AN ABSTRACT OF THE THESIS OF

Catherine Gray Parks for the degree of Doctor of Philosophy in the Department of Forest Science, presented on April 28, 1993. Title: The Influence of Induced Host Moisture Stress on the Growth and Development of Western Spruce Budworm and Armillaria ostoyae on Grand Fir Seedlings.

Abstract Approved:_____

John D. Walstad

This greenhouse study evaluates the influence of separately and simultaneously imposed water stress, western spruce budworm (Choristorneura occidentalis Freeman) defoliation, and inoculation with the root pathogen, Armillaria ostoyae (Romagn.) Herink, on the growth and biochemical features of Abies grandis (Dougl.) Lindl. Seedling biomass, plant moisture status, bud phenology, and allocation patterns of phenolics, carbohydrates, and key nutrients (nitrogen, phosphorus, potassium and sulfur) are reported.

Hypotheses are developed and tested on the impacts of water-stress, defoliation, and root inoculation, on western spruce budworm growth and development, and Armillaria ostoyae-caused mortality and infection.

Western spruce budworm larvae fed on water-stressed seedlings had higher survival rates, grew faster, and produced larger pupae than those fed on well-watered seedlings. There is no clear reason for the positive insect response, but changes in foliage nutrient patterns and phenolic chemistry are indicated.

Insect caused defoliation has been earlier reported to enhance successful colonization of Armillaria spp. on deciduous trees in the forests of the northeastern United States. The positive response of the fungus was attributed to a weakened tree condition. Conversely, although this study conclusively found water-limited trees to have increased susceptibility to A. ostoyae, defoliation significantly lowered Armillaria-caused infection and mortality. The decline in infection success is attributed to defoliation-caused reduction in plant water stress and an alteration of root carbohydrate chemistry.

One and/or two years of defoliation did not appear to weaken the physiological condition of seedlings. Conversely, water-stressed seedlings that were also defoliated produced more buds, had an earlier bud phenology, contained higher total reserve carbohydrates, and had little Armillaria-caused mortality.

The study suggests that during drought, short-term defoliation may be beneficial to grand fir and its associated forest community. Also, the additive effects of simultaneously occurring A. ostoyae and western spruce budworm may not be as severe as conventionally believed. Ecological and forest management implications are explored.

THE INFLUENCE OF INDUCED HOST MOISTURE STRESS ON THE GROWTH AND DEVELOPMENT OF WESTERN SPRUCE BUDWORM AND ARMILLARIA OSTOYAE ON GRAND FIR SEEDLINGS

By

Catherine Gray Parks

A THESIS

Submitted to
Oregon State University

in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Completed April 28, 1993

Commencement June 1993

APPROVED:

Professor and Head, Department of Forest Resources

Head of Department of Forest Science

Dean of Graduate School

Date thesis is presented April 28, 1993

Typed by Catherine Parks

ACKNOWLEDGMENTS

I would like to acknowledge the USDA Forest Service, Pacific Northwest Research Station for supporting this work. My gratitude is extended to my supervisors during the last years, Boyd Wickman and Susan Little, who encouraged this effort and helped me find the financial support to continue.

For productive dialog, I thank my colleagues: Torolf Torgersen, Richard Mason, Philip Wargo, Arthur Tiedemann, and Jack Ward Thomas. For help in chemical analysis I thank Rose Marie Muzika, Carol Glassman, and especially Cathy Rose. I thank Duncan Morrison for supplying the Armillaria isolate and Roy Beckwith for supplying the budworm larvae employed in the experiments. Kathy Howell provided much assistance throughout the experiment and Lisa Aichele in the preparation of the manuscript. For the camaraderie, I thank my fellow graduate students, Kathy Lewis, Blakey Lockman, Brennan Ferguson, and Jane Smith.

I thank my husband, Bruce, for his faithful encouragement and countless sacrifices, and my daughter, Nella, for her love of nature and to have appeared to thrive in-spite-of-it-all. I appreciate many friends with children for the weekends and evenings they offered to Nella.

I am very thankful for the guidance provided by my committee: John Walstad, Everett Hansen, Joe Zaerr, Tim Schowalter, Boyd Wickman, Greg Filip, and Neil Christensen. Special thanks are extended to my mentor Greg Filip whose infectious devotion to Forest Pathology sparked my interest and the inception of this journey.

DEDICATION

To my kinsfolk, who instilled a simple notion in me during my childhood that land mattered. That grass and crops and trees and wild things somehow supremely mattered. And that you were not whole unless you had a daily knowledge of them.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

THE INFLUENCE OF INDUCED HOST MOISTURE STRESS ON THE GROWTH AND DEVELOPMENT OF WESTERN SPRUCE BUDWORM AND ARMILLARIA OSTOYAE ON GRAND FIR SEEDLINGS

INTRODUCTION

Grand Fir Biology

Grand fir (Abies grandis (Dougl. ex D.Don) Lindl.) has a wide geographical distribution in the northwestern United States and southern British Columbia. Its distribution is from latitude 51° to 39° N. and from longitude 125° to 114° W. Figure 1 shows there are two distinct groupings of grand fir within the distribution; a Pacific coast group and a continental interior group. There are no recognized varieties of grand fir, although a "green coastal form" and "grey interior form" are often recognized (Foiles et al 1990). The grey interior form occupies all areas east of the Cascades in Oregon and Washington and in the drier regions of southern Oregon. Significant differences in height growth between trees from sources east and west of the Cascade crest have been reported (Foiles 1965), but the average growth of westside and interior seedlings is generally about the same (Steinhoff 1978).

Grand fir is either a seral or climax species in different forest types within its range. Grand fir sometimes grows in pure stands but is much more common in mixed coniferous and hardwood forests. Regarding growth and yield, grand fir

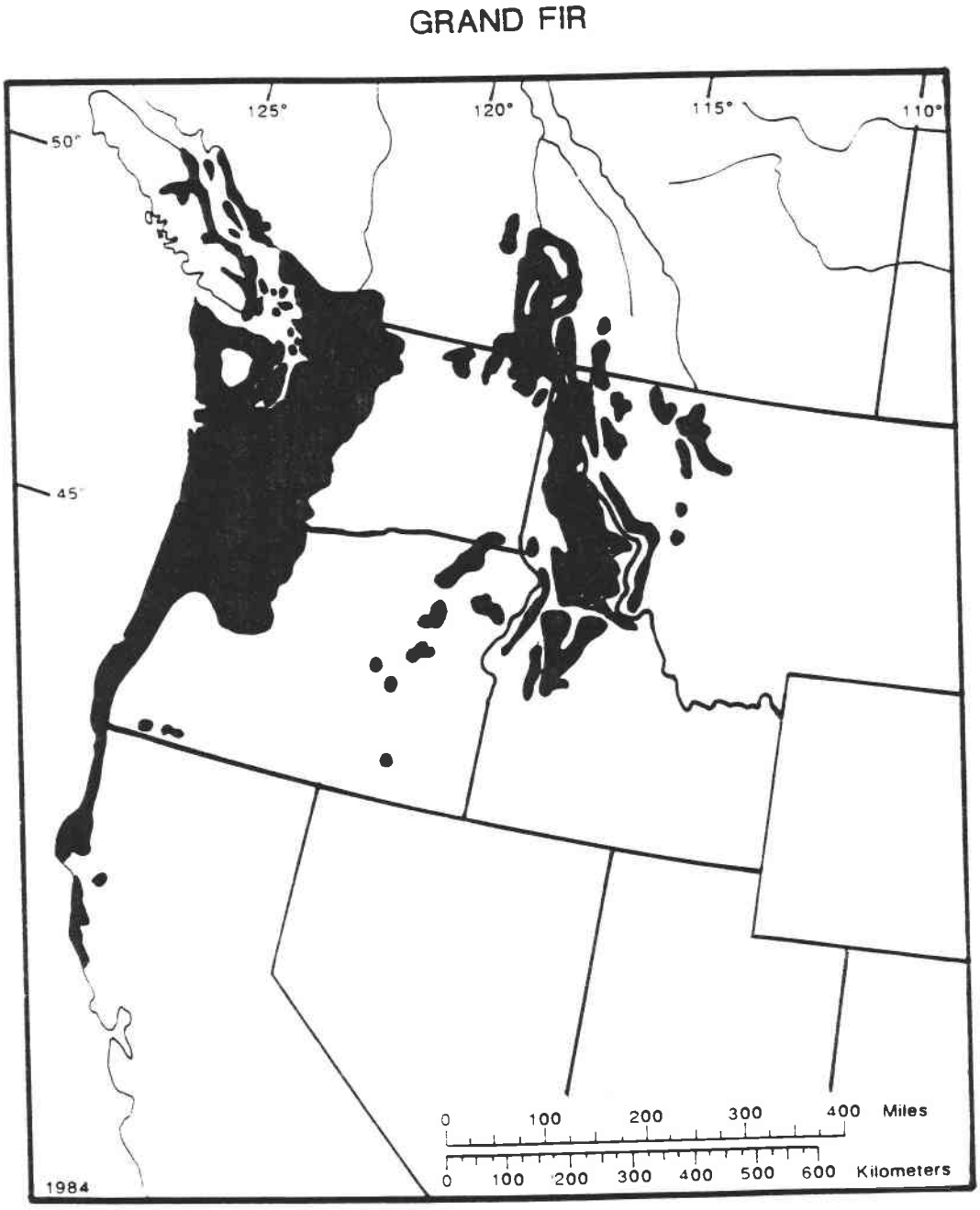


Figure 1. Range map of grand fir, Abies grandis from Foiles et al. (1990)

ranks among the most productive species in all the associations in which it grows (Cochran 1979; Haig 1932; Pfister et al. 1977). Associated forest cover of grand fir varies greatly between the coastal and interior groupings, largely due to precipitation. Generally, coastal-form grand fir can be found growing in areas of high precipitation in deep moist soils or in valleys and stream bottoms having high ground-water levels (Foiles et al. 1990). While the interior form may also be found on rich mineral soils of the valley bottoms grey interior forms often occurs on drier, shallow, exposed soils of mountain ridges and pure pumice soils in central and eastern Oregon, northern Idaho, western Montana, and southern British Columbia.

The grand fir root system is intermediate in development among its associated tree species. Although a relatively deep taproot enables grand fir to survive and grow on rather dry soils and exposed ridges (i.e., interior form), the anchoring taproot does not grow as rapidly nor as deeply as dry site associates such as ponderosa pine (Pinus ponderosa (Dougl. ex D.Don), Douglas-fir (Pseudotsuga menziesii var. glauca (Beissn.) Franco), and lodgepole pine (Pinus contorta (Dougl. ex. Loud). On moist sites (i.e, the coastal-form), the grand fir root system grows faster and deeper than wet site species such as western hemlock (Tsuga heterophylla [Raf.] Sarg.), western redcedar (Thuja plicata Donn ex D. Don), and Engelmann spruce (Picea engelmannii Parry ex Engelm.) which all tend to have little taproot and large numbers of more shallow lateral roots (Foiles 1965).

The adaptable root system and shade-tolerant foliage allows grand fir to produce roots under shaded conditions, enabling it to establish and survive in the

understory. On wet sites (i.e., coastal form) grand fir grows rapidly enough to compete with other seral species in the dominant overstory. In drier interior regions, its shade tolerance allows grand fir to occupy the understory until it can, in the absence of disturbance, assume dominance as climax conditions are approached.

The frequency of grand fir has steadily increased in the interior northwestern United States over the last 100 years. In 1906, the USDA Forest Service started its' policy of fire suppression. Fire control allowed millions of hectares that previously were maintained by periodic light ground fires as ponderosa pine and western larch (Larix occidentalis Nutt.) stands, to convert to shade tolerant, fire intolerant, grand fir and Douglas-fir.

These drier interior West stands where the "grey interior form" of grand fir now proliferates, are being heavily impacted by both Armillaria ostoyae (Romagn.) Herink and western spruce budworm (Choristoneura occidentalis Freeman). It is commonly accepted among forest pathologists and forest managers that interior regions sustain substantially more impact by A. ostoyae than the coastal areas (Morrison 1981). Interior grand fir is considered to be highly susceptible to Armillaria (Filip and Goheen 1984; Entry et al. 1991; McDonald et al. 1988). However, how this increased susceptibility relates to water-stressed sites requires investigation and documentation.

The relationship of dry interior sites with populations of western spruce budworm has been more extensively documented and investigated. Figure 2 shows an outbreak frequency map for western spruce budworm that was developed for

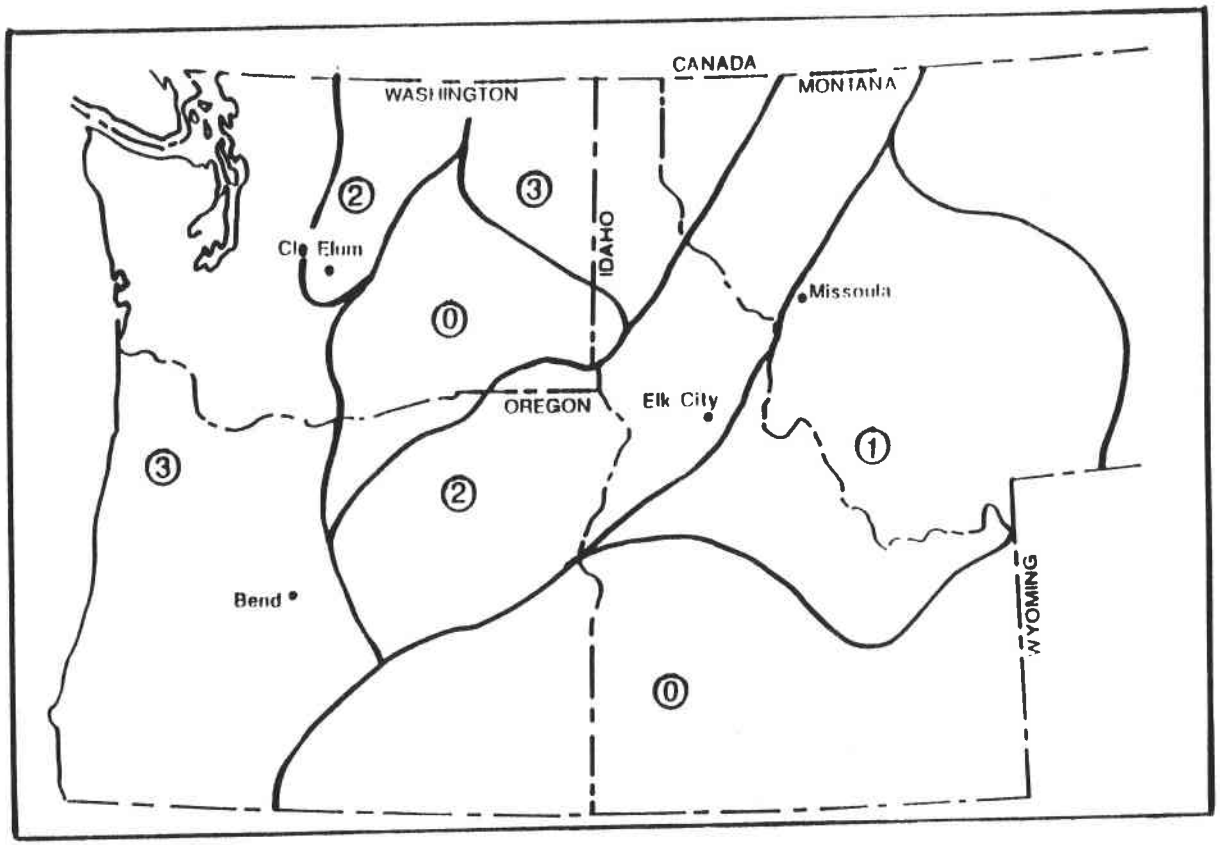


Figure 2. Three classes of outbreak frequency (1947-78) developed for forested areas of Idaho, Montana, Oregon, and Washington (high = 1, medium = 2, low = 3), from Kemp et al. (1985)

forested areas of Idaho, Montana, Oregon and Washington. Coastal areas that coincide with the distribution of "green coastal form" grand fir (Figure 1) are rated as "low" for outbreak frequency. Western spruce budworm exist in endemic populations, rarely increasing to populations capable of causing visible defoliation. Conversely, regions that coincide with "grey interior form" grand fir are rated as medium or high; having shown a historic proclivity for budworm outbreak, especially in recent decades.

Is water-stress the common denominator that brings together these organisms: interior grand fir; western spruce budworm; and A. ostoyae? How can their interrelationships be characterized? How do these relationships interact and affect various other members and functions of the ecosystem? No doubt such co-evolved species have an intricate association with one another. The following literature review outlines the work of many in an effort to elucidate some possible interactions of water stress, grand fir, western spruce budworm, and A. ostoyae. This review will introduce the immediate research and give substance to the Discussion section which ensues.

LITERATURE REVIEW

I. Forest Insect and Disease Outbreaks in Relation to Water Stress

The role of drought in forest insect and disease outbreaks has been much debated during the last 50 years. Few field studies have been conducted to experimentally test the relationship of drought with these outbreaks. Abundant observational reports imply that stress caused by drought increases the impact of forest insects and diseases. Matson and Haack (1987b) maintain that this relationship exists because water stress alters trees and their thermal environment so that stressed trees become progressively more susceptible (through erosion of their defense systems) and suitable (through enhancement of certain constitutive traits) to their adapted consumers, allowing them to achieve faster growth, higher survival, and more successful reproduction. "Drought-stress," in a tree or forest stand, can be induced by either lack of precipitation or by severe competition caused by overstocking or excess vegetation.

Forest Insect Herbivores

A general theory that relates outbreaks of forest insect herbivores to climatic anomalies was first suggested by Graham (1939) and later developed by Wellington (1954) and Greenbank (1956, 1963). The theory postulates that the fluctuations in the abundance of many forest insect herbivores are under long-term climatic control. If a climatic anomaly that favors an increase in fecundity and/or survival persists

over several consecutive generations, its effects on the population may be multiplicative.

Weather has both direct and indirect effects on forest insect herbivore populations. The direct effects of weather on herbivores and their natural enemies are well documented (Martinat 1987). Indirect effects of weather may influence the level of stress in the host plant which in turn may alter its nutritional quality, chemical defenses, or digestibility.

Drought or poor site conditions have often been correlated with outbreaks of forest insects (e.g., Grimalsky 1961; Mason and Tigner 1972; Otto 1970; Mattson and Addy 1975; Kolomiets et al. 1979; Stoszek et al. 1981; Kemp and Moody 1984; Larson and Tenow 1984). Some studies have shown drought to generate an increase of insect performance by improving nutritional quality of foliage (White 1969, 1974, 1976, 1984; Mattson and Haack 1987b). Others have suggested that drought weakens trees' chemical defenses and that, in turn, may lead to an insect outbreak (Rhoades 1979; Cates et al. 1983a, b). Mattson and Haack (1987b) note that experimental tests of the importance of plant moisture stress in producing insect outbreaks are lacking and that evidence that drought leads to insect outbreaks is largely conjectural.

Western Spruce Budworm

Drought has often been suggested as a factor that may trigger western spruce budworm outbreaks. Based on research data collected in the Rocky Mountains,

Carlson (1987) describes stands and forests most susceptible to spruce budworm outbreak as those stands with warm, dry conditions. Carlson reports that fast-growing, healthy stands are less susceptible than stagnated, stressed stands. Foliage quality in drought-stressed stands may be more favorable to eastern spruce budworm and tends to promote insect survival (Mattson and Haack 1987a).

From observations made in forests located in the northeastern United States and Canada, many have concluded that early summer drought, 3-4 years prior, was correlated with spruce budworm outbreaks (Choristoneura fumiferana Clemens) (Greenbank 1956; Hardy et al. 1983; Jennings and Crawford 1985; Pilon and Blais 1961; Wellington et al. 1950). Initially, the hypothesis was based on the observation that sunny, dry weather in the spring enhances continuous larval feeding, whereas cool, cloudy, and rainy conditions interrupt or prolong feeding. Greenbank (1956) showed that the correlations between the development rate and weather conditions were high, such that larval development is completed during a shorter period of time with higher average temperatures and reduced cloudiness and rainfall. Since larval development time is positively correlated with pupal size and fecundity, these weather conditions should result in higher populations the next year (Martinat 1987). Hard et al. (1980), Twardus (1980), and Thompson et al. (1984) concluded that outbreaks of western spruce budworm in British Columbia were related not only to warm, dry summers but also to an optimal synchrony between larval emergence and bud flush. Outbreak collapse appeared to be related to high autumn temperatures following moth flight (Martinat 1987).

Forest Diseases

As with insect outbreaks, it is well known that environmental stress can predispose plants to disease (Crist and Schoeneweiss 1975; Schoenenweiss 1975, 1981, 1983). Experimental tests of the importance of water stress in producing disease outbreaks are lacking and evidence that drought leads to forest disease outbreaks is largely speculative.

By exposing host plants to controlled water stress, increased disease susceptibility to Heterobasidion annosum (Fr.) Brefeld (Fomes annosus [Fr.] Cooke) was reported in loblolly pines (Pinus taeda L.) (Towers and Stambaugh 1968), and in Norway spruce (Picea abies (L.) Karst) (Lindberg and Johansson 1992). Using grand fir seedlings, Puritch and Mullick (1975) found that water-stressed trees had an impaired ability to heal and recover after injury. They propose that the slowing down of the healing process under water-stressed conditions could explain the increased susceptibility of trees to decay organisms and insects after periods of drought. Bier (1959), and later Bloomberg (1962) and Landis and Hart (1967), correlated low levels of bark moisture content with increases in susceptibility of trees to several canker fungi. Although bark moisture content may be a factor in predisposition of bark to colonization by certain pathogens, its relation to disease susceptibility in tissues other than bark has not been clearly established. In those instances where disease is enhanced by drought, the relationship between water stress and infection rate is likely not a linear correlation. Lindberg and Johansson (1992) found that moderate drought stress resulted in a considerable increase in both

the frequency of infection through bark and the growth rate in wood of Norway spruce inoculated with H. annosum. However, a further increase in drought stress led to a decrease in infection frequency and fungal growth rate. The decrease in infection at very low water potentials may be due to the decrease in tissue osmotic potential (Lindberg and Johansson 1992). It has been demonstrated in lab experiments (Boddy 1983) that as tissue dries out and osmotic potentials drop, many wood-rotting fungi exhibit a decrease in growth.

Armillaria

Taxonomy. Armillaria was first described by Fries (1819). Since, the dynamic taxonomy of the type species has produced confusion (Watling et al. 1982). Until recently it was assumed that Armillaria mellea was one polymorphic species with a worldwide distribution and an extremely wide host range. The discovery that an Armillaria species demonstrated a bifactorial sexual incompatibility system led to studies that revealed the existence of several intersterile groups in the Armillaria mellea complex (Korhonen 1978; Anderson and Ullrich 1979). Throughout this document the name "Armillaria mellea" will be followed by the qualifier "sensu lato" when the Armillaria species reported was of a member of the former Armillaria mellea complex. The species of Armillaria currently under the taxonomic name A. mellea (Vahl:Fr.) Kummer will appear without "sensu lato".

Marked differences in host preference and pathogenicity occur among the various species of Armillaria throughout the world (Wargo and Shaw 1985). Some act primarily as saprophytes on dead trees, while others are aggressive pathogens.

One member of the former Armillaria mellea complex, Armillaria ostoyae North American Biological Species I (NABS I), can be a primary pathogen on conifers (Wargo and Shaw 1985). The fungus attacks, colonizes, and kills apparently healthy trees of all ages often creating large disease centers. In dying trees, the fungus continues to advance in the root collar area forming distinct mycelial fans under the bark (Morrison 1981). The disease centers often cover several hectares and can affect up to 25 percent of the trees in a stand (James et al. 1984). Such active disease centers have often been associated with trees predisposed to disease by adverse environmental factors (Wargo and Harrington 1991).

There are many reports, world-wide, to confirm the relationship of drought and Armillaria spp. In their extensive review of the literature of the relationship of Armillaria with drought, Wargo and Harrington (1991) found numerous reports of widespread dying-off of forest stands that authors attributed to drought-induced Armillaria infections. In Europe Twarowski and Twarowska (1959) and Nechleba (1915) indicate that attack of both conifer and hardwoods by Armillaria has been associated with drought since the late 1800's. Parasitism by Armillaria on true fir (Abies spp.) species was reported to increase during dry seasons, while wet seasons favored its saprophytic role (Nechleba 1927, as cited by Wargo and Harrington

1991). It has been observed that droughts often preceded Armillaria-caused deaths of many conifer species in Europe (Müller 1921, Nechleba 1915, both as cited by Wargo and Harrinton 1991). Additionally, early observations of Armillaria-caused oak mortality report drought stress as a predisposing factor (Falck 1918, 1923; Hen 1914, all as cited by Wargo and Harrington 1991).

