.742	0.690	1
141.000	62201	140	3.0	1.190	1.096	2	192.000	75112	096	3.0	0.948	0.900	1
142.000	62202	155	3.0	1.288	0.889	1	193.000	75113	097	3.0	0.948	0.700	1
143.000	62203	152	2.5	1.094	0.783	1	194.000	75114	121	3.0	1.032	0.555	1
144.000	62204	137	2.0	0.696	0.370	1	195.000	75115	122	3.0	1.043	0.715	3
145.000	62205	107	3.0	1.059	0.938	1	196.000	75116	102	3.5	1.341	0.853	2
146.000	62206	100	3.0	0.850	0.954	1	197.000	75117	134	3.5	1.475	1.010	2
147.000	62207	132	3.0	1.029	0.592	1	198.000	75118	105	3.0	0.954	0.883	1
148.000	62208	106	3.0	0.678	0.854	2	199.000	75119	122	3.0	0.796	0.865	1
149.000	62209	133	3.0	1.110	0.643	1	200.000	75120	152	2.5	0.937	0.818	1
150.000	62210	106	3.5	1.120	0.546	1	201.000	75201	135	3.0	1.367	1.066	4

202.000	75202	114	3.0	1.135	1.054	2	253.000	61113	000	000	0.897	0.970	3
203.000	75203	139	3.0	1.500	0.957	1	254.000	61114	000	000	0.874	0.463	1
204.000	75204	118	3.0	1.171	1.102	2	255.000	61115	000	000	1.400	0.830	3
205.000	75205	155	3.0	1.722	1.080	1	256.000	61116	000	000	1.078	0.768	2
206.000	75206	120	3.0	0.690	0.834	2	257.000	61117	000	000	1.100	0.935	2
207.000	75207	152	3.0	1.438	1.267	1	258.000	61118	000	000	1.155	0.888	2
208.000	75208	111	3.5	1.451	1.205	1	259.000	61119	000	000	1.496	1.028	1
209.000	75209	116	3.5	1.561	1.343	1	260.000	61120	000	000	1.296	0.856	1
210.000	75210	120	3.0	1.163	1.031	1	261.000	61201	000	000	0.990	0.743	3
211.000	75211	112	3.0	1.383	1.011	1	262.000	61202	000	000	0.796	0.659	4
212.000	75212	097	3.5	1.376	0.990	2	263.000	61203	000	000	0.809	0.598	1
213.000	75213	105	4.0	1.638	1.144	1	264.000	61204	000	000	1.313	0.849	2
214.000	75214	123	3.0	1.350	0.832	1	265.000	61205	000	000	0.756	0.620	2
215.000	75215	118	3.0	0.980	0.879	1	266.000	61206	000	000	0.928	0.844	2
216.000	75216	150	3.0	1.591	1.121	1	267.000	61207	000	000	1.321	0.851	4
217.000	75217	131	2.5	0.829	0.540	2	268.000	61208	000	000	1.328	1.186	4
218.000	75218	141	3.5	1.701	1.211	2	269.000	61209	000	000	1.110	0.620	2
219.000	75219	134	3.0	1.413	1.398	2	270.000	61210	000	000	1.062	0.854	1
220.000	75220	100	3.0	1.250	0.927	1	271.000	61211	000	000	0.981	0.721	2
221.000	75301	130	3.0	1.152	1.060	2	272.000	61212	000	000	0.406	0.387	3
222.000	75302	155	4.0	2.069	1.282	1	273.000	61213	000	000	1.130	0.728	3
223.000	75303	120	3.5	1.869	0.988	2	274.000	61214	000	000	0.962	0.565	4
224.000	75304	134	3.0	1.143	0.995	2	275.000	61215	000	000	0.751	0.821	3
225.000	75305	107	3.5	1.480	0.708	3	276.000	61216	000	000	0.703	0.666	5
226.000	75306	112	3.5	1.221	1.248	1	277.000	61217	000	000	0.935	0.602	4
227.000	75307	130	3.5	1.490	1.156	1	278.000	61218	000	000	0.986	0.776	3
228.000	75308	100	3.0	0.738	0.864	1	279.000	61219	000	000	0.684	0.602	3
229.000	75309	124	3.5	2.054	0.810	5	280.000	61220	000	000	1.216	0.771	3