In 1939, Ehrlich reported drought as an important predisposing factor in Armillaria-caused mortality of western white pine (Pinus monticola Dougl. ex D. Don). Drought and subsequent Armillaria infection have been reported on radiata pine (Pinus radiata D.Don), western white pine, eastern hemlock (Tsuga canadensis (L.) Carr), balsam fir (Abies balsamea (L.) Mill), scots pine (Pinus sylvestris L.), sugar maple (Acer saccharum Marsh.), black- (Quercus velutina Lam.), red- (Q. falcata Michx var. falcata), and scarlet-oaks (Q. coccinea Muenchh.), and eucalyptus (Eucalyptus spp.) as summarized by Wargo and Harrington (1991).

Poorly developed root systems have been regarded as a possible component in the relationship of moisture stress and Armillaria infection (Ritter and Pontor 1969). Shallow roots and prolonged drought stress (7 years) were found to be associated with the colonization of Armillaria in roots of eastern hemlock (Secrest et al. 1941).

Although the association of Armillaria and drought is one of the most widely speculated interactions of a stress and disease severity, the mechanisms by which drought predisposes trees to Armillaria have not been characterized. Adequate experimental data have not been generated to approach this question.

II. Effect of Water-stress on Plant Traits

Because virtually every plant process is affected during drought, most authors agree that plant-insect, -pathogen relationships must certainly be influenced by water stress. With increasing water stress, a series of physiological and biochemical changes systematically occurs within the plant (Hsiao 1973; Hsiao et al. 1976). As a result, water-stressed plants may at first become more capable, but then less and less capable of defending themselves against herbivore and root disease as stress intensifies (Mattson and Haack 1987a; Houston 1981). In this section I will review some of the morphological, physiological, and biochemical changes that occur in water-stressed plants that are of potential relevance to insect and root pathogen performance.

Stomatal behavior. Water-stressed plants reduce transpiration by means of stomatal closure.

Abscisic acid. Abscisic acid begins to increase in leaf tissues and, to a lesser extent, other tissues including roots (reviewed by Bradford and Hsiao 1982, Salisbury and Marinos 1985). Abscisic acid inhibits shoot growth, further conserving water, and root growth appears to be promoted, which could increase the water acquisition (Salisbury and Ross 1985).

Photosynthesis. Not only does stomatal closure bring about reduced transpiration and increased leaf temperature; it also reduces photosynthesis by inhibiting CO_2 conductance (Hsiao 1973).

Respiration. Respiration is depressed because there is a reduced energy need for cell division and elongation (Begg and Turner 1976). Because photosynthesis is restricted more than respiration, reserve carbohydrates (starches) are usually depleted during drought.

Translocation. The transport system is highly resistant to desiccation and continues to operate at water potentials that severely inhibit photosynthesis (Kramer 1983).

Osmotic adjustment. Osmotic adjustment is a mechanism by which water-stressed plants lower their osmotic potential by accumulating solutes in cells and thereby maintain higher turgor, greater cell enlargement and growth, stomatal opening, and photosynthesis than would otherwise be possible (Kramer 1983). Osmotic adjustment allows for a reduction in water vapor loss and an increase in water uptake from the drying soil (Tyree and Jarvis 1982). Those solutes most frequently accumulated are carbohydrates, sugar alcohols, amino acids, organic acids, and inorganic ions (Salisbury and Ross 1985). Because many of the solutes that increase in concentration in response to water stress serve as feeding stimulants and primary

nutrients of insects, water-stressed plants may be more attractive and nutritious to insects than are non-stressed plants (Mattson and Haack 1987b).

Nutrient uptake and mineral content. Decreases in water potential affect water movement, especially water movement from the soil into roots, thereby reducing mineral uptake. Reduced absorption of inorganic ions from soil also occurs because ion movement is slow in drying soil, root growth is decreased, and increased root suberization decreases root permeability (Pitman 1981; Kramer 1983). Severe water stress, however, can cause a reduction in root suberization (Lindberg and Johansson 1992). Stomatal closure during drought also reduces the "transpirational pull" on water movement and uptake, thereby reducing mineral uptake, as well. Nevertheless, the total mineral ash content of all plant tissue is generally greater in water-stressed plants, probably because less "dilution" has occurred due to restricted growth (Mattson and Haack 1987b).

Nitrogen metabolism. Nitrogen levels, especially soluble nitrogen levels, increase under water stress; however, the effects on total nitrogen are not as clear. Old leaves may senesce during drought and transport their nitrogen out to more juvenile leaves (Viets 1972). In general, protein decreases while amino acids (especially proline) increase in concentration in both twigs and roots (Cyr et al. 1990; Saunier et al. 1968).

Carbon metabolism. Overall, water stress disturbs carbon metabolism so that starch levels generally decrease while sugar levels increase (Dina and Klikoff 1973; Kramer 1983). Matson and Haack (1987b) showed a 2.5-fold increase of foliar sugars in water-stressed balsam fir. However, in very long-term water stress, both starches and sugars can be depleted (Eaton and Ergle 1948; Woodhams and Kozlowski 1954). Long-term water stress may cause an adjustment of the root-shoot ratio. When exposed to drought, the allocation of carbohydrates to root growth may increase, providing more root absorptive area per unit area of foliage and increasing the volume of soil explored.

Secondary Compounds. In addition to the groups of primary compounds just discussed, many other compounds are produced by secondary reactions. These secondary compounds are responsible for many of the differences among plants with respect to color, odor, taste, and resistance to pathogen and insect attack (Kozlowski et al. 1991). They usually are products of metabolic bypaths and most of them can be classified into one of three groups: alkaloids, terpenes, or phenolics. The alkaloids are a large and heterogeneous group of compounds that have few known functions in plants. They include compounds such as caffeine, cocaine and nicotine. The isoprenoids or terpenes include compounds such as the essential oils, which provide most of the odors produced by plants. Terpenes also include resin gums such as the oleoresins, and plant hormones such as gibberellin and abscisic acid.

The most common phenolic compounds are the lignins, which stiffen the walls of wood cells and are second only to cellulose in abundance.

Because growth is limited sooner than photosynthesis, mild to moderate drought stress can result in the accumulation of excess carbon which can be diverted from growth to differentiation products such as phenolics and terpenoids. Few detailed studies exist, but most authors agree these secondary compounds tend to increase in the foliage and roots of water-stressed plants (Gershenzon et al. 1978; Parker and Patton 1975).

Wound healing. Water-stressed plants may be more susceptible to insects and diseases because the process of wound healing is slowed. In Abies species, water stress reduces the rate of wound healing in stem bark and is correlated with susceptibility to the balsam woolly adelgid, Adelges piceae (Puritch and Mullick 1975). Similarly, first periderm formation in trees is delayed by water stress (Borger and Kozlowski 1972).

III. Implications for Insect Defoliator Population Dynamics

Because plant traits are affected by moisture stress, how might this alter population dynamics of defoliating insects? Insects respond on both a behavioral and physiological level to certain classes of plant traits (Mattson and Haack 1982; Ahmad 1983; Haack and Slansky 1987; Mattson and Haack 1987b). A line of

research has evolved to assess how moisture stress might change these critical traits to enhance or inhibit either behavioral or physiological processes of insects.

Sugars

Sugars are substances that have been found to increase in plants under water stress (Vaadia et al. 1961). It is interesting that for many lepidopteran larvae, sugars (sucrose, glucose, and fructose) function as feeding stimulants (Heron 1965; Ouellet et al. 1983; Otto 1970; Ma 1977; Cobbinah et al. 1982). It has been found that late instar budworm (Choristoneura fumiferana) larvae are sensitive to sucrose levels in their food (Mattson and Haack 1987b; Albert et al. 1982). In foliage of unstressed balsam fir, sucrose levels are usually close to 0.004 M, whereas in moisture-stressed fir, sucrose concentrations are nearly threefold higher (0.011 M) (Mattson and Haack 1987a). According to Albert et al. (1982), the peak feeding response to sucrose by sixth-instar budworm larvae occurs between 0.01 and 0.05 M. Therefore, in the case of sucrose, plant water stress would increase sucrose levels and that should increase budworm feeding responses (Albert and Jerrett 1981).

Sucrose has been found to interact synergistically with l-proline to stimulate spruce budworm feeding (Bentley et al. 1982). Proline is a feeding stimulant for many phytophages and usually only at high levels (Cook 1977). This is interesting because proline is not an essential amino acid and it is usually not abundant except under conditions of moisture stress (Matson and Haack 1987a).

Starch

Artificial diet studies have indicated that lepidopterous larvae do not utilize starches extensively; therefore, the decline of foliar starches in water-stressed plants probably does not affect the growth of these insects. Amylase, an enzyme that degrades starch, either has not been found in lepidopterous species or was present in such small quantities that its activity probably was ineffective (Feeny 1970).

Nutrients

It is widely suspected that many herbivores, particularly those of woody plants, are nutrient limited (Bjorkman et al. 1990; White 1974; Mattson 1980; Prestidge and McMeill 1983). It is hypothesized that nutrient balance may be a critical factor influencing budworm performance (Clancy et al. 1988). Water stress may result in nutrients being either better balanced relative to one another or more concentrated in the tree. Nitrogen is thought to be the key nutrient (White 1984; Scriber 1984; Mattson 1980). Increases in nitrogen, sugar, and minerals have been shown to elicit better growth and development of most defoliators (Matson and Scriber 1987). Cates et al. (1983b) and Mattson et al. (1983) reported that low to moderate moisture stress increased the growth of western and eastern spruce budworm, respectively (Mattson and Haack 1987b). Harvey (1974) demonstrated an increase in female pupal body size at a steady rate up to four percent sucrose. Few other experiments have been done to link increased insect performance to water-stressed trees.

Secondary Metabolites

The levels and perhaps kinds of secondary metabolites such as phenolics and terpenes change in trees under water-stress (Mooney and Chu 1974; Ross et al. 1990). In general, there is a tendency for these compounds to increase during moisture stress. Mattson and Haack (1987a) suggest, as others have, that from a consumer's point of view, the tree's increase in secondary metabolites under stress would seem to be inhibiting, and for marginally adapted species it probably is. However, for the well-adapted species, the increases may not be substantial enough to exceed their tolerance; in the case of some compounds, the increase may actually be enhancing. Not much clear evidence exists to determine the effect of moisture stress on phenolics and other secondary metabolites. Many of the secondary metabolites are considered to be key primary attractants to defoliators. Some compounds are reduced; others are increased. From the published studies it is hard to decide whether stress changes those important plant properties in such a way that it either usually augments or diminishes the defoliator's fitness.

Changes in Chemistry due to Defoliation

Little knowledge exists of changes in host chemistry brought about by an extended period of defoliation. Foliar nutrients may be altered by defoliation. New buds from white spruce (Picea glauca [Moench] Voss) heavily defoliated by sawflies (Neodiprion abietis Harris) had higher concentrations of nitrogen, potassium,

phosphorus, and magnesium than did buds of lightly defoliated trees (Cook et al. 1979).

Carbohydrates are the direct products of photosynthesis; thus, any defoliation-caused reduction in photosynthates and the need for photosynthates for growth will change carbohydrate production and storage patterns (Waring 1983; Chapin 1991). Webb (1981) reports reduced starch levels in twigs and roots of trees defoliated by Douglas-fir tussock moth (Orgyia pseudotsugata McDunnough). Wagner and Evans (1985) found the new foliage formed on ponderosa pine after partial defoliation to be more palatable than the old foliage even though it is higher in phenolics. One nutrient-stress hypothesis suggests that when defoliation removes the foliar nutrients of trees growing in nutrient poor soils, it increases nutrient stress which in turn results in a high production of carbon-based secondary compounds (Tuomi et al. 1984).

The production and translocation patterns of plant hormones are likewise affected by defoliation. Most hormones are produced in buds and 1-year-old foliage (Cuddy 1982). Hormones produced at other sites may be affected if they depend on precursors produced in the crown. Needle retention and drop is altered, presumably due to the altered production of growth regulators. Older needles may be held longer, then a heavy drop of old needles may occur once new foliage is produced after the outbreak declines (Van Sickle 1987).

IV. Implications for Root Disease Epidemiology

While most authors agree that moderate levels of water stress elevate levels of total phenolic compounds found in plants (Mooney et al. 1983; Chapin 1991), there has been little research dealing specifically with roots. The influence of these compounds on Armillaria spp. is not clear (Garraway et al. 1991). Phenolics have been reported as having both inhibitory properties (Entry and Cromack 1989; Cheo 1982) and stimulating properties (Shaw 1985).

According to Wargo (1984), A. mellea successfully colonizes the roots of stressed, deciduous trees because the increased levels of both glucose and amino acids enhance its ability to oxidize the normally inhibitory phenolics and even to utilize the products as a source of carbon.

The capacity of Armillaria spp. to utilize the available nitrogen source is largely determined by the amount and type of carbon source (Garraway et al. 1991). The C:N ratio was found to be critical in determining growth of Armillaria spp. isolates (Rykowski 1976). At a given level of nitrogen, an increase in carbon increased fungal biomass. However, after a certain level, an increase in nitrogen was found to cause a decrease in fungal biomass.

Nutrient balance may also be important. Rykowski (1984) found growth of Armillaria spp. increased with additions of potassium, and growth was reduced with additions of nitrogen and phosphorus.

In mesophytic plants, the endogenous levels of abscisic acid and indoleacetic acid have been found to increase with water stress in roots, stems, xylem and

phloem sap (Bradford and Hsiao 1982). Indoleacetic acid has been found to stimulate growth and development of Armillaria spp. (Garraway 1970, 1975). The effect of abscisic acid on Armillaria growth and development has not, to my knowledge been systematically tested.

V. Interactions Among Root Disease and Defoliating Insects

Filip (1989) and Wargo and Harrington (1991) provide a world-wide, itemized review of the reports of interactions between Armillaria spp. and defoliating insects.

Insect-caused defoliation is documented as a biotic stress agent that may predispose trees to root disease. Mortality of defoliated trees is presumed to increase when associated with drought and root disease, but this relationship is not well documented (Van Sickle 1987). Most of the reports are field observations; a few cases report experimentally imposed defoliation and characterize the effects on disease susceptibility and development. As summarized by Filip (1989), almost all of the reports have dealt with broadleaf trees as they interact with Armillaria spp.

The association of Armillaria spp. and defoliated oak (Quercus spp.) has been noted with frequency since the early 1900's in both the United States and Europe. The roles of Armillaria spp., defoliation, and drought have been debated as the cause of widespread oak mortality by several workers. Most consider Armillaria spp. to be a secondary pathogen. Infection of oak trees by Armillaria after gypsy moth (Lymantria dispar L.) defoliation was reported in Massachusetts by

Baker (1941). Increased incidence of Armillaria root disease after defoliation has been reported in Connecticut (Dunbar and Stevens 1975), New Jersey (Kegg 1971, 1973), and Pennsylvania (Karasevicz and Merrill 1986). Dunbar and Stephens (1975) report that Armillaria spp. played only a minor role in oak mortality after gypsy moth defoliation in Connecticut. Wargo (1977), however, suggests that the Armillaria played a significant role in the mortality of defoliated oaks.

Decline of sugar maple has been associated with the maple webworm (Tetralopha asperatella Clemens) and Armillaria mellea (sensu lato), in Wisconsin (Houston and Kuntz 1964). Root systems and root collars of dead trees and stumps, as well as saplings had fans and rhizomorphs of A. mellea (sensu lato). More stumps of defoliated trees (70 percent) were attacked by A. mellea (sensu lato) than were stumps of nondefoliated trees (32 percent). From this work, Houston and Kuntz theorized that the root collar tissues of defoliated trees were more suitable to attack by A. mellea (sensu lato) because of altered carbohydrate content than were those of nondefoliated trees.

Armillaria spp. were also associated with sugar maple mortality in north-central New York after defoliation by the saddled prominent caterpillar, Heterocampa guttavitta Weber (Wargo and Harrington 1991). Wargo and Houston (1974) inoculated both artificially and naturally defoliated sugar maple with an isolate of A. gallica Marxmuller & Romagnesi. They found that successful invasion of the root systems depended on stress from defoliation.

As with broadleaf species, reports of Armillaria spp. attack after defoliation exist for conifers as well. There are, however, little more than observational reports to establish this relationship. Few controlled forest or laboratory studies have been done to experimentally predispose conifers to Armillaria spp. by defoliation or to characterize the effects that insect-caused defoliation may have on infection biology. None have utilized monitored insects to accomplish defoliation, but instead have relied on artificial removal of foliage to simulate insect defoliation. In a greenhouse study using Scots pine (Pinus sylvesteris) seedlings, Wahlstrom (1992) investigated the effect of water stress and defoliation on the infection biology of A. mellea, A. ostoyae, and A. borealis (Marxmuller and Korhonen). He found that exposure to water potentials down to -3 MPa for 10-30 days before inoculation did not affect the infection frequency or mycelial growth of A. ostoyae, but suggests that perhaps the duration of water stress was neither severe nor long enough to promote treatment differences due to water stress. Seedlings that were water stressed "lower than -3 MPa", had less infection than well-watered controls. Wahlstrom found a reduction in the infection frequency of A. ostoyae with increasing defoliation.

Tunnock et al. (1969) report mortality of western larch heavily defoliated by larch casebearer (Coleophora laricella Hubner) to be associated with Armillaria spp. They document that from a total of 48 dead trees, the roots of 12 presented Armillaria when cultured. They concede that their study does not show at what stage of deterioration the sampled trees were invaded by Armillaria spp. and that defoliation is not clearly a predisposing factor.

Sterner (1970) evaluated butt decay of balsam fir that had been defoliated by the eastern spruce budworm in New Brunswick, Canada. He found that trees of higher suppression classes had a higher incidence of Armillaria spp. than trees of lower suppression classes. All trees, however, in this evaluation were defoliated, and no attempt was made to rate defoliation severity. Hence, it is impossible to separate defoliation effects from other suppression agents in the reported "dense stands" of the study area.

Raske and Sutton (1986) report decline and mortality of black spruce (Picea mariana [Mill.] B.S.P.) defoliated by eastern spruce budworm in Newfoundland, Canada. They report that Armillaria spp. was active in stands of various degrees of crown damage but was prominent in recovering trees that had sustained 80 percent or more cumulative total defoliation during the outbreak years. Raske and Sutton further report that these trees also had the highest incidence of successful bark beetle attacks. They continue to speculate:

> "rootlet mortality had occurred during the past years of severe defoliation. Rootlet recovery two to three years after cessation of defoliation lagged behind foliage recovery in trees sampled. This may have led to water stress and favored the establishment of normally secondary organisms."

Raske and Sutton summarize by suggesting that the imbalance between crown recovery and rootlet recovery, combined with bark beetle activity and root pathogen attack, affected the decline and mortality of a large number of severely defoliated black spruce in Newfoundland in the early 1980's.

Filip (1989) reports a low incidence of Armillaria root disease in grand fir stands in eastern Oregon that had been defoliated heavily for three years by the western spruce budworm. Filip suggests that the species of Armillaria involved was perhaps not very pathogenic as cultures of the fungus morphologically resembled known species of low pathogenicity. The species was subsequently identified as North American Biological Species No. 10 (NABS 10) (Filip et al. 1992).

OBJECTIVES

The main objective of this research was to characterize the interaction among drought, defoliation, and root infection when separately and simultaneously imposed on grand fir seedlings.

The specific objectives of this study were:

1. To determine the effects of host drought and defoliation on the growth and development of western spruce budworm and Armillaria ostoyae.

2. To examine the induced change in the production of a secondary metabolite group, the phenolics, in seedlings inflicted with water stress, defoliation and infection.

3. To study the effects of drought, defoliation, and root infection on seedling growth and on the allocation pattern of key nutrients.

PROBLEM STATEMENTS AND HYPOTHESES

Problem Statement 1: Several investigators have shown that feeding on drought-stressed plants led to improved growth, survival, or reproduction of various Homoptera, Lepidoptera, Orthoptera, and mites (Mattson and Haack 1987b). Drought-stressed plants may be more suitable for insect growth, survival, and reproduction because plant nutrients are either more concentrated or better balanced. This may be of particular importance to insects that feed on woody plants because the amounts of nitrogen, sugar, and minerals are often less than optimal (Haack and Slansky 1987; Mattson and Scriber 1987; White 1984). Logically, increasing and/or improving the balance of these nutrients should favor insect performance (Haack and Slansky 1987; House 1974).

Drought may inhibit the inducible defense systems that some plants possess. Foliage concentrations of several classes of allelochemicals tend to increase during drought (e.g., terpenoids and alkaloids) also, the rate of generalized wound healing in grand fir declines during drought (Puritch and Mullick 1975). However, the relationship between drought stress and levels of foliar phenolics has not been clearly demonstrated (Mattson and Haack 1987a; Gershenzon 1984).

Much of the chemical change in foliage of stressed conifers remains poorly understood. These changes could have important implications when related to what is known about the nutritional needs of insects that defoliate conifers.

General hypothesis

Drought-stressed seedlings are more suitable for insect growth, survival, and reproduction.

Test: Null H_1=The survival and pupal weights of western spruce budworm arising from larvae reared on water-stressed seedlings are not significantly different than those from larvae reared on well-watered seedlings.

Null H_2=The total carbohydrate, nitrogen, phosphorus, potassium, sulfur and phenol concentrations in foliage of water-stressed seedlings are not significantly different than in well-watered seedlings.

Problem Statement 2: It is widely accepted among foresters that stands growing under adverse conditions are especially at risk to the root pathogen, Armillaria ostoyae. Armillaria ostoyae is often considered an organism of secondary action (Wargo and Shaw 1985) and is often found associated with trees growing under some environmental stress. Few researchers, however, have questioned how host stress operates to increase the incidence and rate of infection and mortality caused by A. ostoyae.

Determining the stress-induced changes in concentration of nutrients and defensive compounds and the response of A. ostoyae to these changes, is an essential first step in assessing how host stress favors this disease.

General hypothesis

Drought-stressed seedlings are more suitable for Armillaria spp. growth and development.

Test: Null H_3=The percentage of infection and mortality of seedlings inoculated with A. ostoyae is not significantly different in water-stressed vs. well-watered seedlings.

Null H_4=Total carbohydrate, nitrogen, phosphorus, potassium, sulfur, and phenol concentration are not significantly different in the roots of water-stressed vs. well-watered seedlings.

Interactions

Problem Statement 3: Increased tree mortality after defoliation by insects has been associated with Armillaria spp. infection of hardwoods (Wargo and Houston 1974). Studies have shown that some hardwood trees stressed by defoliation are predisposed to invasion by the fungus. However, this line of investigation has not been pursued in conifers.

Tree stress caused by root infection may, like drought, favor insect survival, growth, and reproduction by increasing the nutritive value of the foliage while reducing the accumulation of defensive chemicals. Characterization of those physical and chemical changes induced by defoliation and disease which alter the relationships of the tree with defoliating and root-invading organisms may permit us to manage their impact, perhaps by ameliorating the changes or preventing them from occurring.

General hypotheses

Defoliation, like drought, allows for either increased pathogen growth or a reduction in the rate of host defense reaction.

Infection, like drought, favors insect survival, growth, and reproduction by increasing the nutritive value of the foliage while reducing the accumulation of defensive chemicals.

When defoliation and infection are combined with water stress, these physiological changes are further accentuated to favor the insect or pathogen.

Test: Null H_5=The percentage of infection and mortality of seedlings inoculated with A. ostoyae is not significantly different in seedlings simultaneously water-stressed and defoliated vs. water-stressed only, defoliated only, or non-stressed.

Null H_6=The total carbohydrate, nitrogen, phosphorus, potassium, sulfur and phenol concentrations in root systems of defoliated seedlings are not significantly different than those of undefoliated seedlings.

Null H_7=The total carbohydrate, nitrogen, phosphorus, potassium, sulfur and phenol concentrations in foliage of well-watered and water-stressed seedlings inoculated with A. ostoyae are not significantly different than noninoculated well-watered, or noninoculated water-stressed seedlings.

Null H_8=The survival and pupal weights of western spruce budworm reared on water-stressed/inoculated seedlings are not significantly different than those larvae reared on well-watered seedlings which have not been inoculated with A. ostoyae.

METHODS AND MATERIALS

Two separate experiments were conducted to address the above objectives. **Group I** was started in June of 1989 to study the primary relationships between the organisms. **Group II** was initiated in January of 1990 to examine more specific questions (Table 1).

Growing Conditions

Seedlings

Two-year-old grand fir seedlings were obtained from Wind River Forest Service Nursery, Carson, WA. The seed source was from the eastern slope of Mt. Hood, in north central Oregon. Group I seedlings were planted in June 1989; Group II was planted in January of 1990. All seedlings were planted in 3.6-liter plastic pots filled with a sterile potting medium consisting of commercial potting soil, vermiculite, and perlite in the proportions of 3:2:1, respectively. A 25-cm long tree tube was planted along side each seedling to facilate the inoculation process that was to occur in 3 months. Seedlings were kept in outdoor cold frames for 9 to 11 months before moving them into a 23 °C greenhouse under an 18-hour light cycle with daylight supplemented with greenhouse lights. Seedlings, dormant when brought into the greenhouse, began new shoot growth after approximately six weeks.

Table 1. Chronological events of experimental Groups I and II.

Group	Planting Date	# of seedlings in each treatment cage	Inoculation date	Moved to Greenhouse date	Water stress treatments started	Date larvae applied	# of larvae per cage	Instar when applied	Harvest date
I	June 1989	9	August 1989	Feb 1990[1]	February 1990	April 1990	20	4 th	August 1990
II	January 1990	9	March 1990	Feb 1991[2]	February 1991[3]	April 1991[4]	30	2 nd	July 1991

[1] Corvallis, OR
[2] La Grande, OR
[3] Water-stressed treatments were stressed the previous year along with Group I
[4] Those treatments in Group II with 2-year defoliation were also artificially defoliated in March 1990

Insect rearing

Spruce budworm larvae used in this experiment were obtained from USDA Forest Service, Forestry Sciences Laboratory, Corvallis, OR. Larvae received were from the 4th generation of a lab-reared stock-colony stored at 5 °C as overwintering 2nd instars enclosed in their hibernacula on gauze strips.

The larvae used in the Group I experiment were 2nd instars removed from the cooler and left at room temperature for 48 hours. Before Group I larvae were transferred to seedlings they were first reared to the 4th instar by repositioning them every other day into petri dishes with fresh, new-foliage cut from a group of potted seedlings identical to those used in the experiment. It took an average of 11 days for Group I larvae to develop from newly emerged, 2nd instar larvae, to 4th instar larvae.

The larvae used in the Group II experiment were directly transferred onto seedlings as 2nd instars that were newly emerging from their hibernacula after being removed from the cooler and left at room temperature for 48 hours.

Rearing and Defoliation

Seedlings of both Groups were contained in wooden cages covered with cloth. Each cage held nine seedlings. The framework of the insect cages was formed from 5 cm x 3 cm wood boards. A cover tailored from fine-mesh mosquito-netting fit tightly over the cage structure (55 cm x 55 cm x 66 cm) and was secured with hot melt glue. Foam stripping was adhered to the bottom of the cage to fill

any gaps that might allow crawling larvae to escape the cage. The entire cage was set upon a plywood base.

Only active larvae were transferred to the newly flushed buds of the nine seedlings enclosed in cages of Group I (4th instar) and II (2nd instar) treatments. Twenty larvae were placed in the Group I cages; 30 larvae were placed in the Group II cages. Since each cage held nine seedlings that were spaced closely enough for branches to intermingle, larvae were distributed across the tops of seedlings by placing individual larvae on individual buds. Larvae were free to access all seedlings in the cage. After 10 days in Group I and 20 days in Group II, the cages were checked daily for recently pupated insects. Immediately after each insect shed its last larval skin, the pupa was removed from its cage. Pupae were sexed and weighed 24 hours after collection and frozen. Spruce budworm pupae can be sexed by the location and shape of the genital opening. The opening spans the 8th abdominal segment in female pupae and is found on the 9th segment in male pupae (Jennings and Houseweart, 1978). At the end of each experiment same-sex pupae from each treatment were combined and dried in a forced air oven at 65 °C for 48 hours.

Treatments in Group II with more than current year, 1991 (larval) defoliation, involved seedlings artificially defoliated in March 1990 (Table 1). Artificial defoliation was achieved by continually pinching off small amounts of newly flushed foliage through March and April. Subjectively, the final level of artificial defoliation of new foliage was visually estimated to be 80 to 90 percent of

the potential foliage for the 1990 growth season. Group II seedlings were then left in the outdoor coldframe until late fall when they were moved to an outdoor lath house located at the PNW Research Station, La Grande. In February, 1991 Group II seedlings were transferred to the greenhouse.

Inoculation Techniques

Isolate SP-28-82 (Morrison et al. 1991) of Armillaria ostoyae (NABS I), was grown on 3 percent malt agar. The isolate was obtained from Canadian Forestry Service, Pacific Forestry Research Centre, Victoria, BC.

Living mountain alder (Alnus incana [L.] Moench) stems 3-cm diameter x 10-cm long, were washed and placed in a 0.89 L container with 50 ml of malt extract medium. The stems and medium were autoclaved for 60 minutes at 1.46 kg/sq. cm., then allowed to cool. Three 10-mm diameter plugs from petri dishes containing the Armillaria ostoyae isolate were placed on the alder stems. Alder stems were incubated at room temperature in the dark for eleven months and were well colonized by the fungus before seedling inoculation.

The seedling inoculation method followed that described by Shaw (1975). Three months after planting the seedlings with a sterile tree tube, the tube was removed and a single alder-stem inoculum was inserted into the hole left by the tube. This placement put the inoculum in direct contact with the primary root of the seedling. Seedlings of non-inoculated treatments each received a sterile alder stem

that had been prepared exactly as the inoculum stems except A. ostoyae was not introduced into the jar.

Description of Treatments

The two separate experiments, Group I and Group II, had a slightly different series of treatments and study objectives.

Group I

Eight treatments were established comparing: 1) insect performance as rated by survival and pupal weight; 2) seedling infection and mortality; 3) plant moisture status; and 4) starch, sugar and phenolic content of roots and current year foliage. The Group I treatments were:

Treatment	Abbreviation
Well-watered:	
1) Control	H2O+/Control
2) Defoliated	H20+/Defol
3) Inoculated	H20+/Inoc
4) Defoliated and Inoculated	H2O+/Defol/Inoc
Water-stressed:	
5) Control	H2O-/Control
6) Defoliated	H20-/Defol
7) Inoculated	H20-/Inoc
8) Defoliated and Inoculated	H2O-/Defol/Inoc

Each treatment had two replications of nine seedlings each. Treatment and inoculation dates are shown in Table 1.

Group II

Sixteen treatments were established to evaluate: 1) insect performance as judged by development rate and sex ratio; 2) seedling infection and mortality; and 3) resource allocation pattern as estimated by nutritional qualities of roots and new shoots, phenolic content of new shoots during the period of peak larval feeding, and phenology, and biomass production of experimental seedlings.

The Group II treatments were:

Treatment	Abbreviation
Well-watered:	
1) Control	H2O+/Control
2) Defoliated 1990	H20+/Defol90
3) Defoliated 1991	H20+/Defol91
4) Defoliated 1990-91	H2O+/Defol90/91
5) Inoculated	H2O+/Inoc
6) Defoliated 1990 & Inoculated	H20+/Defol90/Inoc
7) Defoliated 1991 & Inoculated	H20+/Defol91/Inoc
8) Defoliated 1990-91 & Inoc.	H2O+/Defol90/91/Inoc
Water-stress:	
9) Control	H2O-/Control
10) Defoliated 1990	H20-/Defol90
11) Defoliated 1991	H20-/Defol91
12) Defoliated 1990-91	H2O-/Defol90/91
13) Inoculated	H2O-/Inoc
14) Defoliated 1990 & Inoculated	H20-/Defol90/Inoc
15) Defoliated 1991 & Inoculated	H20-/Defol91/Inoc
16) Defoliated 1990-91 & Inoc.	H2O/Defol90/91/Inoc

Nine seedlings were in each treatment; treatments were not replicated.

Water Measurements

To obtain a clear measure of plant moisture status (PMS) among treatments, a PMS pressure chamber was used to monitor twig water potential. Generally, the procedures followed were those recommended by Cleary and Zaerr (1980). Xylem water potentials were measured in the annual shoots. Immediately after excision, the shoots were placed in a pressure chamber with the cut end facing the microscope. Gas pressure was applied until a drop of water was visible on the cut surface. Because the process requires clipping of branches, each treatment had ten extra seedlings that were used for these measurements. Frequent mid-day (1 to 3 P.M.) PMS readings were made at irregular intervals. Four or five of the extra seedlings were sampled on each day of measurement.

Seedlings in the well-watered treatment groups were thoroughly watered every-other-day with a garden hose. Water-stressed treatments received 250 ml of tap water each day that a sub-sample average of the treatment averaged a PMS value that was twice the value of the corresponding well-watered treatment. For example, if the well-watered inoculated treatment (H20+/Inoc) had an average PMS reading of -1.2 Mega Pascals (MPa), the water-stressed inoculated (H20-/Inoc) treatment received 250 ml of water when the daily average PMS was -2.4 MPa.

Plant moisture status (PMS) was not as precisely tracked for group II as it was for Group I. Measurements were made at irregular intervals to assure that water-stressed treatments did not lapse into severe water deprivation. Records were not kept, however, to establish the PMS trend of each treatment.

Harvest Methods

Verification of Infection

At harvest, seedling tops were severed at soil level. Roots of inoculated seedlings were visually examined for mycelial mats underneath the bark: 1) at the root collar; 2) on all dead roots; and 3) on 10 live roots, if present, greater than 2mm in diameter. Isolations were made onto 3 percent malt agar plates to verify the presence of A. ostoyae. Seedlings were rated as 1) uninfected and living, 2) infected and living, 3) infected and dead, or 4) uninfected and dead.

A sub-sample of the alder stem inoculum sections was recovered from the pots and isolations made into malt agar media to assess inoculum viability.

Root And Shoot Weight

The current year foliage, roots, and shoots of each seedling in Group II treatments were weighed and dried separately in a forced air oven at 70°C. Oven-dried weights were recorded separately. Dry weight of the current year foliage was subtracted from the fresh weight to determine foliar moisture content. The dry weights of the remaining shoots, current year foliage, and roots were summed to determine total seedling dry weight; root weight was divided by shoot weight to determine root:shoot ratios.

Phenology

The development rate of the newly flushing buds was measured at one point in time at the onset of the Group II experimental period. The number of buds that had reached the "brush stage" as defined by Shepherd (1983) were measured on March 22. This number was later divided by the total number of buds that had flushed on each individual seedling to calculate a percentage of total flush on March 22.

Laboratory and Analytical Methods

Soluble Sugars

Dried tissue of current year foliage and secondary roots was ground to pass a 40-mesh sieve. Samples of approximately 100 mg were weighed to the nearest .1 mg onto a filter paper. The sample was rolled-up in the paper to form a sealed tube (Rose et al. 1991). The sample, folded in the filter paper tube, was placed in a test tube with about 10 ml of 100 percent acetone and left overnight. The acetone extract was poured off, and the extraction was repeated until the extract was colorless. Acetone extracts were discarded.

The acetone-extracted sample, still folded in filter paper was placed in a 100-ml test tube and covered with 80 percent ethanol. The tubes were placed in a water bath at a temperature at which the ethanol gently boiled. The tube was covered with a small glass funnel blocked with a marble to prevent ethanol evaporation that would change the ethanol concentration and therefore the solvent characteristics of

the extracting solution. After one hour the extract was decanted into a beaker and saved. The extraction was repeated three times. Subsequent extractions of a given sample were combined.

One-hundred *ul* of $Pb(OAc)_2$ (saturated neutral lead acetate) solution was added and mixed into the ethanol solutions (Joslyn 1970). After at least thirty minutes, 500 *ul* saturated sodium oxalate solution was added, precipitating any lead still in solution. The samples were brought to volume and allowed to stand overnight. The following morning, the uppermost 10 ml in the volumetric flask was poured through a filter paper. The hexose concentration of the filtrate was then determined using the anthrone reaction (Yemm and Willis 1954).

An aliquot of .50 ml of sample solution was placed into a test tube in a cold water bath. Five ml of anthrone reagent was added and mixed on a vortex mixer. The tubes were then returned to an ice water bath. The tubes were heated in a boiling water bath for exactly 12 minutes, then cooled for a few minutes in tap water. Absorbance was read at 625 nm using undiluted anthrone reagent as a blank. A set of glucose standards was run with each set of samples and treated in exactly the same way as the samples.

Starch

After the soluble sugars and other interfering substances were removed, the residue was processed to extract starch. The methods are described by Rose et al.

(1991) as "enzyme method 3" in their publication that evaluates the accuracy and precision of six colorimetric methods of starch determination.

Each residue sample was scraped from the filter paper into a centrifuge tube. The tissue was dried by placing tubes in a hot water bath. Five ml of distilled water was added to each sample and the tube was capped with a marble. Tubes were autoclaved at 1.05 kg/cm^2 for 45 minutes at 121°C and left to cool overnight. Exactly 5 ml of amylogluccosidase solution were pipetted into each tube and tubes were covered with paraffin film. The tissue/enzyme mixture was mixed by gently inverting the tube. Tubes were incubated overnight in a 30°C water bath.

Each tube was brought to a volume of exactly 10 ml by adding .5 ml of distilled water and mixed well. Tubes were then centrifuged at 1500 rpm for 5 min. Aliquots of .25 ml were transferred to small test tubes and 2.5 ml of glucose oxidase/peroxidase-o-dianisidine solution were added. Tubes were incubated in a 37°C water bath for 30 min. After 30 min, the absorbance was read on a Milton Roy Spectronic 20D spectrophotometer at 450 nm.

Numerical Analysis of Soluble Sugar and Starch

Glucose concentrations in the samples of roots and foliage were determined by calculating a regression equation for ppm of standard solutions based on readings from the spectrophotometer. The regression equation was then used to calculate sample values in ppm and convert this value to concentration of chemical fractions using the following equations:

Soluble Sugars:

A x B/C = mg sugar per g dry wt. of sample

where:

A = absorbance reading in ppm

B = sample volume of .1 L

C = sample dry wt in g

Starch :

A x (B/C) x D = mg starch per g dry wt. of sample

where:

A = absorbance reading in ppm

B = sample volume of .1 L

C = sample wt.

D = extract dilution ratio.

Phenolics

The dried needles of the current-year growth were removed from branches and then ground with mortar and pestle to pass a 40-mesh sieve. Secondary roots were dried and ground in a Wiley mill to pass a 40-mesh sieve. Samples of approximately .01 g of ground material were weighed into a test tube. One ml of 100 percent acetone was added and the test tubes were placed in a sonicator for 30 min. after which the acetone was transferred into another flask. The acetone

extraction was repeated three times, twice with 50 percent acetone. Following the acetone extraction, the plant material was filtered and the acetone was removed. Each sample was extracted three times with methyl chloride. The extract was taken to volume in a 50-ml volumetric flask. This solution was then partitioned for Folin-Ciocalteu total phenolic analysis.

Exactly 10 ml of this aqueous solution were placed in a 25 ml volumetric flask for Folin-Ciocalteu total phenolic analysis. The process is a modification of the Folin-Ciocalteu method by Singleton and Rossi (1965). Folin-Ciocalteu solution (1.25 ml) was added to the 10 ml aqueous extract. After 30 seconds, but before 8 minutes had passed, 3.75 ml of 20 percent Na_2CO_3 solution was added, and the solution was brought to volume. After two hours, absorbance was measured at 765 nm with a Bausch and Lomb Spectronic 100 spectrophotometer. Total phenolics were expressed as gallic acid equivalents (mg/L) by comparison with calibration curves prepared from standard solutions (Muzika 1989).

Nitrogen, Phosphorus, Potassium, and Sulfur

A sample of dried current-year foliage and secondary roots from each treatment of Group II was analyzed for nitrogen, phosphorus, potassium, and sulfur. A sub-sample of .5 g was ashed at 525 °C in a muffle furnace. The ash was dissolved in 10 percent HNO_3 and brought to 50 ml volume (Jackson 1958) and analyzed for P and K. Total N was analyzed by standard microKjeldahl techniques (Bremner and Mulvaney 1982). Phosphorus and potassium were analyzed by atomi

absorption. Nitrogen, potassium, and phosphorus were analyzed by the Plant Analysis Laboratory, Forest Science Department, Oregon State University.

The level of sulfur in seedling tissue was determined by oxidation of plant material in a furnace and determining SO_4 -S by Ba SO_4 turbidity (Tabatabai and Bremmes, 1970). Sulfur was analyzed by the Plant Analysis Laboratory, Department of Soil Science, Oregon State University.

The ratios of plant sugars, phenolics, and minerals to nitrogen were also calculated.

Experimental Design

The experiment was designed as a 2^3 factorial; two levels each water, defoliation, and inoculation. Treatments in Group I were replicated; those in Group II were not. Grand fir seedlings were randomly assigned to all treatments; insects were randomly assigned to defoliated treatments; inoculum was randomly assigned to inoculated treatments. Every effort was made to avoid bias in comparisons among treatment means by systematic known or unknown extraneous sources of variation.

Complete randomization was not employed, however, as there was a non-random watering order in both Group I and Group II experiments. Although random assignment was made prior to placing treatments on tables, all well-watered seedlings were grouped on one large table and all water-stressed seedlings were grouped on an adjacent table. Decisions as to the watering effect and location in the greenhouse were made mindful of potential for bias. Dangers inherent in a

randomized watering order seemed larger than the chosen arrangement because of the higher risk of watering errors. Although there may have been some correlation between the grouping and the amount of water provided to adjacent plants due to splashing, I feel that watering is reasonably represented as individually applied. I also feel confident that although full randomization was not obtained, the locations used in the greenhouse did not in themselves introduce bias into my experimental results.

It is not uncommon for researchers to use something less than complete randomization for the sake of practicality. Cochran and Cox (1957) state that "Randomization is somewhat analogous to insurance, in that it is a precaution against disturbances that may or may not occur, and that may or may not be serious if they do occur." But they also state, "The occasions on which randomization is required vary with the type of experiment and must be left to the judgement of the experimenter."

Statistical Methods

Insect Performance Variables

Group I western spruce budworm performance was measured by computing percent larval survival (4th instar to pupation) for the budworm larvae caged together on the nine seedlings of each replicate (20 larvae on each replicate). Mean pupal dry wt (mg) was calculated for pooled, same-sex larvae collected from each cage.

The only insect variables presented for Group II are the length of development period (days to pupation), and the sex ratio of surviving pupae.

Seedling Infection and Mortality

For both groups the percent infection and mortality of grand fir seedlings caused by A. ostoyae was averaged for each treatment cage (replicate).

Chemical Analysis

The Group I and Group II foliage and root variables of phenolic, sugars, starch and elemental nutrients were estimated by using two chemical analysis runs of pooled sub-samples of tissue collected from the replicate.

All Group I data were analyzed using analysis of variance for a 2^3 factorial with F tests set at a probability of $P < 0.05$ (Solo Statistical System 1991). These tests examined the main and interactive effects of water stress, inoculation and defoliation (Steele and Torrie 1980).

Group II data analysis was accomplished using an analysis of variance (SAS Institute 1982). Group II analysis, because of lack of replication, was accomplished by using estimates of error that were all obtained by assuming some interaction terms to be zero. The sum of squares which would have been attributable to these interactions were pooled and used as sum of squares error (Larry Bednar, personal communications).

Both Group I and Group II utilized a cage as an experimental unit with one exception, the phenology analysis. In the phenology analysis where bud flush was addressed, individual plants were used as an experimental unit.

The validity of the assumptions made in the ANOVA were tested. Since the numbers of observations involved are in most cases quite low, it is difficult to say with assurance that the residuals are not distributed according to a normal distribution. In all but one data set the assumptions tested valid. In the phenology data, the ranges of the response variables were somewhat large and the residuals were funnel shaped. Log transformation was performed on the data and the results presented in the Group II results section.

RESULTS

Group I

Insect Performance

Insect survival. Western spruce budworm fed on water-stressed seedlings had a significantly higher (p=.007) survival-to-pupation rate than did budworm fed on well-watered seedlings (Table 2). Of the 80 4th-instar larvae placed on water-stressed treatments, 85 percent survived to become pupae. Well-watered treatments had a budworm survival rate of 59 percent (Table 3). Figure 3 shows the percentage of female and male survivors collected from each treatment. Inoculation did not have a significant effect on larval survival.

Table 2. Group I p-values as determined by analysis of variance for performance of western spruce budworm larvae fed on grand fir seedlings that were well-watered or water-stressed, and/or inoculated with Armillaria ostoyae.

Source	df	Insect Survival	Female Pupal wt.	Male Pupal wt.	Female:Male
Water	1	.007	.005	.08	.38
Inoc	1	.82	.76	.21	.36
W x I	1	.82	.40	.27	.41
TOTAL	11				

Pupal weights. Female pupae collected from water-stressed treatments were significantly heavier than those females collected from well-watered treatments (p=.005). Likewise, male pupae reared on water-stressed treatments were heavier

than those on well-watered treatments (p=.08). Inoculation did not influence pupal weights of either sex.

Sex ratio. The ratio of females to males was not statistically different with water treatment or inoculation. However, the female:male ratio for pupae was highest in the most stressed treatment (H20-/Defol/Inoc), where it was 2.34, and lowest in the least stressed treatment (H20+/Defol) at 1.23. (Table 3).

Table 3. Group I pupal weights, survival rates, and sex ratios for western spruce budworm larvae that were fed on grand fir seedlings that were well-watered or water-stressed, and/or inoculated with Armillaria ostoyae.

Treatment[1]	% Survival	Pupal Weights (mg)		Sex Ratio
		Female[2]	Male[3]	Female:Male[4]
H2O-/Defol	85	24.20	13.25	1.28
H2O-/Defol/Inoc	85	25.40	13.55	2.34
H2O+/Defol	60	14.90	8.45	1.23
H2O+/Defol/Inoc	58	12.40	12.20	1.30

[1] n=40 insects per treatment
[2] Standard error = .002
[3] Standard error = .001
[4] Standard error = .544

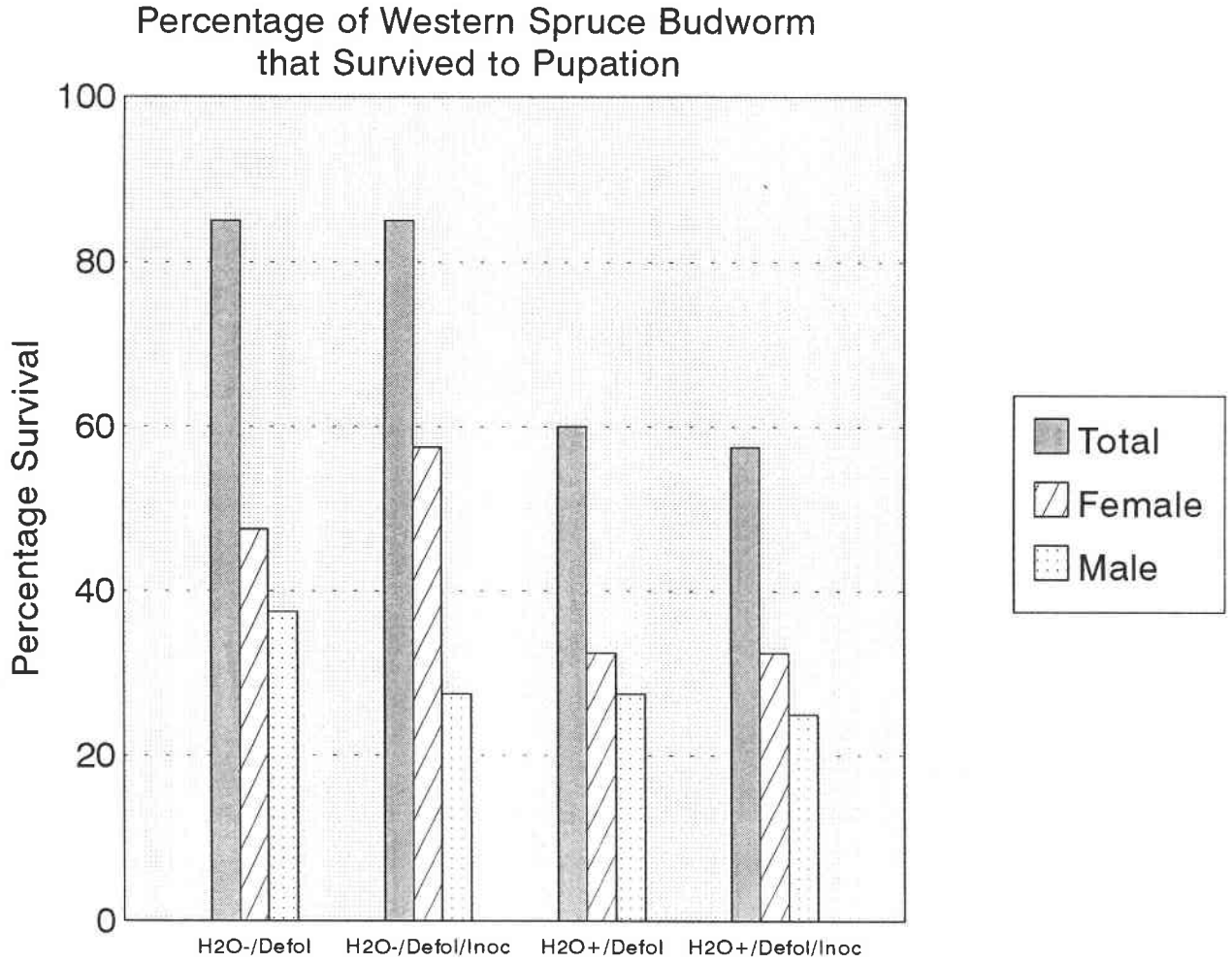


Figure 3. Group I percentage of western spruce budworm larvae that survived to pupation

Development rate. The development rate for Group I insects was not formally tracked. Nonetheless, it appeared that the western spruce budworm reared on water-stressed treatments pupated in fewer days than budworm on well-watered treatments. All pupae were collected and the water-stressed treatments of the experiment were terminated eleven days before the last pupal collection for well-watered treatments.