230.000	75310	135	3.0	1.101	0.890	2	281.000	61301	000	000	0.280	0.463	1
231.000	75311	124	3.0	1.346	0.695	2	282.000	61302	000	000	2.046	1.360	1
232.000	75312	090	3.5	1.586	1.032	1	283.000	61303	000	000	1.012	0.661	2
233.000	75313	173	3.5	1.620	0.940	5	284.000	61304	000	000	1.479	1.312	2
234.000	75314	146	3.5	1.087	0.881	3	285.000	61305	000	000	0.690	0.567	3
235.000	75315	123	3.5	1.268	0.958	2	286.000	61306	000	000	0.507	0.866	2
236.000	75316	130	3.5	1.099	0.930	1	287.000	61307	000	000	1.206	1.024	2
237.000	75317	134	3.0	1.412	0.913	1	288.000	61308	000	000	0.594	0.523	2
238.000	75318	101	2.0	0.632	0.458	1	289.000	61309	000	000	0.603	0.400	2
239.000	75319	105	3.0	0.770	0.539	1	290.000	61310	000	000	0.489	0.382	1
240.000	75320	110	3.0	1.068	0.850	1	291.000	61311	000	000	0.677	0.367	3
241.000	61101	000	000	0.829	0.574	2	292.000	61312	000	000	0.585	0.606	1
242.000	61102	000	000	1.250	0.958	2	293.000	61313	000	000	1.605	1.414	2
243.000	61103	000	000	1.364	0.576	1	294.000	61314	000	000	0.532	0.444	1
244.000	61104	000	000	0.839	0.748	3	295.000	61315	000	000	0.303	0.255	3
245.000	61105	000	000	1.055	0.810	3	296.000	61316	000	000	0.676	0.467	2
246.000	61106	000	000	1.215	0.801	1	297.000	61317	000	000	0.254	0.214	2
247.000	61107	000	000	0.704	0.725	1	298.000	61318	000	000	0.618	0.610	4
248.000	61108	000	000	1.103	0.744	4	299.000	61319	000	000	0.800	0.773	3
249.000	61109	000	000	1.522	0.796	3	300.000	61320	000	000	0.503	0.533	1
250.000	61110	000	000	1.327	0.982	2	301.000	10101	000	000	0.930	0.821	1
251.000	61111	000	000	1.316	0.660	3	302.000	10102	000	000	1.166	0.771	2
252.000	61112	000	000	0.681	0.610	1	303.000	10103	000	000	0.846	0.547	1

304.000	10104	000	000	1.109	0.764	2	355.000	10315	000	000	0.867	0.596	2
305.000	10105	000	000	1.649	0.621	2	356.000	10316	000	000	1.279	0.674	1
306.000	10106	000	000	0.527	0.286	1	357.000	10317	000	000	0.595	0.330	1
307.000	10107	000	000	1.269	0.838	1	358.000	10318	000	000	0.822	0.613	2
308.000	10108	000	000	1.617	1.179	1	359.000	10319	000	000	0.636	0.289	2
309.000	10109	000	000	1.510	0.842	2	360.000	10320	000	000	1.413	0.839	1
310.000	10110	000	000	1.318	0.753	1	361.000	14101	000	000	1.931	0.731	0
311.000	10111	000	000	0.958	0.725	1	362.000	14102	000	000	1.433	0.642	0
312.000	10112	000	000	0.515	0.337	1	363.000	14103	000	000	1.216	0.483	0
313.000	10113	000	000	1.404	1.155	1	364.000	14104	000	000	1.211	0.623	0
314.000	10114	000	000	1.087	0.941	2	365.000	14105	000	000	1.380	0.645	0
315.000	10115	000	000	0.383	0.293	1	366.000	14106	000	000	1.531	0.727	0
316.000	10116	000	000	1.589	1.009	1	367.000	14107	000	000	1.324	0.688	0
317.000	10117	000	000	2.081	1.100	1	368.000	14108	000	000	1.191	0.711	0
318.000	10118	000	000	1.237	0.878	1	369.000	14109	000	000	1.887	0.781	0
319.000	10119	000	000	1.640	0.762	1	370.000	14110	000	000	1.790	0.879	0