Seedling Infection and Mortality

Non-inoculated Seedlings

During the Group I experimental period, there was no seedling mortality in any treatment that did not include inoculation. There was 100 percent survival in H20+/Control and H20-/Control. Likewise, no mortality was recorded in H20+/Defol and H20-/Defol. A. ostoyae was thought to be the only cause of seedling death in Group I.

Inoculated Seedlings

Mortality (dead infected). Treatment H20-/Inoc exhibited 50 percent seedling mortality (nine of 18 seedlings); significantly higher ($p=.04$) than H20+/Inoc which had 16.6 percent mortality (Table 4). Defoliation had a significant effect on mortality ($p=.008$) (Table 5). Defoliated treatments of both watered and water-stressed treatments suffered less mortality than undefoliated treatments. Furthermore, there was a significant interaction between H20 treatment and

defoliation (p=.04). Treatment H20-/Defol/Inoc had 5.5 percent mortality (one seedling) as did H20+/Defol/Inoc.

Table 4. Group I infection and mortality of grand fir seedlings that were well-watered or water-stressed, and/or defoliated, and/or inoculated with Armillaria ostoyae.

Treatment[1]	Live-Infected	Dead-Infected	Healthy	Total Infected
	% (actual number)			
H2O-/Inoc	11.1 (2)	50.0 (9)	38.9 (7)	61.1 (11)
H2O-/Defol/Inoc	0	5.5 (1)	94.5 (17)	5.5 (1)
H2O+/Inoc	11.1 (2)	16.6 (3)	72.3 (13)	27.7 (5)
H2O+/Defol/Inoc	5.5 (1)	5.5 (1)	89.0 (16)	11.0 (2)

[1] n=18

Live-infection. There was not a significant difference in the number of live-infected seedlings between water treatments. Water-stressed treatment H20-/Inoc had an infection rate of 11.1 percent, as did H20+/Inoc. Defoliation was the only significant factor (p=.04) in live-infection rates, seeming to prevent infection from occurring. Water-stressed defoliated seedlings (H20-/Defol/Inoc) had no detectible root infection. Examination of roots of H20+/Inoc/Defol revealed one infected seedling (5.5 percent).

Table 5. **Group I p-values as determined by analysis of variance for infection and mortality rates of grand fir seedlings that were well-watered or water-stressed, and/or defoliated, and/or inoculated with Armillaria ostoyae.**

Source	df	Infection	Mortality
Water	1	.37	.04
Defoliation	1	.04	.008
W x D	1	.37	.04
TOTAL	7		

Lab isolations

At the time of seedling harvest, a sub-sample of the alder dowel inoculum from each treatment were tested for viability. Armillaria ostoyae was recovered from 100 percent of the sampled dowels. Likewise, all of the culture attempts to verify colonization by Armillaria ostoyae in root tissues of seedlings suspected to be infected produced the fungus.

Plant Moisture Status

Treatment averages of Scholander pressure chamber measurements (Table 6) signified two distinct water regimes in the H2O-/Control and the H20+/Control groups. The xylem pressure potential averages per sample period for the two treatments remained separated throughout the experiment (Figure 4).

Xylem pressure potential averages of water-stressed defoliated treatments (H20-/Defol, H20-/Defol/Inoc), although starting with values similar to H20-/Control early in the experiment, soon diverged. Defoliated seedlings of H20-/Defol and H20-/Defol/Inoc quickly developed a water status pattern not unlike that of H20+/Control (Figure 4). Conversely, non-defoliated seedlings of treatments H20-/Inoc developed a water status pattern with values equal or lower (more water stressed) than that of the H20-/Control treatment, eventually becoming quite low (-3 and -5 MPa).

There was little variation in plant moisture status of any of the well-watered treatments (Table 6). Defoliation (H20+/Defol; H20+/Defol/Inoc) and/or inoculation (H20+/Inoc) did not cause dramatic variation from H2O+/Control water status values.

Table 6. **Group I plant moisture status (MPa) of grand fir seedlings that were well-watered or water-stressed, and/or defoliated, and/or inoculated with Armillaria ostoyae.**

Treatment	Monthly Averages					Average MPa for Experimental Period
	March	April	May	June	July	
H2O-/Control	- 2.39	- 2.12	- 1.81	- 2.10	- 1.98	- 1.94
H2O-/Defol	- 2.35	- 1.19[1]	- 1.02	- 0.84	- 1.02	- 1.28
H2O-/Inoc	- 2.57	- 2.19	- 3.84	- 4.68	- 2.57	- 3.17
H2O-/Defol/Inoc	- 2.03	- 1.54[1]	- 1.25	- 1.07	- 1.40	- 1.46
H20+/Control	- 1.28	- 1.27	- 1.11	- 1.50	- 1.25	- 1.28
H2O+/Defol	*	- 1.06[1]	- 0.78	- 1.30	- 1.20	- 1.09
H2O+/Inoc	*	- 1.59	- 1.40	- 1.13	- 1.13	- 1.31
H2O+/Defol/Inoc	- 1.12	- 1.29[1]	- 0.97	- 2.10	- 1.35	- 1.37

* missing values
[1] larvae applied

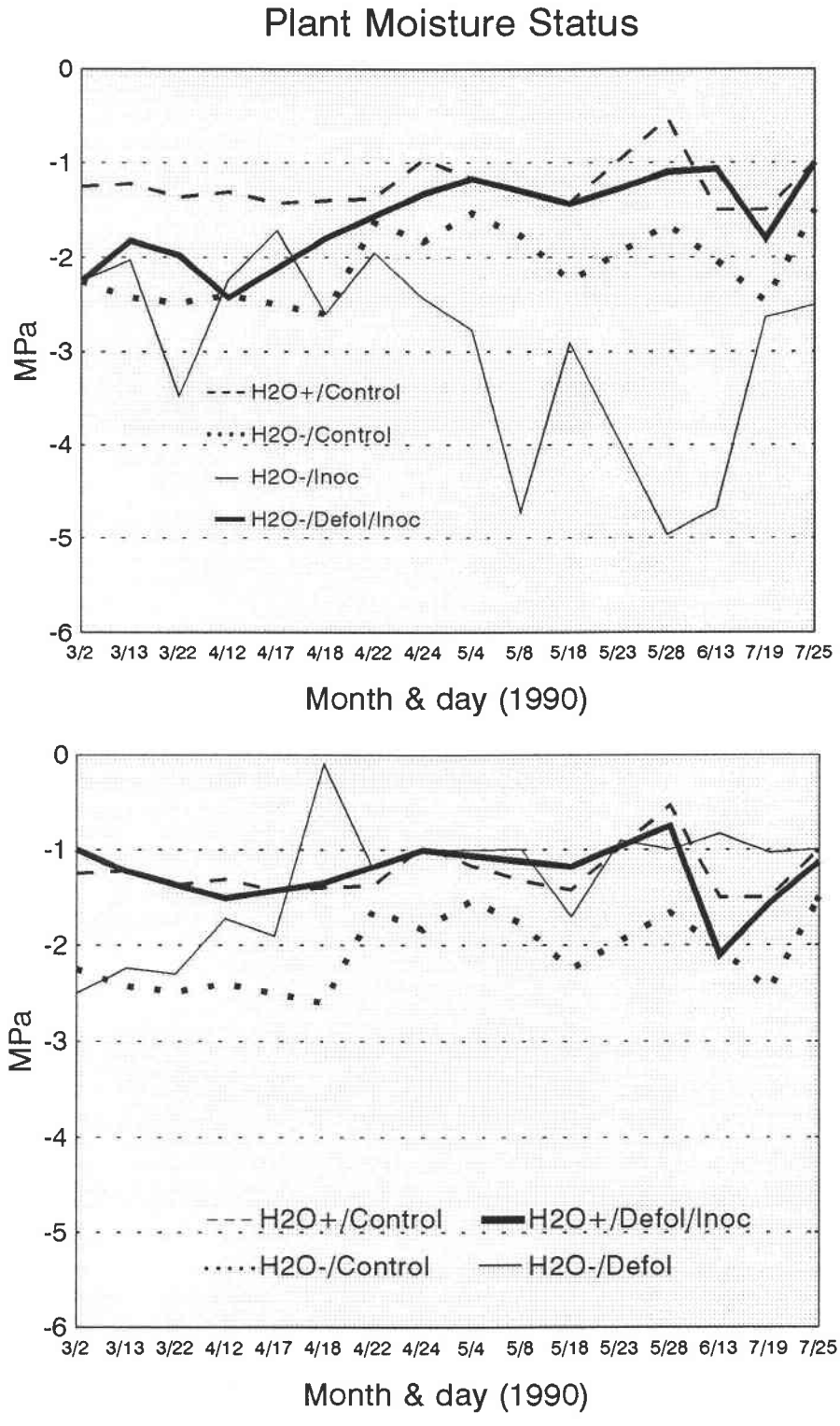


Figure 4. Plant moisture status for selected treatments in Group I

Biochemical Features

Phenolics

Foliage. There was no significant difference in the phenolic concentrations in foliage of well-watered and water-stressed seedlings. However, there was a significant effect (p=.001) due to defoliation (Table 7). Defoliated seedlings of both H20+ and H20- treatments showed an increase in foliage phenolics. The interaction between defoliation and water treatment (Water x Defol) was significant (p=.006). Foliage of well-watered defoliated treatments (H20+/Defol and H20+/Defol/Inoc) showed a larger increase than water-stressed defoliated treatments (H20-/Defol and H20-/Defol/Inoc). Foliage from H20+/Defol contained 24 percent more phenolic equivalents than H20+/Control (Table 8).

Inoculation significantly increased foliage phenolics (P=.03) in H20- treatments. The highest foliage phenolics in both water regimes were found in the treatments with both inoculation and defoliation. However, the 3-way interaction of water, defol and inoc was not quite significant (p=.07).

Seedlings in H20+ treatments, that were defoliated and inoculated had large foliage phenol increases, compared to controls (Figure 5). Treatment H20-/Defol/Inoc had a sample average of 17 percent more phenolic equivalents than H20-/Control. The highest phenolic level was found in foliage from H20+/Defol/Inoc which had 39 percent more phenolic equivalents than foliage from H20+/Control (Table 8).

Table 7. **Group I p-values as determined by analysis of variance for phenolics, sugars, and starch in grand fir seedlings that were well-watered or water-stressed, and/or defoliated, and/or inoculated with Armillaria ostoyae.**

Source	df	------Phenolics------		--------Sugar-----		------Starch-----	
		Foliage	Root	Foliage	Root	Foliage	Root
Water	1	.71	.003	.01	.001	.045	.002
Defol	1	.001	.06	.08	.28	.16	.01
W x D	1	.006	.89	.18	.11	.14	.002
Inoc	1	.03	.27	.72	.72	.96	.90
D x I	1	.45	.28	.75	.13	.32	.62
W x I	1	.78	.01	.47	.12	.17	.86
WxDxI	1	.07	.08	.97	.66	.10	.46
TOTAL	15						

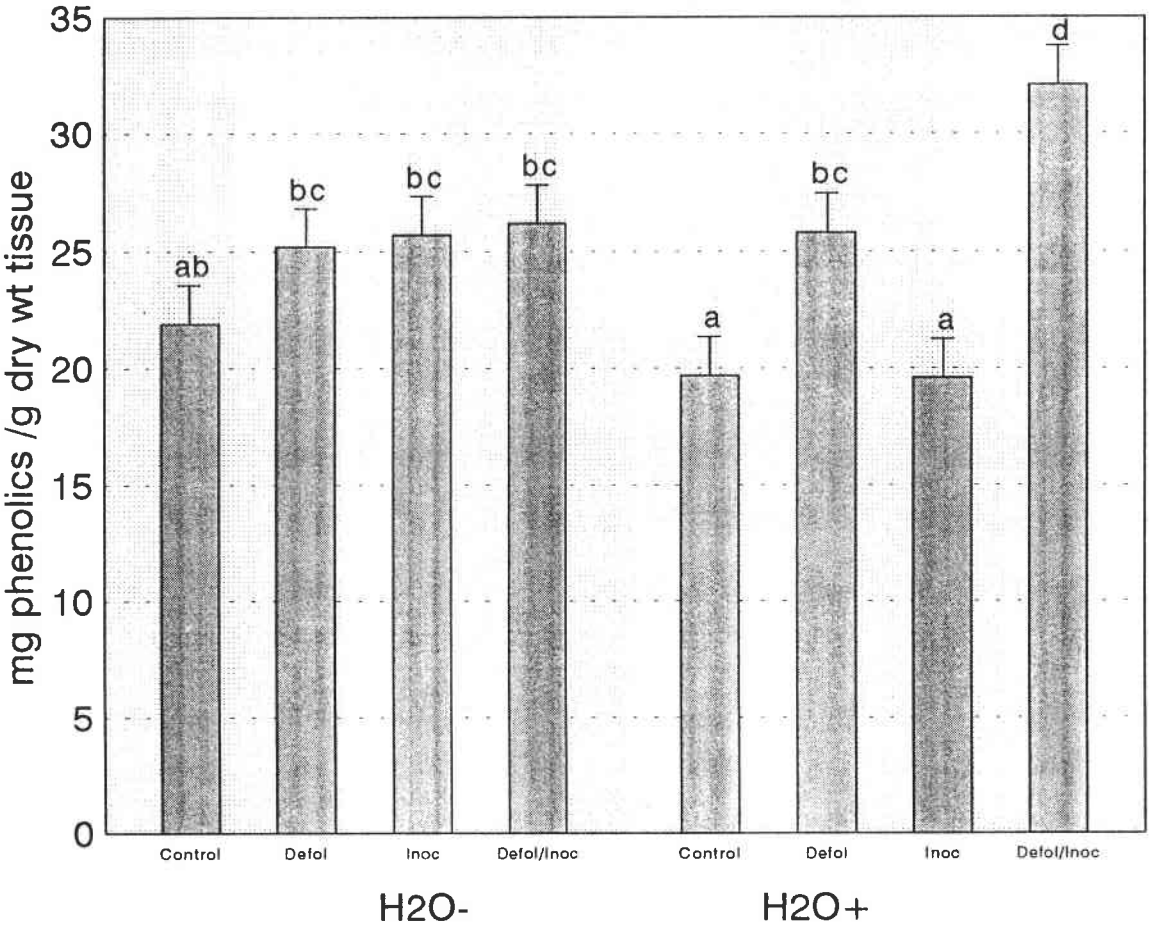


Figure 5. Group I total Folin-Ciocalteu foliage phenolics (gallic acid equivalents) of grand fir seedlings that were well-watered or water-stressed, and/or defoliated by western spruce budworm larvae, and/or inoculated with Armillaria ostoyae. Mean values with the same letter are not significantly different ($p<0.05$)

Roots. The combined seedlings of water-stressed treatments had significantly (p=.003) higher root phenol content than well-watered seedings.

Defoliated treatments had less root phenolics than undefoliated controls in both H20- and H20+ groups (Table 8). The difference between defoliated and undefoliated was nearly (p=.06), but not quite, statistically significant at the 0.05 significance level (Table 7).

Inoculation, alone, did not cause a significant difference in root phenolics. The interaction between water and inoculation was significant (p=.01). Water-stressed (H20-/Inoc) seedling roots had lower levels of phenolics than did the roots of H20-/control seedlings (Figure 6). Likewise, the roots of H20+/Inoc seedlings had slightly lower levels of total phenolics. There was not a statistical interaction between inoculation and defoliation as related to phenolic levels, nor was the three-way interaction between water, defoliation, and inoculation significant.

Table 8. **Group I concentrations (values expressed in mg/g dry tissue) of phenolics, sugars, and starch in grand fir seedlings that were well-watered or water-stressed, and/or defoliated, and/or inoculated with Armillaria ostoyae.**

	------Phenolics-----		------Sugar-------		----Starch---	
Treatment	Foliage	Root	Foliage	Root	Foliage	Root
H2O-/Control	21.9	19.7	98	30	27	15
H2O-/Defol	25.2	18.4	71	25	25	24
H2O-/Inoc	25.7	15.8	98	27	26	16
H2O-/Defol/Inoc	26.2	12.7	76	25	28	23
H2O+/Control	19.7	13.9	69	21	27	24
H2O+/Defol	25.8	8.0	63	20	25	23
H2O+/Inoc	19.6	12.7	59	22	26	24
H2O+/Defol/Inoc	32.1	13.7	57	23	24	23

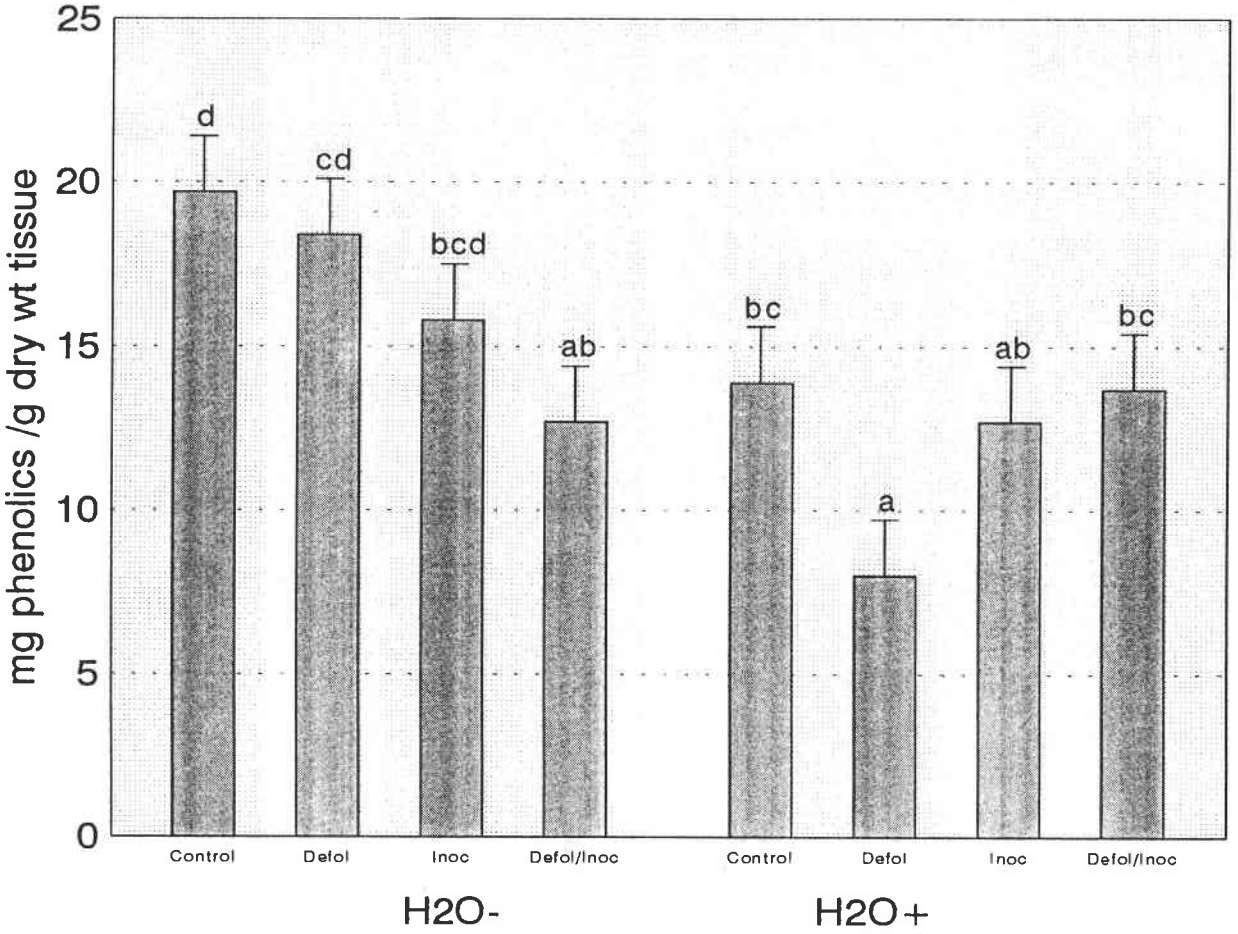


Figure 6. Group I total Folin-Ciocalteu root phenolics (gallic acid equivalents) of grand fir seedlings that were well-watered or water-stressed, and/or defoliated by western spruce budwrom larvae, and/or inoculated with Armillaria ostoyae. Mean values with the same letter are not significantly different ($p<0.05$)

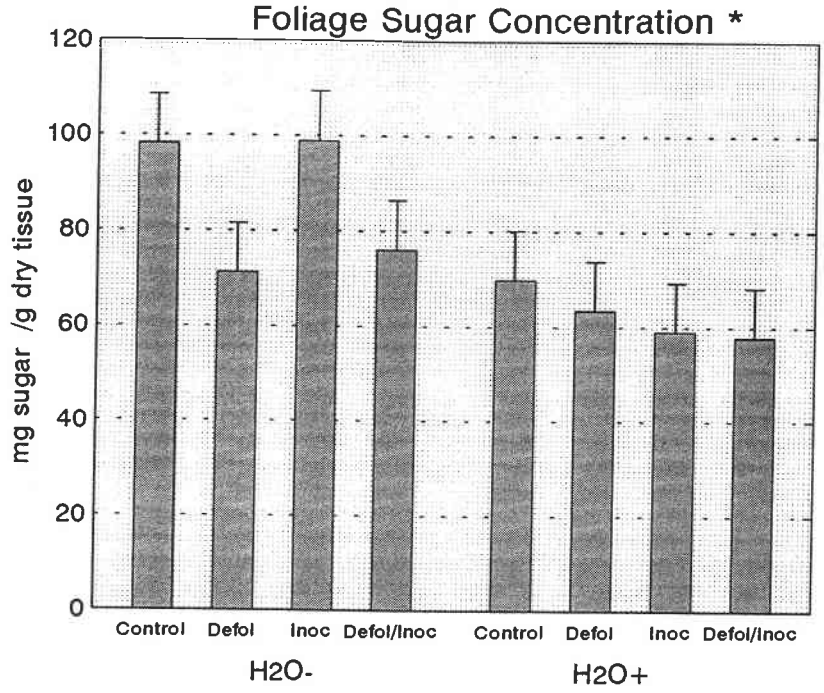
Sugars

Foliage. Water-stressed seedlings had significantly more (p=.01) soluble sugars in needle tissue than did well-watered seedlings (Table 7). Defoliation caused a decrease in soluble sugars in both water treatments, but the difference was not statistically significant (p=.08). Inoculation did not significantly alter the foliage soluble sugar content (Figure 7). Interactions among treatments were not significant.

Roots. Seedlings of combined water-stressed treatments had significantly more soluble sugars in the secondary roots than did well-watered seedlings (p=.001). Roots of H20-Defol seedlings had a significantly lower level of sugar than nondefoliated controls (Figure 7). There were no interactive effects with defoliation or inoculation.

Starch

Foliage. Foliage from water-stressed seedlings was higher in starch content (p=.045) than foliage of well-watered seedlings. Defoliated treatments had less foliage starch than undefoliated, but the difference was not significant (p=.16) (Figure 8).



* Combined water-stressed treatments had significantly higher foliage sugars. However, there were no differences between individual treatments.

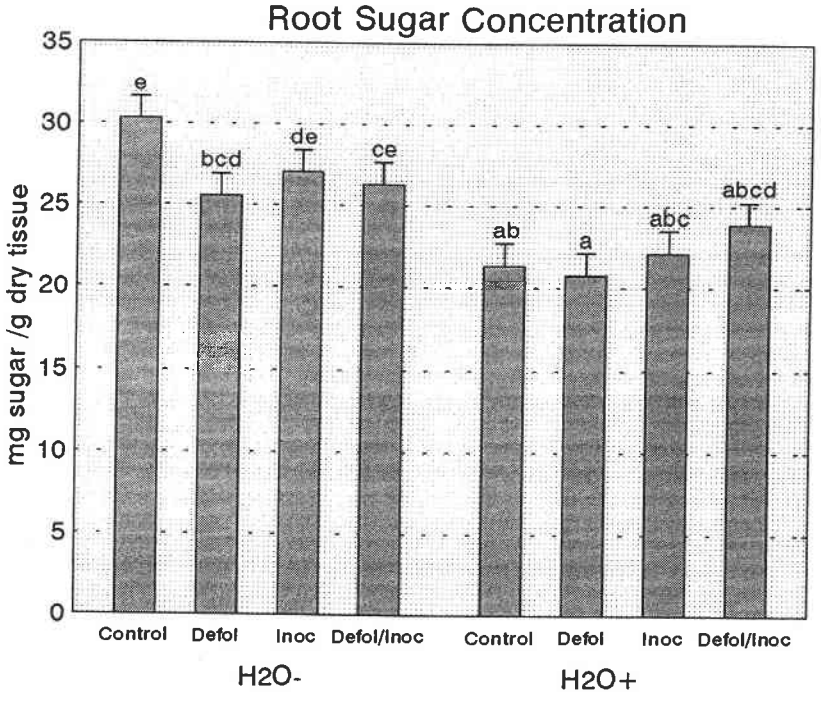
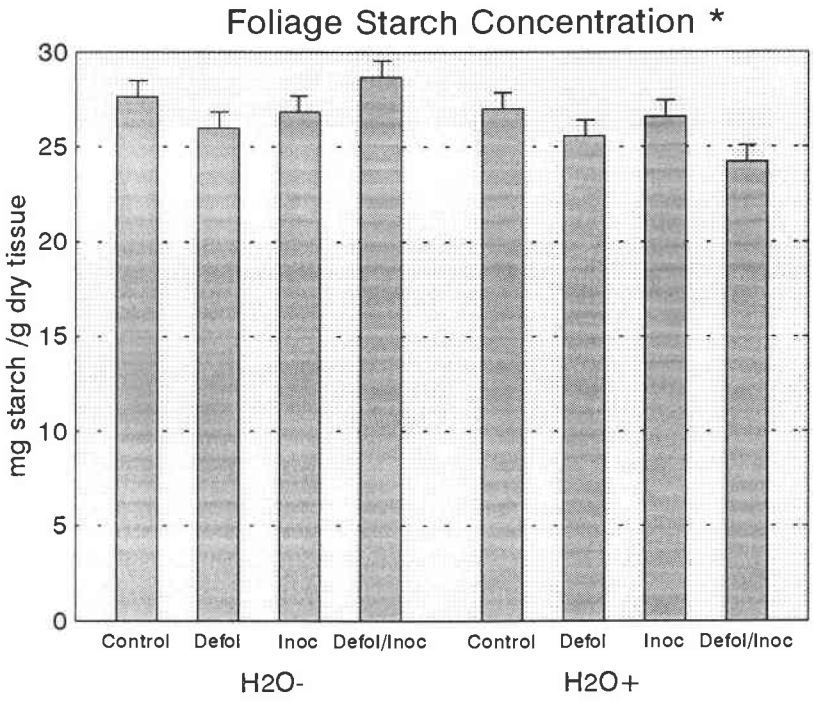


Figure 7. Mean values of sugar concentrations in foliage and roots of Group I treatments. Mean values with the same letter are not significantly different ($p<0.05$)



* Combined water-stressed treatment had significantly higher foliage starch. However, there were no differences between individual treatments.

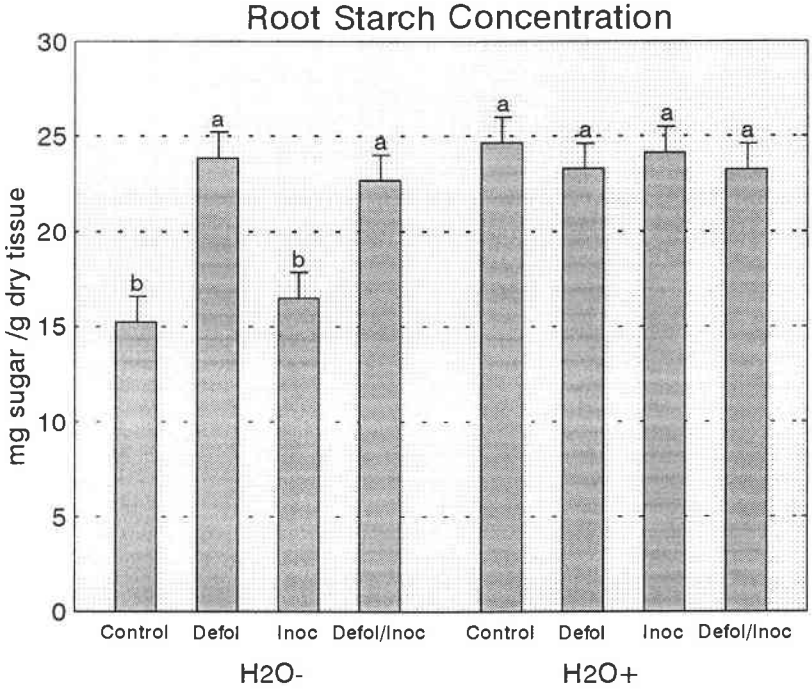


Figure 8. Mean values of starch concentration in foliage and roots of Group I treatments. Mean values with the same letter are not significantly different ($p<0.05$)

Roots. Roots of water-stressed seedlings had significantly less starch (p=.002) than roots of well-water seedlings. Defoliation, however, appeared to cause an increase in root starch of water-stressed seedlings; H20-/Defoliated treatments had significantly more starch in root tissue (p=.01) than did H20-/Control. Water-stressed roots of H20-/Defoliated had a root starch content close to that of watered controls (H20+/Control) (Figure 8). The interaction between water and defoliation (Water x Defol) was statistically significant with a probability factor of .002. Inoculation was not a significant factor in root starch, nor was the three-way interaction of water, defoliation, and inoculation.

Group II

Insect Performance

Development rate

The development rate for western spruce budworm reared on water-stressed treatments was faster (p=.001) than budworm reared on well-watered treatments (Table 9). The mean number of days to pupation for larvae reared on combined water-stressed treatments was 26 days. This was eight days less than the mean of 34 days needed for larvae reared on well-watered treatments (Table 10). Larval development rate was not significantly influenced by previous defoliation or inoculation.

Table 9. **Group II p-values as determined by analysis of variance for western spruce budworm larvae development rate and sex ratio. Larvae were fed on grand fir seedlings that were well-watered or water-stressed and/or inoculated with Armillaria ostoyae.**

Source	df	Development Rate	Female:Male
Water	1	>.001	.003
Inoc	1	.687	.100
W x I	1	.991	.209
TOTAL	11		

Sex ratio

The ratio of females to males in water-stressed seedlings was significantly higher (p=.003) than in well-watered treatments (Table 9). Combined water-stressed treatments had an average female:male ratio of 1.68 compared to .64 for well-watered treatments. Inoculation and defoliation level did not influence sex ratio (Table 10).

Table 10. Group II sex ratio and development rate of western spruce budworm larvae fed on grand fir seedlings that were well-watered or water-stressed and/or inoculated with Armillaria ostoyae.

Treatment	Sex Ratio Female:Male	# of Days to Pupation	
		Female	Male
H2O-/Defol 91[1]	*	*	*
H2O-/Defol 90-91	2.14	28.5	23.5
H20-/Defol 91/Inoc[1]	*	*	*
H2O-/Defol 90-91/Inoc	1.20	29.9	24.3
H20+/Defol 91	1.20	41.0	34.2
H20+/Defol 90-91	.60	32.8	30.9
H20+/Defol 91/Inoc	.19	30.0	35.6
H2O+/Defol 90-91/Inoc	.57	33.7	33.3

[1] seedlings did not produce new foliage thus no defoliation or budworm development was possible
* missing data

Seedling Infection and Mortality

One seedling died during the Group II experimental period from causes other than Armillaria. Treatment H20-/Defol-91/Inoc had one dead seedling that had no evidence of root disease. The cause of death is unknown. All other seedling mortality is thought to have occurred as a result of, or in conjunction with Armillaria colonization.

Armillaria ostoyae

Mortality (dead infected). More seedlings died as a result of Armillaria infection in water-stressed treatments than in watered treatments (Table 11). As in Group I, defoliated treatments of both water regimes sustained less mortality than undefoliated treatments. As with Group I, the highest level of mortality occurred in the H20-/Inoc treatment where 44 percent of the seedlings died. Treatment H20-/Defol-91 (the treatment that was actually undefoliated because of absence of new foliage upon which larva must feed) had a mortality rate of 22 percent. One seedling in the well-watered group (H20+/Inoc.) died during the experiment.

Live infected. There were one or two live-infected seedlings in each treatment group except those that were both inoculated and defoliated. Treatments of both water regimes that had been both defoliated and inoculated had no visible signs of infection (Table 11).

Table 11. Group II Armillaria ostoyae infection and mortality of grand fir seedlings.

Treatment[1]	Live-Infected	Dead-Infected	Healthy	Total Infected
	----------% (actual number)----------			
H2O-/Inoc	22 (2)	44 (4)	33 (3)	66 (6)
H2O-/Defol 90/Inoc	11 (1)	0	88 (8)	11 (1)
H2O-/Defol 91/Inoc[3]	22 (2)	22 (2)	44 (4)[2]	44 (4)
H2O-/Defol 90-91/Inoc	0	0	100 (0)	0
H2O+/Inoc	22 (2)	11 (1)	66 (6)	33 (3)
H2O+/Defol 90/Inoc	22 (2)	0	77 (7)	22 (2)
H2O+/Defol 91/Inoc	22 (2)	0	77 (7)	22 (2)
H20+/Defol 90-91/Inoc	0	0	100 (0)	0

[1] n=9 seedlings
[2] includes one uninfected dead seedling
[3] no actual defoliation occurred because there was no new foliage

Total infected. The number of dead-infected and live-infected seedlings were combined to calculate the total infected. Treatment H20-/Inoc had the highest total infection where 66 percent of the seedlings were either live infected or dead infected.

Lab isolations

At the time of seedling harvest, a sub-sample of the alder dowel inoculum from each treatment were tested for viability. Armillaria ostoyae was recovered from 100 percent of the sampled dowels. Likewise, all of the culture attemps to verify colonization by Armillaria ostoyae in root tissues of seedlings suspected to be infected produced the fungus.

Biochemical Features

Phenolics

Fifth Instar Foliage Collection. Defoliation had a notable effect on phenolics of foliage collected during the period when the majority of experimental budworm were in the 5th instar (p=.07). Treatments of both water regimes that were defoliated in '90 only, had higher levels of phenolics than foliage collected from other treatments (Figure 9). The main effects of water regime and inoculation were not statistically significant in foliage phenolics. Generally, well-watered seedlings had lower foliage phenolics than water-stressed seedlings during this sample analysis.

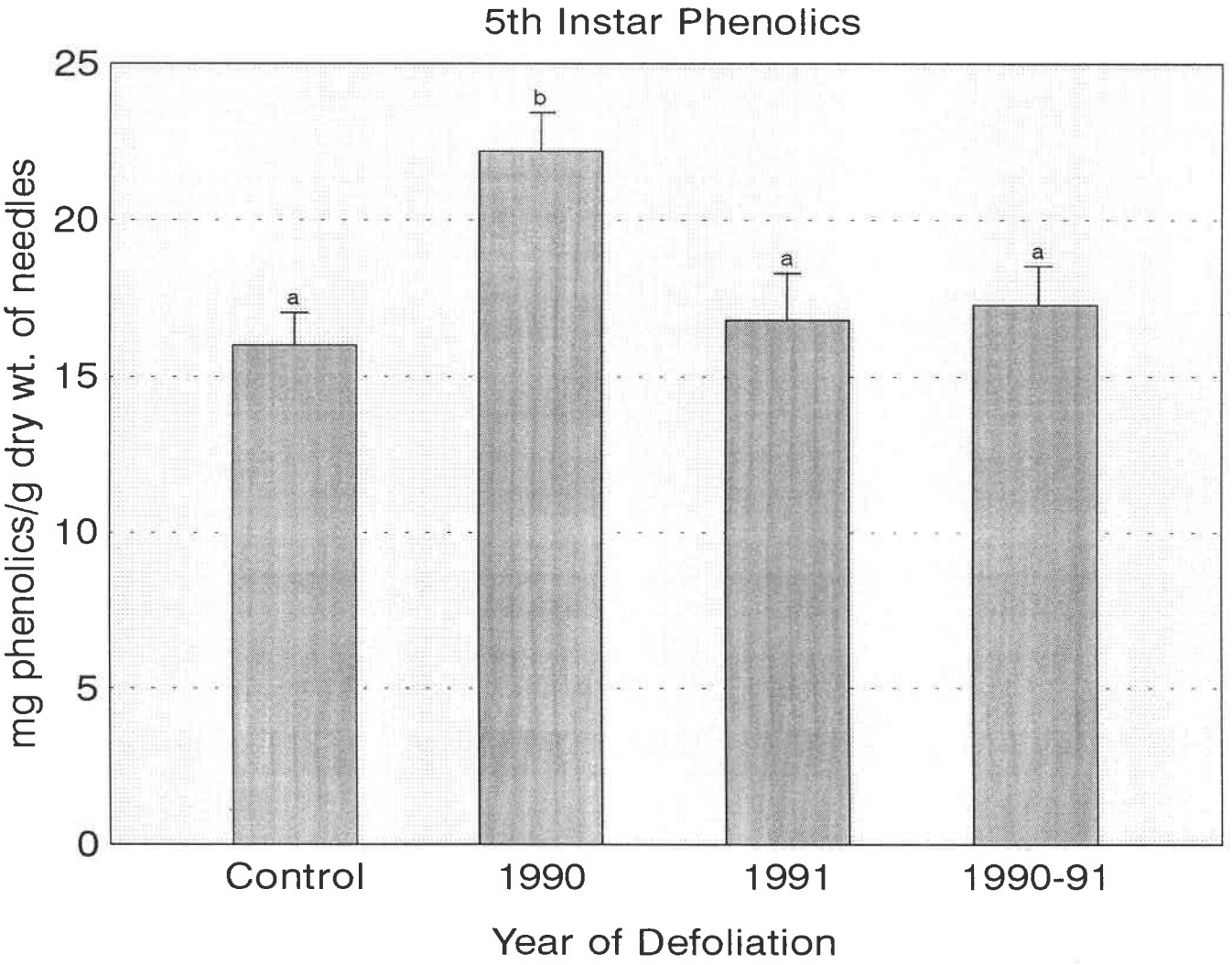


Figure 9. Group II total Folin-Ciocalteu phenolics (gallic acid equivalents) collected from grand fir with different levels of defoliation. Foliage was collected when most of the experimental budworm were in the 5th instar. Means values with the same letter are not significantly different ($p<0.05$)

Nitrogen, Phosphorus, Potassium, and Sulfur

Foliage

Foliar concentrations of N were not statistically different between well-watered and water-stressed treatments (Figure 10). Defoliation, however, altered foliage N (Figure 11). Foliar concentrations of P were significantly affected by treatment. Foliage P increased with water-stress (p=.002) (Figure 10), and decreased (p=.02) with previous year defoliation (90 and 90-91) (Figure 11). There was a significant interaction (P=.02) of water and defoliation due to the greater reduction in P of water-stressed seedlings defoliated in 1990, and due to only a slight reduction in P from undefoliated controls in H20+ treatments. There were no significant differences in levels of foliage K related to treatment. Sulfur levels were lower (p=.05) in treatments defoliated in the previous year (90 and 90-91) than in treatments undefoliated or defoliated in 1991, only. Foliar sulfur did not vary with water treatment or inoculation. Generally, there was no significant response of N, P, K or S to inoculation.

Ratios. The ratio of foliar sugar to N was significantly higher in water-stressed treatments (p=.05) (Figure 12). The sugar:N was not different with defoliation or inoculation. The ratio of P to N was not different with H20 or inoculation but was affected by defoliation (p=.06) (Figure 13), where it decreased in treatments defoliated in 90 and 90-91. Likewise, K:N levels were significantly lower (p=.009) in treatments defoliated in '90 and 90-91 and were unaffected by water-stress or

defoliation. As with K:N and P:N, the S to N ratio was lower in treatments defoliated in 90 and 90-91 ($p=.001$), and unaffected by water treatment or inoculation.

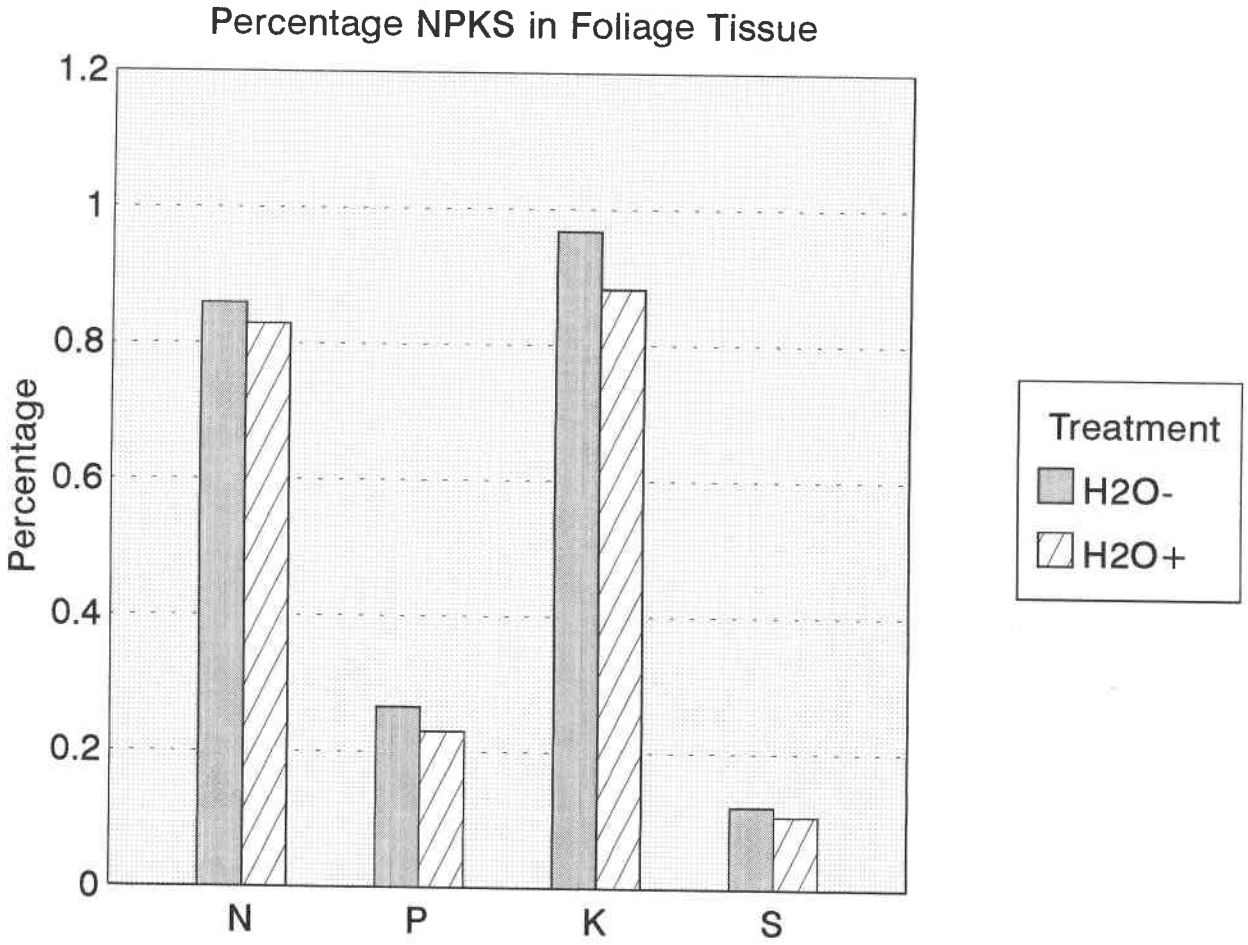


Figure 10. Group II foliage nutrients of well-watered and water-stressed grand fir seedlings

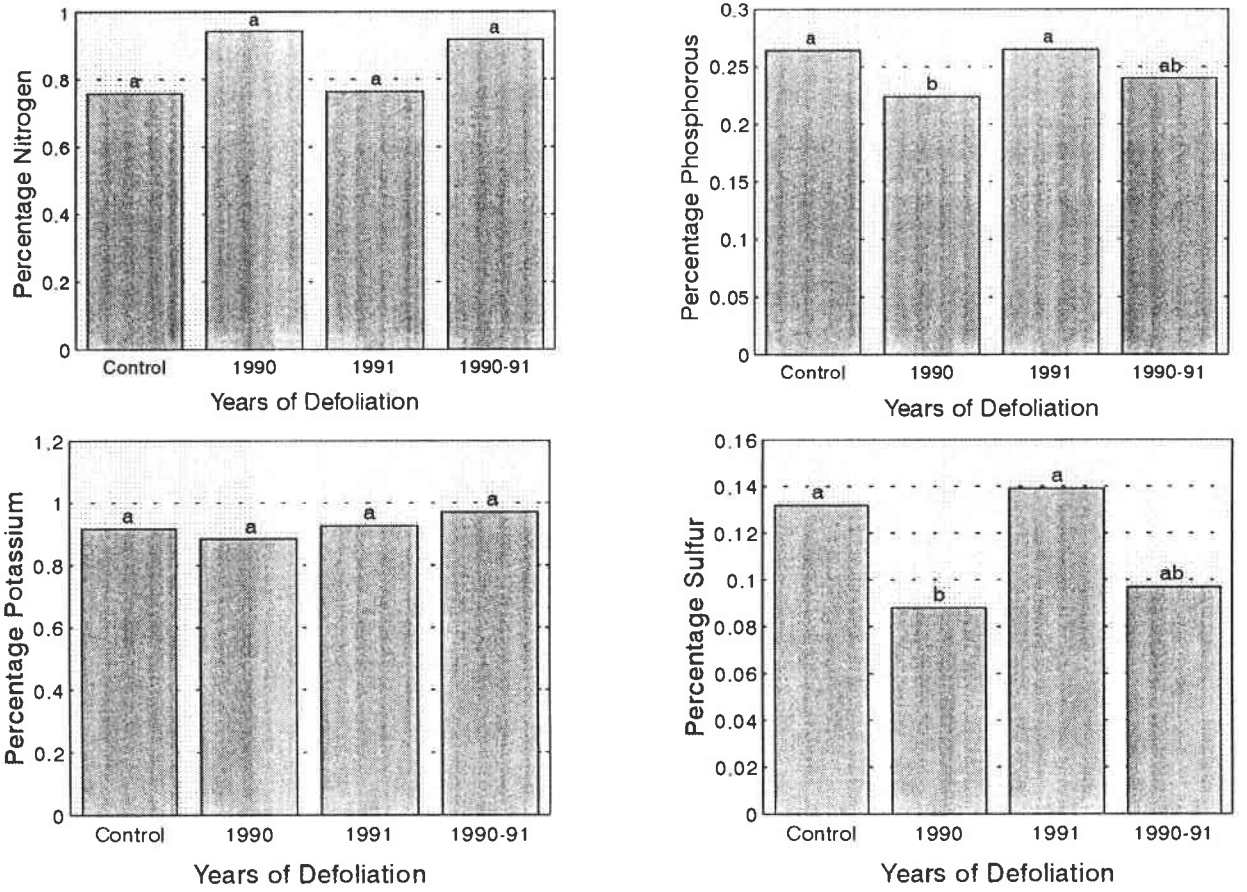


Figure 11. Percentage of foliage N, P, K, and S in Group II grand fir that were undefoliated (control), defoliated in the year prior to harvest (1990), defoliated in the same year as harvest (1991), and defoliated in both years (1990-91). Mean values with the same letter are not significantly different ($p<0.05$)

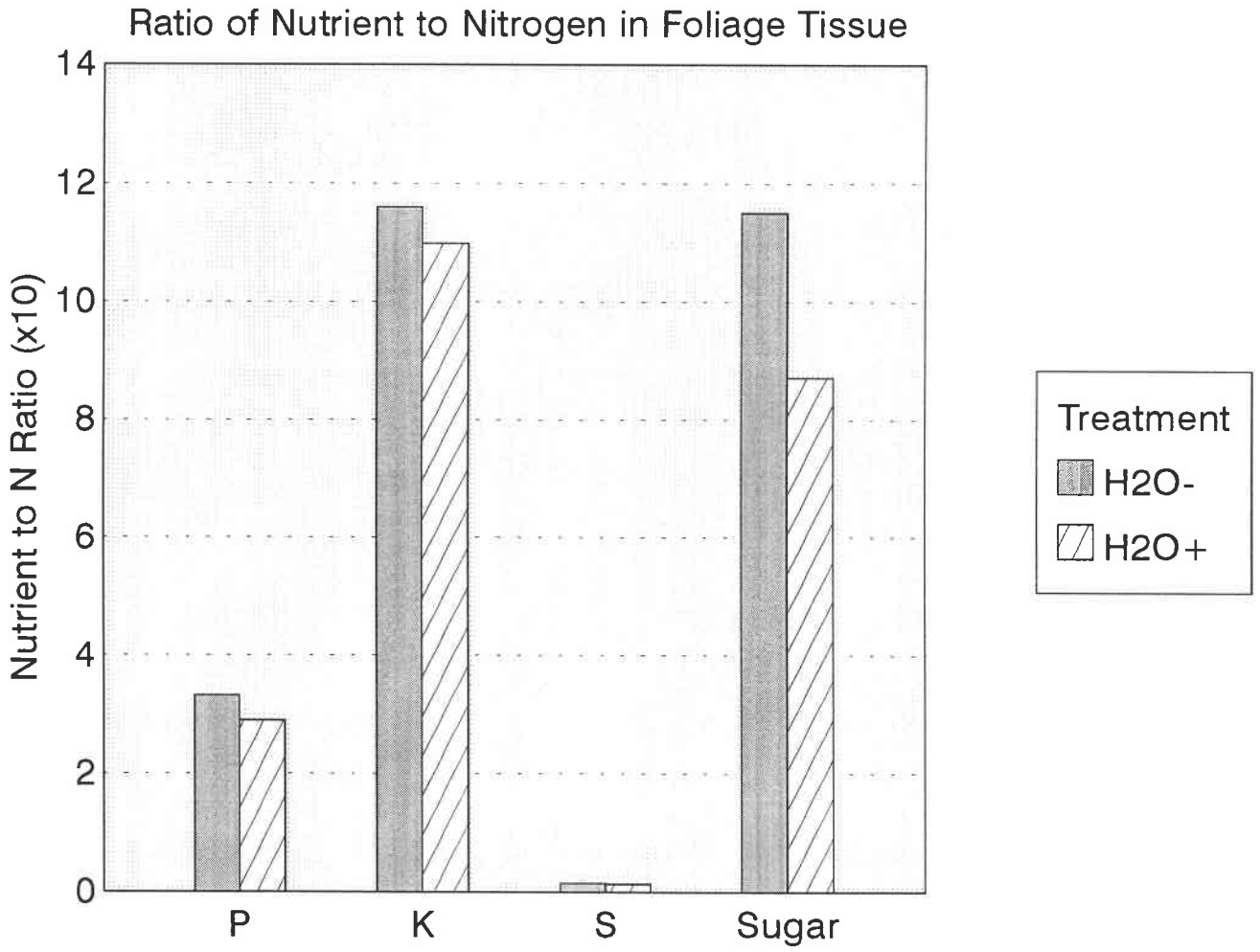


Figure 12. Group II nutrient to N ratio of foliage from well-watered and water-stressed seedlings