320.000	10120	000	000	1.348	0.921	1	371.000	14111	000	000	0.961	0.432	0
321.000	10201	000	000	1.030	0.433	1	372.000	14112	000	000	1.452	0.758	0
322.000	10202	000	000	1.189	0.668	1	373.000	14113	000	000	1.532	0.735	0
323.000	10203	000	000	0.939	0.724	2	374.000	14114	000	000	1.299	0.760	0
324.000	10204	000	000	1.043	0.845	3	375.000	14115	000	000	1.653	0.770	0
325.000	10205	000	000	1.400	0.822	2	376.000	14116	000	000	1.878	0.749	0
326.000	10206	000	000	0.884	0.804	1	377.000	14117	000	000	0.470	0.261	0
327.000	10207	000	000	1.180	0.767	1	378.000	14118	000	000	1.657	0.631	0
328.000	10208	000	000	1.125	0.718	1	379.000	14119	000	000	1.144	0.557	0
329.000	10209	000	000	0.815	0.476	1	380.000	14120	000	000	1.070	0.489	0
330.000	10210	000	000	0.238	0.301	1	381.000	14201	000	000	1.553	0.649	0
331.000	10211	000	000	0.680	0.563	1	382.000	14202	000	000	1.711	1.166	0
332.000	10212	000	000	1.202	0.749	3	383.000	14203	000	000	1.674	0.738	0
333.000	10213	000	000	1.413	0.741	1	384.000	14204	000	000	1.433	0.946	0
334.000	10214	000	000	1.365	0.733	1	385.000	14205	000	000	1.460	0.603	0
335.000	10215	000	000	1.134	0.980	1	386.000	14206	000	000	1.256	0.673	0
336.000	10216	000	000	0.879	0.988	1	387.000	14207	000	000	1.076	0.860	0
337.000	10217	000	000	1.238	0.981	1	388.000	14208	000	000	0.982	0.422	0
338.000	10218	000	000	0.914	0.650	3	389.000	14209	000	000	1.396	0.656	0
339.000	10219	000	000	0.926	0.736	2	390.000	14210	000	000	1.801	0.932	0
340.000	10220	000	000	2.025	1.419	1	391.000	14211	000	000	1.576	0.964	0
341.000	10301	000	000	1.537	0.847	2	392.000	14212	000	000	1.942	0.964	0
342.000	10302	000	000	0.941	0.764	1	393.000	14213	000	000	2.236	1.118	1
343.000	10303	000	000	1.164	1.025	1	394.000	14214	000	000	1.643	0.642	0
344.000	10304	000	000	0.952	0.811	3	395.000	14215	000	000	1.567	0.992	0
345.000	10305	000	000	0.918	0.555	1	396.000	14216	000	000	0.770	0.344	0
346.000	10306	000	000	1.509	0.564	1	397.000	14217	000	000	1.086	0.520	1
347.000	10307	000	000	0.501	0.346	1	398.000	14218	000	000	1.843	0.678	0
348.000	10308	000	000	1.792	1.325	2	399.000	14219	000	000	1.514	0.953	0
349.000	10309	000	000	0.471	0.281	1	400.000	14220	000	000	1.892	1.004	0
350.000	10310	000	000	0.400	0.232	1	401.000	14301	000	000	0.593	0.412	0
351.000	10311	000	000	0.900	0.697	2	402.000	14302	000	000	1.521	1.095	0
352.000	10312	000	000	1.146	0.782	3	403.000	14303	000	000	1.292	0.857	0
353.000	10313	000	000	1.442	0.578	2	404.000	14304	000	000	1.463	1.242	0
354.000	10314	000	000	0.669	0.438	3	405.000	14305	000	000	1.955	0.972	0

406.000	14306	000	000	1.043	0.691	0	457.000	18217	000	000	0.450	0.181	0
407.000	14307	000	000	2.027	1.353	0	458.000	18218	000	000	0.763	0.368	0
408.000	14308	000	000	1.586	0.763	0	459.000	18219	000	000	1.392	0.670	0
409.000	14309	000	000	1.162	1.017	0	460.000	18220	000	000	0.660	0.338	0
410.000	14310	000	000	1.742	0.635	0	461.000	18301	000	000	1.523	0.636	0
411.000	14311	000	000	1.123	0.659	0	462.000	18302	000	000	0.784	0.461	0
412.000	14312	000	000	1.522	0.998	0	463.000	18303	000	000	1.327	0.679	0
413.000	14313	000	000	1.912	1.001	1	464.000	18304	000	000	2.083	1.167	0
414.000	14314	000	000	1.679	0.720	0	465.000	18305	000	000	0.473	0.273	0
415.000	14315	000	000	0.956	0.440	0	466.000	18306	000	000	1.762	1.018	0
416.000	14316	000	000	1.690	0.890	0	467.000	18307	000	000	1.445	0.820	0
417.000	14317	000	000	1.398	0.713	0	468.000	18308	000	000	1.698	0.751	0
418.000	14318	000	000	1.675	0.949	0	469.000	18309	000	000	1.381	0.783	0
419.000	14319	000	000	1.971	0.991	0	470.000	18310	000	000	1.359	0.571	0
420.000	14320	000	000	0.604	0.391	0	471.000	18311	000	000	0.592	0.213	0
421.000	18101	000	000	1.274	0.637	0	472.000	18312	000	000	1.473	0.731	0
422.000	18102	000	000	1.257	0.641	0	473.000	18313	000	000	2.256	0.940	0
423.000	18103	000	000	1.142	0.513	0	474.000	18314	000	000	0.618	0.358	0
424.000	18104	000	000	1.337	0.633	0	475.000	18315	000	000	1.370	0.556	0
425.000	18105	000	000	1.766	0.676	0	476.000	18316	000	000	1.291	0.752	0
426.000	18106	000	000	0.896	0.354	0	477.000	18317	000	000	1.520	0.805	0
427.000	18107	000	000	1.272	0.784	0	478.000	18318	000	000	0.637	0.330	0
428.000	18108	000	000	1.991	0.735	0	479.000	18319	000	000	0.745	0.342	0
429.000	18109	000	000	0.689	0.311	0	480.000	18320	000	000	0.740	0.325	0
430.000	18110	000	000	1.353	0.511	0	* EOF hit after 480.000						
431.000	18111	000	000	0.846	0.566	0	*END						
432.000	18112	000	000	1.919	1.012	0	!BYE						
433.000	18113	000	000	1.334	0.608	0							
434.000	18114	000	000	0.757	0.347	0							
435.000	18115	000	000	0.893	0.349	0							
436.000	18116	000	000	1.172	0.547	0							
437.000	18117	000	000	2.711	0.930	0							
438.000	18118	000	000	1.788	0.927	0							
439.000	18119	000	000	0.319	0.186	0							
440.000	18120	000	000	1.262	0.500	0							
441.000	18201	000	000	1.697	0.951	0							
442.000	18202	000	000	0.593	0.321	0							
443.000	18203	000	000	1.178	0.749	0							
444.000	18204	000	000	1.521	0.792	0							
445.000	18205	000	000	0.453	0.195	0							
446.000	18206	000	000	2.068	0.888	0							
447.000	18207	000	000	1.502	0.442	0							
448.000	18208	000	000	1.895	0.733	0							
449.000	18209	000	000	1.735	0.746	0							
450.000	18210	000	000	1.459	0.726	0							
451.000	18211	000	000	1.963	0.958	0							
452.000	18212	000	000	0.420	0.239	0							
453.000	18213	000	000	1.682	0.764	0							
454.000	18214	000	000	1.760	0.854	0							
455.000	18215	000	000	0.316	0.136	0							
456.000	18216	000	000	1.238	0.576	0							

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