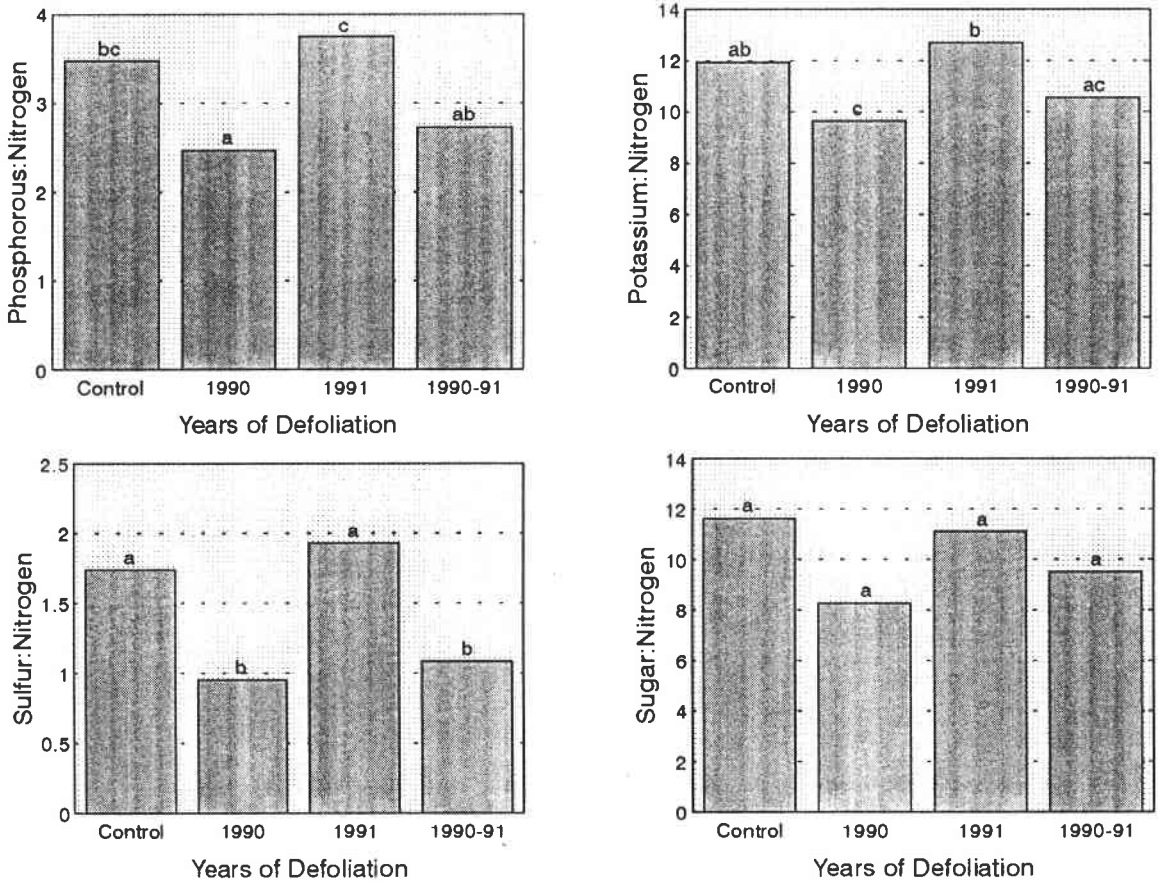


Figure 13. Ratio of nutrient to N in foliage in Group II grand fir that were undefoliated (control), defoliated in the year prior to harvest (1990), defoliated in the same year as harvest (1991), and defoliated in both years (1990-91). Mean values with the same letter are not significantly different ($p<0.05$)

Roots

There were no detectible differences in root N concentrations with water-stress (Figure 14) or inoculation. Defoliation however, was a significant factor (p=.001). The roots of seedlings with 1990 defoliation, and 1990-91 defoliation had higher levels of root N than those treatments without defoliation or with only 91 defoliation (Figure 15). The roots of water-stressed seedlings had lower concentration of P than well-watered seedlings (p=.04). There were no detectible differences with inoculation but defoliation was a significant factor (p=.02). Treatments with '90 and 90-91 defoliation had higher levels of P in the root tissue. Water-stressed treatments had lower levels of K than well-watered treatments (p=.001). Defoliation and inoculation caused no detectable difference in K levels of experimental groups. Water-stressed treatments had less S in root tissue than well-watered treatments, but this difference was not statistically different (p=.08). Sulfur levels were not significantly affected by defoliation.

Ratios. The ratio of sugars to N was not significantly different with water treatment (Figure 16) but was affected by defoliation level (p=.005) (Figure 17). The highest sugar:N ratio was in the roots of undefoliated seedlings. Previous year defoliation (90 and 90-91) caused a significant reduction in the sugar:N. Inoculation did not significantly affect the sugar:N ratio. The P:N ratio was significantly affected by water-stress (p=.0007). Water-stressed treatments had lower P:N ratios than well-watered treatments. Inoculation and defoliation did not significantly influence P:N

ratios. Water-stress caused a significant reduction in K:N values (p=.0007). Defoliation and inoculation caused no detectible differences in the K:N ratio. Sulfur to N ratios were lower in water-stressed seedlings (p=.07) than well-watered seedlings and lower in seedlings with 90 and 90-91 defoliation (p=.003).

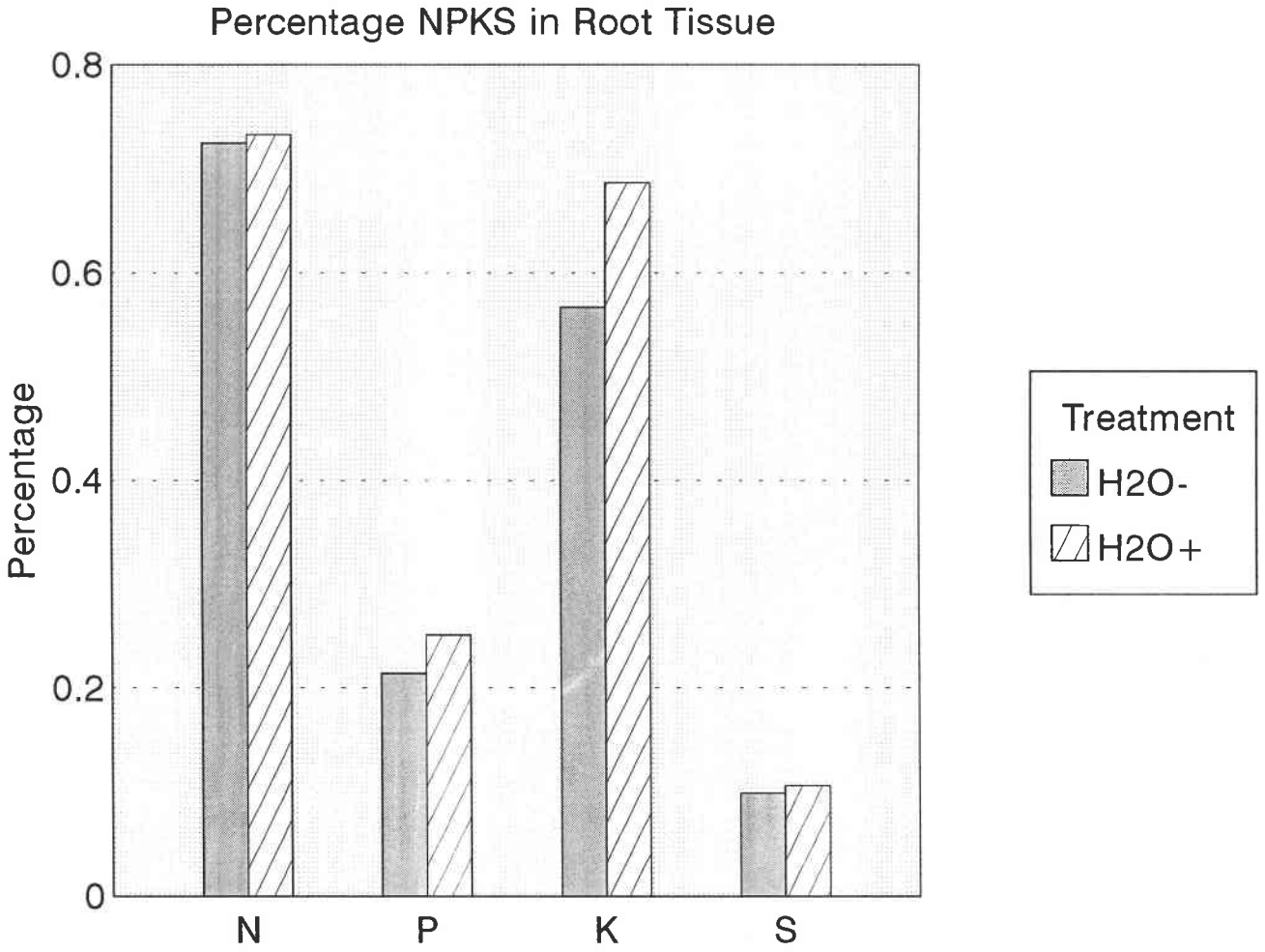


Figure 14. Group II root nutrients of well-watered and water-stressed grand fir seedlings

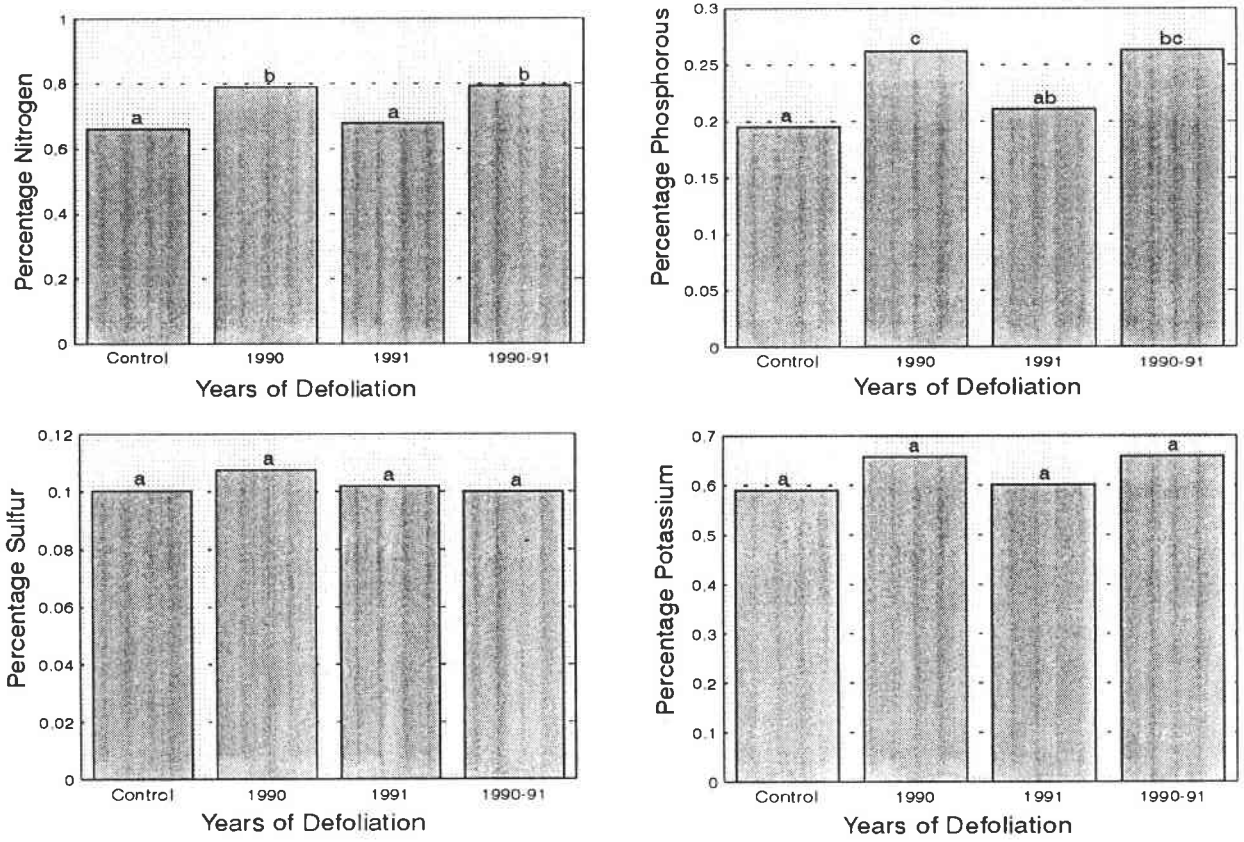


Figure 15. Percentage of root N, P, K, and S in Group II grand fir that were undefoliated (Control), defoliated in the year prior to harvest (1990), defoliated in the same year as harvest (1991), and defoliated in both years (1990-91). Mean values with the same letter are not significantly different ($p<0.05$)

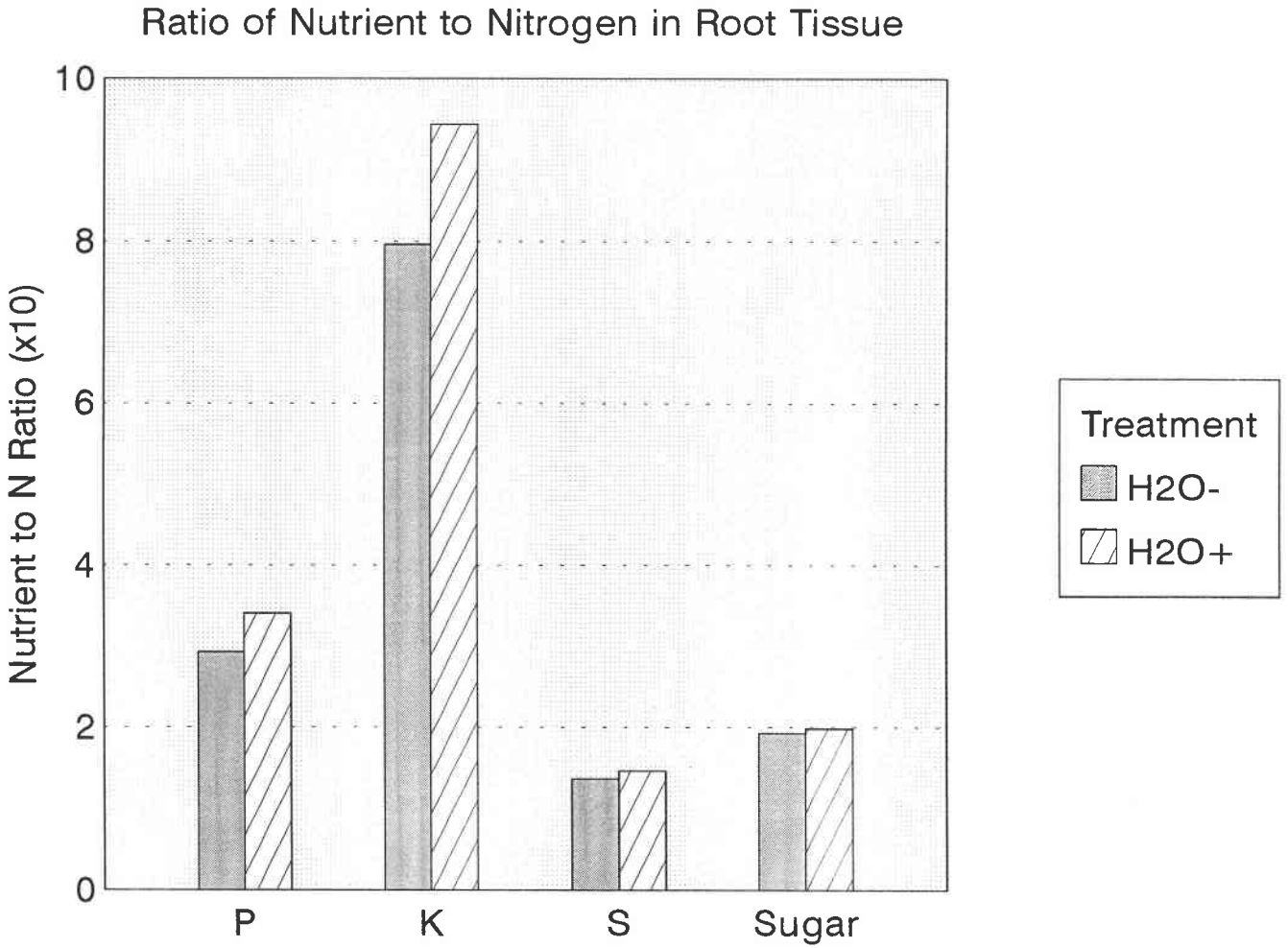


Figure 16. Group II nutrient to N ratio of roots from well-watered and water-stressed grand fir seedlings

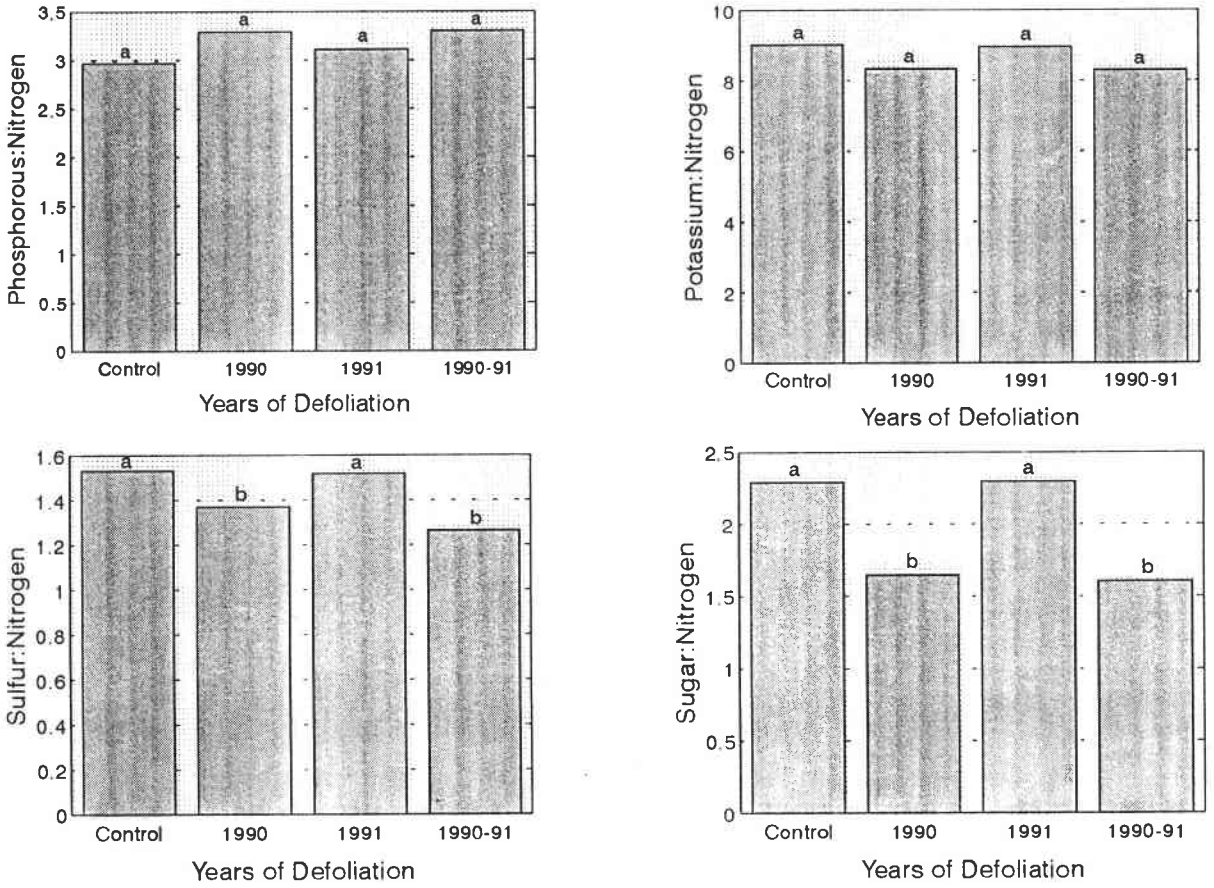


Figure 17. Ratio of nutrient to N in roots in Group II grand fir that were undefoliated (Control), defoliated in the year prior to harvest (1990), defoliated in the same year as harvest (1991), and defoliated in both years (1990-91). Mean values with the same letter are not significantly different ($p<0.05$)

Phenology

Bud Flush

Seedlings of H20+ treatments flushed earlier than those of H20- treatments (p=.0001) (Figure 18). The interaction between water and defoliation was also significant (p=.003) (log trans =.0001). Seedlings of H20-/Defol had a high rate of increase from H20-/Control. Inoculated seedlings had a significantly later bud flush than non-inoculated (p=.03). Inoculation did not significantly interact with other treatments.

Foliage Quality

Percentage Moisture

There was not a statistically significant difference due to water treatment in the percentage moisture content of current year needles. Water-stressed treatments averaged 64.5 percent moisture; well-watered treatments averaged 65 percent moisture (Table 12). Defoliation had a significant effect on percentage moisture of new needles (p=.03). Seedlings that were defoliated in 1990 or in both 1990 and 1991 had higher mean moisture content of 66.4 percent in the new foliage than seedlings that were not defoliated in 1990 or were defoliated in 1991 only. Seedlings not defoliated in 1990 averaged a mean moisture content of 64.3 percent.

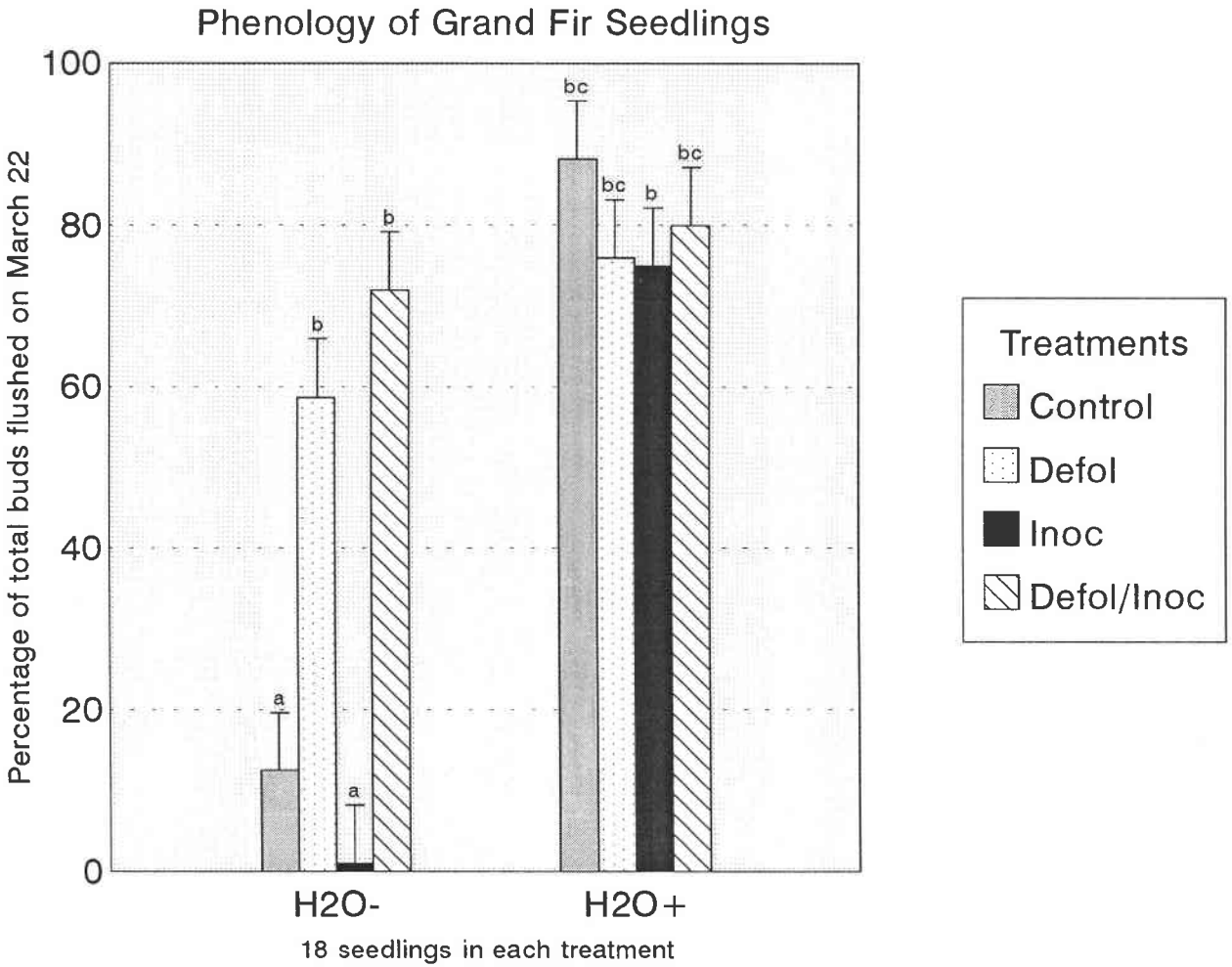


Figure 18. Group II bud development phenology. Mean values with the same letter are not significantly different ($p<0.05$)

Seedling Morphology and Biomass Production

Bud numbers

As shown in Figure 19, seedlings in well-watered treatments had more developing buds than those of water-stressed treatments (p=.0001). Previously defoliated seedlings also had more buds than did undefoliated seedlings (p=.0001). The interaction between water and defoliation was also significant (p=.05), as water-stressed seedlings had a higher rate of increase between total buds of H20-/Control and H20-/Defol treatments than did comparable H20+ treatments. Inoculation was not a significant factor in the number of buds.

Table 12. Group II average oven-dry weight of roots and shoots per seedling.

Treatments[1]	Shoots			Roots Weight (grams)	Root to Shoot Ratio
	Total Top (grams)	New Foliage (grams)	% Moisture in New Foliage		
H2O+/Control	9.37	2.44	64.53	9.77	1.09
H2O+/Defol 90	6.75	2.73	65.79	5.27	.82
H2O+/Defol 91	8.20	1.52	64.30	9.48	1.20
H2O+/Defol 90-91	5.31	1.22	67.55	5.43	1.06
H2O+/Inoc	9.62	2.65	63.52	10.88	1.12
H2O+/Defol 90/Inoc	8.79	3.15	67.73	7.39	.86
H2O+/Defol 91/Inoc	8.85	.82	64.91	12.01	.37
H2O+/Defol 90-91/Inoc	7.28	2.11	66.42	6.31	.89
H2O-/Control	12.11	0	*	11.99	1.02
H2O-/Defol 90	5.91	1.49	64.83	6.23	1.05
H2O-/Defol 91	11.44	0	*	13.27	1.16
H2O-/Defol 90-91	5.06	.40	67.57	6.13	1.22
H2O-/Inoc	11.72	0	*	13.37	1.17
H2O-/Defol 90/Inoc	6.21	1.28	66.39	6.89	1.10
H2O-/Defol 91/Inoc	12.29	0	*	11.63	.97
H2O-/Defol 90-91/Inoc	5.22	.30	64.94	6.12	1.20

[1] n=9 seedlings
* missing data

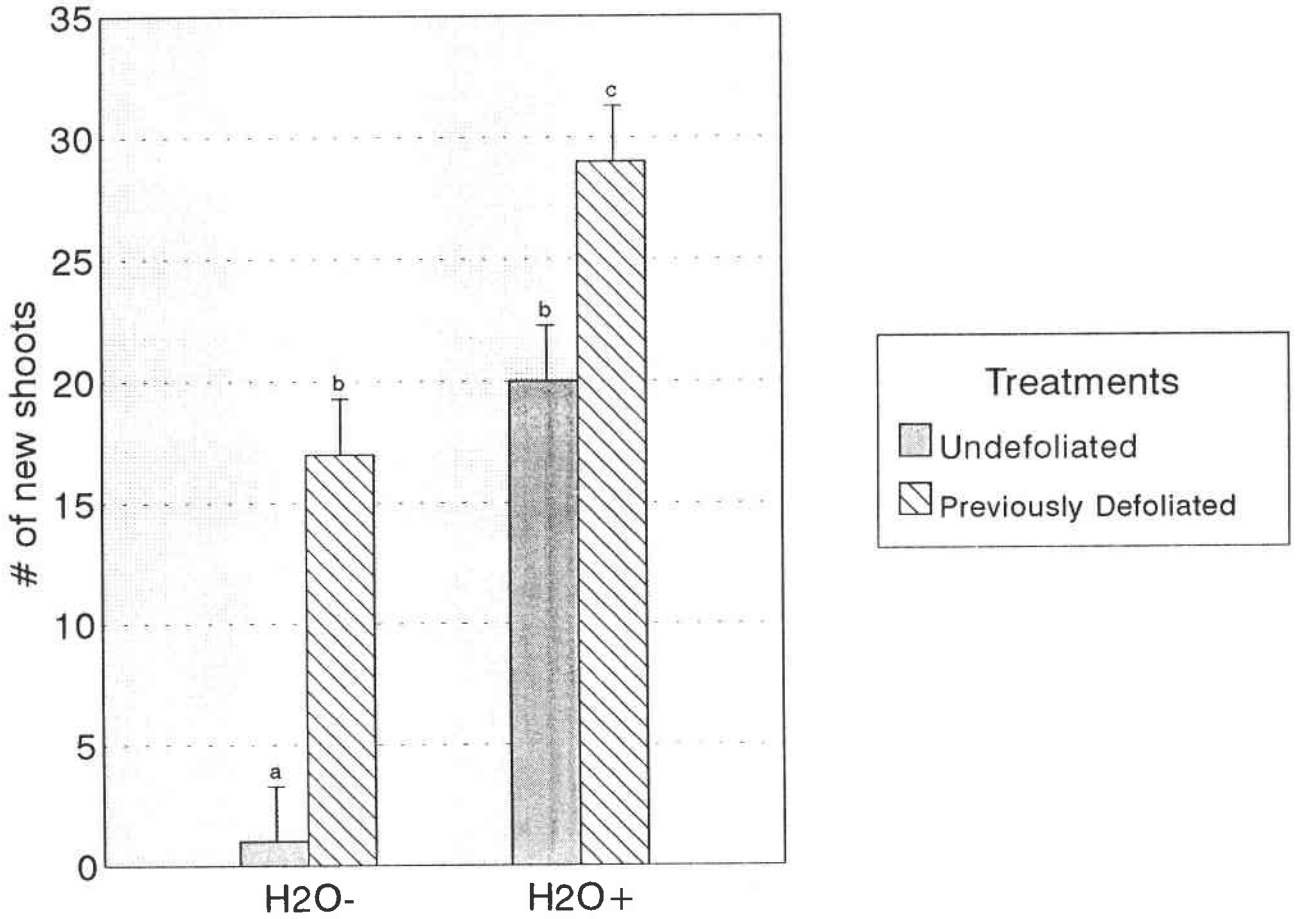


Figure 19. Group II total number of new shoots on previously defoliated grand fir seedlings. Mean values with the same letter are not significantly different ($p<0.05$)

Roots

Seedlings of water-stressed treatments had a higher total root mass than seedlings of well-watered treatments (p=.03). Defoliation level had a highly significant effect on root mass (p=.0001). Defoliation of current year foliage of both water regimes (H20-/Defol-91 and H20+/Defol-91) produced a root biomass similar to undefoliated controls (Table 12). Seedlings defoliated in the previous year (H20-/Defol-90 and H20+ Defol-90) and seedlings defoliated for two years (H20-/Defol-90, 91 and H20+/Defol-90, 91) had reduced root biomass compared to undefoliated controls. Inoculation and interactions were not significant.

Shoots

Even though water-stressed seedlings were more heavily defoliated by spruce budworm than well-watered seedlings, the mean weight for seedling shoot (above ground) biomass was greater for combined water-stressed treatments than the above-ground biomass for well-watered seedlings (p=.03). Water-stressed, undefoliated seedlings had the highest above ground biomass (Table 12). Defoliation, of course, had a significant effect on top biomass (p=.0001). When compared to controls of the same water regime, results show a 51 percent reduction in total top biomass in H20-/Defol-90 from H20-/Control; a six percent reduction in H20-/Defol 91; and a 57 percent reduction in H20-/Defol-90, 91. Likewise, when compared to H20+/Control, H20+/Defol-90 had a defoliation caused reduction of total top biomass of 28 percent; a reduction of 12 percent in H20+/Defol-91; and a reduction

of 22 percent in H20+/Defol-90, 91. There was a significant interaction of water and defoliation (p=.0001) as the amount of reduction (foliage consumed by budworm) was higher in the H20- treatments. Inoculation did not significantly influence top biomass.

Root:Shoot

The ratio of root biomass to shoot (top) biomass was slightly higher in H20- treatments, but not significantly so (p=.07). Defoliation caused a significant effect on root:shoot ratios (p=.004) (Figure 20). As a main variable for well-watered seedlings, defoliation caused a reduction from the ratio of undefoliated controls in seedlings defoliated in 1990, it caused an increase in the seedlings defoliated in 1991, and there was no difference in seedlings defoliated in both 1990 and 1991. Analogous trends were not apparent for water-stressed seedlings. There was a highly significant interaction of water and defoliation (p=.0004). Water-stressed seedlings defoliated only one year, in either year, (H20-/Defol-90 and H20-/Defol-91) had root:shoot ratios comparable to those of H20-/Control (Table 12). Seedlings defoliated two years (H20-/Defol-90, 91) had significantly higher root:shoot.

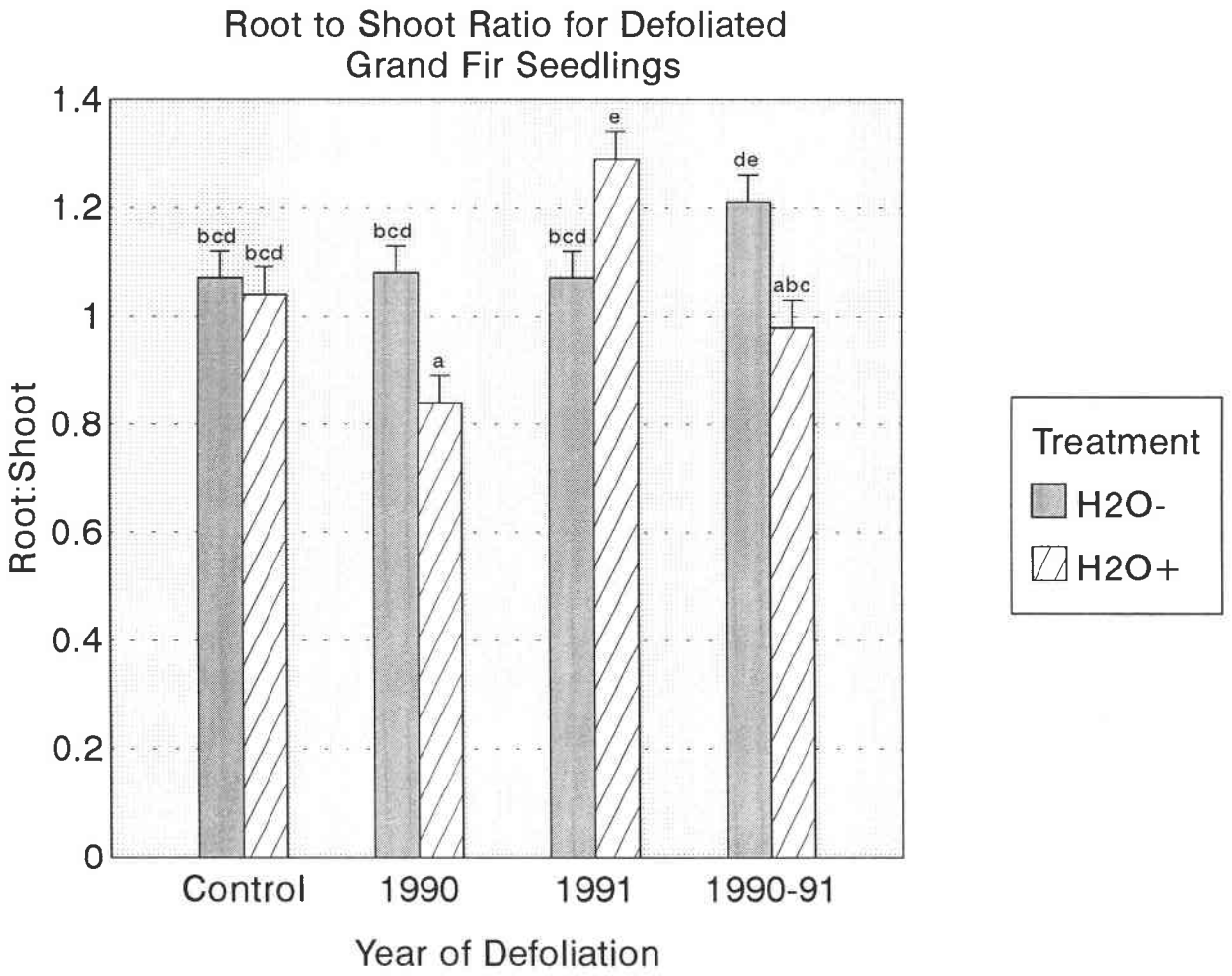


Figure 20. Root to shoot ratios for well-watered or water-stressed seedlings with different levels of defoliation. Mean values with the same letter are not significantly different ($p<0.05$)

HYPOTHESES SUMMARY

In reference to Hypothesis 1 the null is rejected; water-stressed seedlings were more suitable for insect growth, survival and reproduction.

As metabolic pathways for the substances analyzed are all different, both the null and the alternative are true for Hypothesis 2, depending on the substance. In terms of phenolic concentration, no strong evidence of change was found with water regime. Carbohydrate allocation was altered by water-stress, and higher concentrations of both sugars and starch were apparent in the current year foliage of water-stressed seedlings. Concentrations of N, P, K, and S were all somewhat elevated in water-stressed tissue, but the increase was significant only for P.

Hypothesis 3 was rejected because water-stress significantly enhanced successful infection and mortality of experimental seedlings.

As with Hypothesis 2, both the null and the alternative were true for Hypothesis 4. Phenolic levels were higher in water-stressed roots. The overall pattern in root tissue was lower N, P, K, and S, only the difference was not significant for N, as it was for P, K, and S.

Defoliation negated the enhanced effect on A. ostoyae colonization success due to water stress. Thus, the null is rejected for Hypothesis 5. Defoliated, water-stressed seedlings seemed to be protected from the water-stress induced changes that made seedlings highly susceptible to infection and mortality. Defoliated seedlings had the lowest Armillaria-caused mortality in both water regimes.

Most evaluated nutrients and elements of root tissues were affected by defoliation (Hypothesis 6). The roots of defoliated seedlings of both water regimes had higher levels of starch and N, and lower levels of P and S. Only K was unaffected by previous defoliation.

The null was accepted for Hypothesis 7 for carbohydrates, N, P, K, and S because they were unaffected by inoculation. Alternatively, inoculated seedlings had a mean foliar phenol concentration that was higher than noninoculated seedlings, thereby necessitating a rejection of Hypothesis 7 for phenolic substances.

Regarding Hypothesis 8, the null was rejected because larvae reared on water-stressed and inoculated seedlings produced heavier pupae than larvae reared on well-watered and inoculated seedlings.

DISCUSSION AND CONCLUSIONS

Western Spruce Budworm

Factors Affecting Performance

Water Stress. Western spruce budworm mortality was lowest in water-stressed treatments. The results of these experiments support the work of others that suggest that feeding on drought-stressed plants may increase the fitness of co-evolved insect herbivores. Western spruce budworm grew larger, faster, and produced more females on water-stressed treatments. The implications of these changes in fitness in nature are as follows:

1) Because pupal size is directly correlated with adult fecundity (Miller 1957), experimental results suggest that western spruce budworm exponentially increase in reproductive potential when fed on water-stressed grand fir seedlings.

2) If larval growth and development are accelerated during periods of water deficits, there is relatively less time for parasitism, predation, and infection by lethal diseases per given life stage. Consequently, the reduction in mortality would result in more females contributing to the next generation.

3) Sex ratios of budworm, normally 1:1 (Campbell et al. 1983), were affected by water treatment. Higher female to male ratios suggest that more females are surviving on water-stressed foliage. This indicates that the foliage of water-stressed seedlings is relatively more nutritive to developing female larvae than to developing male larvae. Since any one male can mate several females, a differential shift toward an increase in females would contribute to growth in the next generation.

Foliage Phenolics. The role of phenolic compounds on the performance of western spruce budworm has been a much debated topic among entomologists (Cates et al. 1983a, 1983b; Mooney et al. 1983; Mattson et al. 1983; Wagner and Blake 1983; Cates and Redak 1988). It is now widely accepted that phenolics have defensive functions. It is, however, far less clear to what extent the defensive functions really explain the evolution of phenol metabolism in the plant. A plant character can, for instance, evolve primarily for drought resistance, and as a side effect deter herbivore feeding (Tuomi 1992). Other factors, for example, resource availability, may constrain secondary metabolism and, thereby, plant defensive responses. Rhoades (1979) summarized the basic tenets of the optimal defense theory. The theory assumes that there is a limited amount of resources that a plant can devote to defense, and that there are alternative demands for these limited resources (e.g., growth). Selection is expected to favor an optimal defense allocation that

maximizes plant fitness, as defenses are costly. Following this theory, plant parts most valuable in terms of fitness should be most effectively defended.

The phenolic patterns reported in Group I suggest that the foliage phenolics of new needles were not higher in undefoliated well-watered plants than water-stressed plants; conversely, they were lower than levels of all water-stressed treatments. Well-watered, defoliated seedlings, however, showed a large increase in foliage phenolics from undefoliated controls. Water-stressed treatments did not show a comparable increase in foliage phenolics when defoliated. This suggests an "induced" reaction catalyzed by defoliation in well-watered seedlings that was not present in water-stressed treatments.

Reports of induced secondary chemical production in tree/herbivore relationships are few but interest in this area of research has been increasing. Both artificial damage and insect damage appear to increase levels of phenolics in birch foliage (Hanson and Havir 1981; Haukioja and Niemala 1979) and in sugar maple and poplar (Hartley 1988).

Furthermore, Bloom et al. (1985) suggest that plants growing in a resource limited environment are less plastic in carbon allocation patterns than those plants growing in a resource rich condition. It is possible that water-stressed seedlings were unable to respond to defoliation with an increased production of phenolics because the resources were not available to do so; especially since they had elevated levels of phenolic compounds already.

Although foliage phenolics of well-watered defoliated seedlings were higher than those of well-watered controls they were not higher than water-stressed groups. Hence, it is unlikely that phenolics were responsible for the decrease in budworm performance on well-watered treatments. This, of course, assumes that similar phenolic compounds were being produced by both well-watered and water-stressed seedlings. It is possible that, in response to defoliation, the well-watered seedlings were actually producing a phenol or other compound which was deleterious to the budworm, and because of the nonspecific methods used for testing of total phenolics, it was undetectable.

Phenolics were measured twice during the Group II experimental period. The first measurements of current year foliage were made during the period that most experimental budworm were in the fifth instar. Measurements were made during this larval period because the fifth and sixth stages consume 90-95 percent of the total diet (Miller 1977). Foliage collected at this time generally contained lower amounts of phenolics than foliage of the second collection that was made approximately eight weeks later when seedlings were harvested. It has been suggested that the new foliage of conifers is the most dispensable tissue and, given the cost of defending, may frequently contain less secondary metabolites, even though the risk of insect attack to that tissue is high. Higher phenolics in foliage from seedlings defoliated the previous year, 1990, may indicate that more resources are dedicated to defense if a tree has been previously exposed to foliovores and has ample resources to produce the secondary metabolites. This rise in phenolics was

not found in foliage from trees under current defoliation or trees defoliated for two consecutive years which may suggest they did not, yet, have time to acquire these defenses.

Foliage Textural Quality. I observed budworm feeding differently on well-watered treatments and water-stressed treatments. The feeding pattern on needles of well-watered trees was more of a "window feeding" where the surface of one side of the needle (top or bottom) was skimmed but the entire needle cross section was not consumed. Conversely, the needles of water-stressed treatments were fully ingested from the outer edge of the needle, inward. In the cases where the entire needle was not eaten, it was severed from the branchlet and thus fell to the potted soil or cage bottom.

The difference in feeding pattern suggests that the quality of the needles of well-watered seedlings was somehow inferior to those needles of water-stressed hosts. Although no difference in moisture content of well-watered verses water-stressed foliage was detected at the time of the post-pupation sample, it is possible that water content and/or "toughness" of needles were different during the larval feeding period that occurred prior to sampling. Toughness is related to the levels of compounds that together comprise "fiber" (lignin, silica, pectin, cellulose, hemicellulose, etc.) and structural components such as sclerencyma fibers and bundle sheaths (Hagan and Chabot 1986; Mattson and Scriber 1987). Lawrence (1990) found higher levels of needle water-content to be positively correlated with

spruce budworm performance. Toughness, though not measured in this experiment, has frequently been reported as negatively correlated with both leaf water content and insect performance (Feeny 1970; Huang and Fuhrer 1979; Hagen and Chabot 1986). Additionally, toughness steadily increases in newly elongating foliage; water percentage steadily decreases in aging foliage (Lawrence 1990). Hence, sampling for these variables should expressly be done during larval development and not post-pupation, as was performed in this experiment.

There may have been an effect due to microclimate in the developmental differences of larvae in the water-stressed verses well-watered groups. Because of profuse foliage and alternate day waterings of well-watered cages, the environment inside the insect cages was different than the drier, less shady environment of the water-stressed cages. Because budworm development is likely affected by leaf temperature, and perhaps moisture and solar radiation, these unmeasured microclimatic variables may have had a significant effect on insect response to treatment.

Foliage Nutritional Quality. Reduced nutrition may explain a decline in budworm performance on well-watered seedlings.

Carbohydrates -- Well-watered foliage was lower in the concentration of both soluble sugars and starch than water-stressed foliage. Sucrose and monosaccharides are likely to be important in the diet of western spruce budworm larvae, especially

during late larval development. Thorsteinson (1960) reported that "for bees, flies, and butterflies, the feeding response to sucrose is proportional to the concentration, i.e., the modal response occurs at the highest concentrations obtainable." In support of Thorsteinson's statement, Harvey's 1974 study showed that spruce budworm females responded with an increase in weight on up to a 4.0 percent sucrose diet, the highest level tested in Harvey's study. Additionally, there is some evidence that sucrose acts as a phagostimulant for many insect species (Akeson, et al. 1970; Harvey 1974; Heron 1965).

Starch on the other hand, is not thought to be important in the diet of lepidopertous insects. Artificial diet studies have shown that spruce budworm do not utilize starches extensively (Harvey 1975; Feeny 1970). Feeny (1970) has suggested that energy needs of lepidopterous larvae are probably met by free sugars and, perhaps, by nitrogenous compounds.

Nitrogen -- Converse to what has been found in other experiments (Kramer 1983; Mattson and Haack 1987a), water stress did not alter N levels in this experiment. In their review of studies measuring herbivore response to water deficits, Waring and Cobb (1992) found that in published research there is no clear response of N to water stress, nor is there predictable herbivore response to water stress-related increases in the nitrogen fraction.

Unlike water treatment, defoliation did influence the nitrogen level of current year foliage in Group II. Those seedlings that had been defoliated in 1990 and in

1990-91 had higher levels of foliar N than did undefoliated seedlings or those defoliated in 1991 only. Mattson et al. (1983), who studied the response of spruce budworm, report that larval growth was consistently and positively linked to foliar N, although survival rates were not. Clancy et al. (1993) reported the results of a field study that measured levels of foliar nutrients including N in trees she considered to be "resistant" (i.e. undefoliated) and "susceptible" (i.e., defoliated). She suggested, as have others, that foliage from resistant trees had a different nutrient profile from susceptible trees which probably led to their escape from budworm feeding. Although this may indeed be the case in the Clancy study, my results indicate that defoliation itself may be the cause of the nutrient pattern difference, and that the patterns were not a pre-existing inherent trait that rendered some trees "resistant" or "susceptible." No other studies, to my knowledge, have been designed to look at nutrient profiles where defoliation is an independently evaluated treatment variable.

Phosphorus, Potassium and Sulfur -- Foliar phosphorus levels were higher in water-stressed seedlings than well-watered seedlings. Some studies have shown a positive insect response to plants fertilized with phosphorus (Waring and Cobb 1992), but many show no response. Potassium and sulfur were not affected by water stress but sulfur showed a similar pattern of reduction to phosphorus in seedlings that had been defoliated in 1990 and 1990-91, strengthening the evidence that past defoliation significantly alters the nutritional pattern of current year foliage.

Ratios -- Although it is speculated that most insects are nitrogen limited, this study found the foliage that was most favorable to budworm development had higher nutrient to N ratios. All ratios of foliar nutrients to N were higher in foliage of water-stressed seedlings. The higher sugar to N ratio found in water-stressed seedlings may likely be a main factor in the positive insect response to water treatment. Both sugars and nitrogen have a critical impact on insect physiology. Additionally, sugars act as a feeding stimulant. The ratio of sugar to N may be closer to optimum in water-stressed seedlings and, thereby, be responsible for the enhanced budworm growth and survival. It is interesting to note that previous year defoliation lowered the ratio of P, K and S to N in all cases.

Armillaria Ostoyae

Factors Affecting Performance

Water stress. The effect of water stress on mortality rate was prominent (56 percent mortality in Group I; 33 percent in Group II). Significantly higher mortality rates in the undefoliated water-stressed seedlings were accompanied by the observation that water-stressed seedlings became symptomatic and died rapidly as compared to well-watered seedlings. Although there was a low level of Armillaria-caused mortality in well-watered treatments (22 percent in Group I; 5 percent in Group II), these seedlings became chlorotic and gradually and slowly died. There was also a difference in the degree of colonization of the root system of water-stressed vs. well-water seedlings. Dead water-stressed seedlings usually had signs of resinosis

above the soil line in the pot; often accompanied by root collars that were completely colonized. Conversely, only one dead well-watered seedling had evidence of colonization at the root collar and no well-watered, infected seedlings had produced basal resinosis. Rather, well-watered seedlings seemed to have a few colonized secondary roots and perhaps a lesion on the distal portion of the tap root. The basal resinosis suggests that the water-stressed trees were extensively colonized before dying and were not simply a better substrate after death, than well-watered seedlings (Shaw 1977, 1980).

It is possible that soil moisture played some part in the preponderance of infection and mortality of water-stressed seedlings by affecting the growth and viability of the inoculum. Although low soil moisture was not found to be a factor on growth of A. mellea (sensu lato) (Garrett 1956; Redfern 1970), it is possible that waterlogging may inhibit growth. Risbeth (1978), found growth restricted and rhizomorph formation of wide selection of isolates inhibited by water logged soils. Whereas the pots in my well-watered treatments appeared to be well drained, they were always in a moist condition due to alternate day waterings. The possible influence of high moisture conditions is supported by the fact that field reports of Armillaria spp. on permanently wet soils with a high peat accumulation are rare (Redfern and Filip 1991). The potting mix used in this experiment was one-third peat, and although the soil moisture conditions of well-watered seedlings could not be described as waterlogged, they were maintained in a permanently moist condition.

Defoliation. Soil moisture conditions cannot entirely explain the differences in Armillaria-caused infection and mortality because not all water-stressed treatments had high rates of mortality or live-infection. Defoliated seedlings in both water regimes had less live-infection and mortality than did undefoliated seedlings. This finding departs from a two-decade paradigm espoused by forest pathologists that defoliation contributes to enhanced incidence and spread of Armillaria spp. (Wargo and Harrington 1991). Evidence to support this paradigm was originated with a series of well designed studies established to evaluate the relationship of defoliated oaks and maples with A. mellea (sensu lato) in the Northeastern United States (Wargo and Houston 1974; Wargo and Montgomery 1983).

The relationship between insect defoliation and enhanced severity of Armillaria spp. on deciduous hardwood species has been irrefutably established. This relationship for conifer species, although commonly accepted, has not been validated by controlled research.

Two major differences exist between the environment of the hardwood-defoliator-Armillaria relationship and that of the conifer-budworm-Armillaria association. First, the annual carbohydrate and nutrient allocation patterns are different in deciduous species vs. evergreen species; the flux being greater in the deciduous species. These differences likely remain in tree-response to defoliation. Second, the defoliators involved and the mode of defoliation are different between the hardwood complex and the conifer/budworm complex. Hardwoods set buds in the fall and flush all at once in the spring with foliage that is all of similar age and

metabolic function. Thus, hardwood defoliators have a different effect on plant metabolic function than do budworm on their conifer hosts. Western spruce budworm feed almost exclusively on current year foliage; early instar budworm developmental rates are closely tied to bud flush phenology. This mode of defoliation, except in the youngest trees or after multiple years of defoliation, leaves a complement of past year(s) foliage. Research has found that on conifer species, each age of foliage has a unique contribution to the whole-tree metabolic process. These differences become important topics for discussion because the paradigm of defoliation-enhanced Armillaria infection and mortality is centered on chemical changes found in the roots of stressed hardwood trees that have been proven to nutritionally enhance Armillaria growth (Parker 1970; Parker and Houston 1971; Wargo 1972). It is my belief that, because of these differences in hardwood vs. conifer physiology, plus lack of supporting field evidence, available data cannot be projected into conifer species. Each of the three conifer-budworm-Armillaria observational reports published, reports an enhancement of disease with budworm defoliation but each reports additional confounding factors as well (See pages 29 and 30 in the Literature Review section for pertinent review).

Only two controlled experiments have been performed, to my knowledge, that may illuminate the conifer-defoliation-Armillaria complex. Wahlstrom (1992) found defoliation to both increase and decrease Armillaria infection depending on Armillaria species. Evaluating the effects of defoliation on the infection of Scots pine Wahlstrom (1992) found a decrease in infection success of A. ostoyae. The

method for defoliation, however, was manually removing all but a few needles on each tree as reported: "seedlings were stressed by cutting off 90 percent of their needles, leaving only a tuft of needles at each branch tip." Although this method may supply some empirical knowledge about the interaction, it does not emulate the feeding pattern of any forest insect guild. Therefore, the results of the test are difficult to project to insect-caused defoliation conditions. The other experiment, performed by Filip (1989), found no increase in Armillaria infection in artificially defoliated grand fir. Filip tried to mimic western spruce budworm feeding by gradually removing newly flushing foliage. In his discussion, Filip attributed this lack of infection to be possibly caused by low virulence of the fungus, when in fact defoliation may have caused the unanticipated reduction in infection success.

Root Phenolics. Water-stressed seedlings had the highest level of root phenolics. Within the water-stressed treatments, inoculated, and inoculated and defoliated seedlings had lower root phenolics. Because phenolics have been shown to have both inhibitory effects and enhancement effects on the growth of Armillaria spp., it is difficult to interpret these results. Wargo (1984) suggests that A. mellea (sensu lato) successfully colonizes the roots of stressed, deciduous trees because their increased levels of both glucose and amino acids enhance its ability to oxidize the normally inhibitory phenolics and even to utilize the products as a source of carbon. It is unlikely that the drop in root phenolics of water-stressed inoculated seedlings is due to the phenolics being utilized by the root pathogen because seedlings in the

inoculated and defoliated (H2O/DEFOL/INOC) treatment had lower root phenolics as well, and few were found to be successfully infected by Armillaria. A more plausible explanation of the lower phenolics found in inoculated roots would be that they did not have the resources needed to produce phenolics or that on a whole plant basis more phenolics were allocated to the above ground portion of tissue.

Root Nutritional Quality. Enhanced nutrition may explain an increase in A. ostoyae performance on water-stressed seedlings.

Carbohydrates -- Entry and Cromack (1989) found A. ostoyae to grow faster in the presence of phenolic compounds in media supplemented with higher concentrations of easily degradable carbohydrates. In my experiment, higher soluble sugars were found in the roots of water-stressed seedlings. Wargo (1972) found higher sugars in defoliated sugar maple and attributed, in part, increased A. mellea (sensu lato) success to the sugar increase. In my defoliated grand fir, however, I did not find higher sugars concentrations; conversely, defoliated roots had a pronounced decrease, even though this decrease was not statistically significant. Water-stressed, inoculated and defoliated seedlings which had low incidence of Armillaria infection had both lower sugars and higher starch than water-stressed, inoculated and undefoliated treatments which had high levels of infection and mortality.

In contrast to my results, Wargo (1972) found low root starch to be associated with defoliation and increased Armillaria-caused mortality of sugar

maple. It is possible that my results of higher starch in root tissue of defoliated seedlings is an artifact of tree age, and that similar results may not be obtained in mature A. grandis. Past research provides little information on the effect of defoliation on the below ground system. Webb (1980) found mature defoliated white fir (Abies concolor Gord. and Glend.) Lindl.) to have lower starch in all plant parts, including roots, with heavy defoliation by the Douglas-fir tussock moth. In a companion study, Webb (1980) found the same starch reduction in artificially defoliated Douglas-fir. It is not possible to compare the results of Webb to my study, however, as unlike western spruce budworm, the tussock moth defoliates all ages of needles, as did Webbs' artificial defoliation process. Although in my study 80 to 90 percent of the new foliage was defoliated in some treatments for two consecutive years, root starch remained high. Presumably, the high levels of root starch are due to a reduction in seedling growth potential because of defoliation and water-stress, during which a major complement of foliage is still present to produce and transport photosynthates to the roots where they are subsequently stored as reserve carbohydrates.

Nitrogen and Phosphorus -- The nitrogen and phosphorus levels were significantly lower in roots of water-stressed undefoliated, or current year only defoliated seedlings. Increased impacts due to Armillaria in plantations and forests have been related to soils that are low in N and P (Singh 1970; Shields and Hobbs 1979). This relationship has been demonstrated experimentally, as well (Entry et al. 1986; Singh

1983; Rykowski 1984). Interestingly, a classical theory in mycorrhiza research, "Bjorkman's Carbohydrate Theory" (Nylund 1988), submits that the best host environment for mycorrhizal infections is one of low N and P and high carbohydrates (i.e., sugars; not starch). These are the conditions that were found in the root tissue of the seedling group most susceptible to Armillaria infection in my study. Other mycorrhizal work (Richards and Wilson 1963) found a high carbohydrate to nitrogen ratio to be positively correlated with mycorrhiza formation. Higher carbohydrate to N conditions were found in all of my water-stressed seedlings except those that were defoliated. Defoliation increased levels of root nitrogen and reduced sugars, perhaps rendering the host less suitable for establishment of A. ostoyae.

Seedling Morphology and Biomass Production

Bud Numbers

Seedlings in both water regimes that had been previously defoliated produced more buds the following year. Water-stressed seedlings produced few buds unless they had also been defoliated. It has been reported for Douglas-fir in New Mexico that heavy budworm feeding apparently induces latent buds to flush and expand as shoots; similar studies found white fir to have few such activated latent buds (Brookes et al. 1977). The abundant flush of foliage the year following defoliation in water-stressed seedlings may indicate an over-all superior seedling condition of that group verses the undefoliated controls; on the other hand, such a response may

be due to defoliation-caused disruption to hormones that regulate bud flush. Additionally, although bud numbers were greater in the previously defoliated seedlings, the amount of foliage produced per shoot may have been less. Wickman et al. (1992) found that budworm-infested fertilized grand fir produced fewer buds than unfertilized, but more foliage per shoot. They suggest that this resulted in increased tree growth because the larger shoots were not as often destroyed by budworm feeding as smaller shoots.

Projecting these results to the field suggests that if the same phenomenon occurs in grand fir of all ages, that defoliation is beneficial to the tree during periods of short-term drought. This benefit disappears, however, after multiple years of annual defoliation obliterates foliage to the point where foliage is insufficient to supply the energy needs of the tree (estimated to be six years for mature Douglas-fir, Alfero et al. 1982).

Phenology

Not only did previous defoliation cause a production of more buds in water-stressed seedlings but buds were produced sooner. Host-insect synchronization is often important to the survival of the insect. Witter and Waisanen (1978) found a six-fold difference in the mean proportion of buds infested by Choristoneura spp. between early and late flushing clones of Populus tremuloides Michaux.

The late flushing of buds in undefoliated, water-stressed control and inoculated seedlings may reflect poor condition of these groups. Defoliated water-

stressed seedlings entered into the growing season early and with plentiful buds which may enhance their growth potential. On the other hand, early flushing may provide an advantage to the budworm that, while closely tied to the bud phenology, usually develops slightly earlier. In infrequent years of late bud flush the budworm can be limited by insufficient food source. An early source of suitable foliage would likely enhance budworm survival.

Field studies evaluating Douglas-fir that were "susceptible" to defoliation and "resistant" to defoliation, indicated that those trees that appeared to be resistant had a delayed bud flush compared to those that appeared susceptible (Clancy et al. 1993; Muzika et al. 1993). Results from my study suggest that the difference in bud flush timing found by Clancy et al. (1993) and Muzika et al. (1993) may have been a result of differing defoliation history between resistant and susceptible trees as opposed to some genetically based resistance factor.

Root:Shoot Biomass

Surprisingly, combined water-stressed treatments had the highest above soil biomass. Undefoliated, water-stressed groups produced more top growth than any of the other treated groups. Visually, the differences between water-stressed and well-watered seedlings were prominent; well-watered seedlings were a mass of foliage, lush green, and visually appeared to have more above soil biomass. Conversely, the water-stressed groups appeared to have sparse foliage, short internodes and an unthrifty color and appearance. Results of the shoot biomass analysis were

unexpected. These results perhaps may be explained by a theory proposed by Whitmore and Zahner (1966). The theory proposes that periodic water stress is needed for wood formation. The theory is based on the evidence that when water stress is low and mother cells are actively producing new derivatives, little secondary cell wall thickening occurs. During periods of water stress, the zones of mother cell activity are reduced and existing cells have less competition for phloem substrates and considerable wall thickening takes place. Thus, experimental seedlings in the undefoliated, water-stressed groups may have been producing denser, heavier plant tissue verses the actively growing, and foliage producing activities of well-watered groups.

The net effect of water stress on secondary wall thickening in a tree growing under field conditions apparently varies considerably. Under moderate environmental water deficit, in which the rate of new cell production is merely slowed and derivatives are permitted a long life span, many exceptionally thick-walled xylem cells may be formed in the annual ring. At the extreme, under severe water stress which essentially stops production of derivatives by mother cells and also strongly reduces wall assimilation, the final ring may contain only a few moderately thick-walled cells (Zahner 1968).

The experimental groups with the highest successful A. ostoyae colonization also produced the largest root biomass. It seems unlikely, however, that a larger root system would increase the susceptibility of the seedling in a pot test such as this one. Although an abundant root system would enhance the points of contact

with the inoculum source, this hypothesis would be more reasonable under field conditions. My observations were that the soil of most pots of all treatment groups had been thoroughly occupied by seedling root systems. Yet, the possibility exists that larger root biomass was a factor in increased infection and mortality by A. ostoyae.

Plant Moisture Status

Water-stressed and inoculated seedlings, which had the highest level of Amillaria-caused mortality, also exhibited the highest levels of measured water stress. Feiler et al. 1992 report Armillaria-infected spruce showed increased osmotic potential and reduced water content compared to non-infected controls. Presumably, the low PMS readings associated in this treatment group, even in the absence of symptomatic tops, indicated that the root systems were already colonized by the fungus and disease had began to interrupt the water relations of the whole plant.

Defoliation, because it reduced transpiration, was found to significantly raise the Plant Moisture Status. The new foliage is the foliage tissue with the highest transpiration rate. Once the new tissue is removed, the older tissue has stomata that are more efficient at controlling water loss than younger tissue. Seedlings in the defoliated treatments started out with a water status pattern similar to that of the water-stressed control seedlings; a few days after insects were applied, this pattern began to shift to one that more closely resembled the well-watered controls. Even when the pot soil was extremely dry, the defoliated seedlings maintained a PMS

reading close to that of well-watered controls. It is likely that defoliation-caused reduction in plant moisture stress is involved in the abatement of successful A. ostoyae infection and mortality of defoliated, water-stressed seedlings. Defoliated seedlings, even when in a dry soil environment, did not develop high negative plant moisture readings and the associated changes in root biochemical factors (e.g., low starch) expressed by water-stressed, undefoliated seedlings.

If this experiment can be extended to mature trees, the PMS results suggest that Abies grandis is well adapted to dry summers. In my attempts to apply and monitor water stress during the experimental periods, I observed that water stress was regularly obtained in shorter intervals (i.e., mean 8 days) after water additions to seedlings early in the experimental period, during bud flush. When the new foliage was a few weeks older, or in some groups consumed by budworm, all groups of experimental seedlings could exist in dry soil and not show the steady, rapid increase in plant moisture stress that they did earlier in the experiment. This suggests that in field conditions the timing of drought is critical. Late spring and early summer drought may affect the physiological condition of the forest component of grand fir more severely than extreme late summer and fall drought which may have little or no effect. The pattern of high moisture early in the spring and summer, and little or no moisture later in the growing season is a pattern that accompanies grand fir throughout much of its range. An aberration of this pattern is not historically common, but has been known to occur. Infrequent dry springs may favor the biochemical and perhaps physical host conditions needed by western

spruce budworm and A. ostoyae for rapid growth and development, thus enhancing their impact on the grand fir and subsequently grand fir's other ecosystem associates.

Experimental Design Limitations

It goes without saying that any conclusions that are drawn from this study are limited by the circumstances of the experimentation process. First of all, the experimental unit was a group of nine seedlings; replication was small in Group I and lacking in Group II. Although I project the results to field conditions and infer relationships that include mature trees, these projections are made from seedlings grown in artificial conditions and may not be valid under other circumstances. Likewise, the use of lab-reared insects, artificial inoculum, and commercial potting soil could each impose impact to the results. Many opportunities for unknown systematic error are available for an experiment that studies the relationship of three living organisms, each classified in a separate kingdom, and each with a unique but overlapping natural history.

Future Research

The results and implications of these experiments need to be field validated. Fruitful additional areas of study may include:

1) Investigations of the relationship of stress-induced changes in total N and how this relates to important amino acids; Cyr et al., (1990) found amino acids to "pool" in roots of three water-stressed conifers.

2) To ascertain the effect of early flushing on western spruce budworm population dynamics. Early flushing may be important as Campbell (1989) found that spruce budworm fed on earlier flushing trees grew 20 percent larger than budworm on late flushing trees. Careful correlation of site meteorological and phenological data with budworm populations may determine if early-dry springs, verses wet-late springs affect budworm fitness.

Information available from past studies of the impact of stress on plants and their consumers is fraught with contradictory results. This is, in part, due to varying methods used to experimentally induce stress. Mechanisms of experimentally inducing water stress, such as root trenching, xylem girdling, or with the osmotic agent polyethylene glycol, are still being used despite strong evidence to suggest that they alter plant metabolic processes in ways that do not emulate natural water stress.

Likewise, studies to assess the effects of defoliation have included methods such as removing the upper half of the seedling or tree (to measure "50 percent

defoliation" effects) and other easily quantified but unrealistic methods of simulating insect defoliation.

The design of a study can have a strong influence on the results in stress research. Levels of stress, as well as timing and duration, influence herbivores and pathogen responses to stress. Any future research in this area of study should incorporate keen observation of organism response, as well as experimentally sound, but nature-mimicking methods of producing plant stress. A better understanding of the details of naturally induced water stress will improve our understanding of its effects on herbivore-plant-pathogen interactions.

Implications for Forest Management

The interrelationships of the three organisms depicted in this work serve as illustration of the interwoven character of the ecosystems that contemporary land managers are commissioned to administer.

Drought may benefit the defoliator by producing more nutritious host foliage. The defoliator, in turn, may benefit the tree (at least in the short term) by alleviating water stress and thereby enhancing tree fitness by increasing reserve carbohydrates and vegetative buds.

Defoliation during drought may benefit the stand (on a long term basis) by reducing the uptake of nutrients and water by budworm hosts, thereby, liberating them to be used by non-hosts that are perhaps better adapted to periodic drought conditions. Since non-hosts of budworm (e.g., ponderosa pine or larch) use less

water per unit biomass than budworm hosts (e.g., grand fir and Douglas-fir), excess water is then available to replenish drought impacted soils and then eventually available to stream flows. Stream flow studies have shown a higher rate of water yield in defoliated stands than in nondefoliated stands (Helvey and Tiedemann 1978). In an era where land managers are also concerned about managing for anadromous fish and other riparian dwellers, water yield becomes a critical issue.

Depending on the severity and duration of defoliation, insecticidal spray programs aimed at "saving foliage" may actually increase the risk of tree death in the stand. Saving foliage by eliminating defoliators on drought-stressed stands may reduce tree vigor by increasing water stress and thereby enhancing colonization by endemic A. ostoyae, bark beetles and secondary pathogens.

As land managers maneuver towards developing risk ratings systems for Interior West stands, overstocked and drought prone stands may be a primary assessment factor in determining risk of impact by western spruce budworm and Armillaria. Research results from this study suggest, however, that the additive impact due to the co-association of budworm and Armillaria on Interior West conifer stands may not be as severe as conventionally believed.

Regarding long-term management, it is possible that there is a selective advantage for the stand community for overcrowded trees growing on water and nutrient limited sites to be more palatable to their adapted consumers.

Throughout the Interior West, fire suppression has produced large landscapes of highly susceptible budworm and Armillaria hosts; drought, caused by a decade of

low precipitation and by overstocking, has increased the host's suitability to these consumers. In the absence of fire, both budworm and Armillaria function as primary regulators, largely by thinning and increasing plant diversity, and thereby bring stability to the system.

REFERENCES

Ahmad, I.; Larher, F.F.; Stewart, G.R. 1979. Sorbitol, a compatible osmotic solute in Plantago maritima. New Phytol. 82: 671-678.

Akeson, W.R.; Gorz, H.J.; Haskins, F.A. 1970. Sweetclover weevil feeding stimulants: Variations in levels of glucose, fructose, and sucrose in Melilotus leaves. Crop Science 10: 477-479.

Albert, P.J.; Jerrett, P.A. 1981. Feeding preferences of spruce budworm (Choristoneura fumiferana Clem.) larvae to some host-plant chemicals. J. Chem. Ecol. 7: 391-401.

Albert, P.J.; Cearley, C.; Hanson, F.; Parisella, S. 1982. Feeding responses of eastern spruce budworm larvae to sucrose and other carbohydrates. J. Chem Ecol. 8: 233-239.

Alfaro, R. I.; VanSickle, G. A.; Thomson, A. J.; Wegwitz, E. 1982. Tree mortality and radial growth losses caused by the western spruce budworm in a Douglas-fir stand in British Columbia. Canadian Journal of Forest Research. 12(4):780-787;1982.

Baker, W.L. 1941. Effect of gypsy moth defoliation on certain forest trees. J. of For. 39: 1017-1022.

Bednar, Larry. 1993. Personal communications. Portland Forestry Sciences Laboratory, 1221 S. W. Yamhill Street, Suite 200, Portland Or 97208.

Begg, J.E.; Turner, N.C. 1976. Crop water deficits. Adv. Agron. 28: 161-217.

Bently, M.D.; Leonard, D.E.; Leach, S.; Reynolds, E.; Stoddard, W.; Tomkinson, B.; Tomkinson, D.; Strunz, G., and Yatagai, M. 1982. Effect of some naturally occurring chemicals and extracts of non-host plants on feeding by spruce budworm larvae, Chroristoneura fumiferana. Maine Agric. Exp. Stn., Tech. Bull. 107.

Bier, J.D. 1959. The relation of bark moisture to the development of canker diseases caused by native facultative parasites. II. Fusarium canker on black cottonwood. Can. J. Bot. 37: 229-38.

Bjorkman, Christer; Larsson, Stig; Gref, Rolf. 1991. Effects of nitrogen fertilization on pine needle chemistry and sawfly performance. Oecologia. 86: 202-209.

Bloom, A.J.; Chapin, F.S.; Mooney, H.J. 1985. Resource limitations in plants--an economic analogy. Annual Review of Ecology and Systematics. 16: 363-392.

Bloomberg, W.J. 1962. Cytospora canker of poplars: Factors influencing the development of the disease. Can. J. Bot. 40: 1271-1280.

Boddy, L. 1983. Effect of temperature and water potential on growth rate of wood-rotting basidiomycetes. Trans. Br. Mycol. Soc. 80(1): 141-149.

Borger, G.A.; Kozlowski, T.T. 1972. Effects of water deficits on first periderm and xylem development in Fraxinus pennsylvanica. Can J. For. Res. 2: 144-151.

Bradford, K.J.; Hsiao, T.C. 1982. Physiological responses to moderate water stress. In: Lange, O.L.; Nobel, P.S.; Osmond, C.B.; Ziegler, H. eds. Physiological Plant Ecology II, Water Relations and Carbon Assimilation. 263-324. In: Pirson, A.; Aimmermann, M.H. ed. Encyclopedia of Plant Physiology, New Series. Berlin, Heidelberg, New York: Springer-Verlag: Vol. 12B.

Bremner, H.M.; Mulvaney, C.S. 1982. Nitrogen--Total. In: Page, P.A.; Miller, R.H.; Keeney, D.R. eds., Methods of Soil Analysis Part 2. Chemical and Microbial Properties, Second Edition. American Society of Agronomy Inc., Madison, Wisconsin.

Brookes, M.H.; R.W. Campbell; J.J. Colbert; R.G. Mitchell, and R.W. Stark, Tech. Coords. 1987. Western spruce budworm. USDA Forest Service, Coop. State Res. Serv. Tech. Bull. No. 1694. Washington, D.C. 198 pp.

Campbell, I.M. 1989. Does climate affect host-plant quality? Annual variation in the quality of balsam fir as food for spruce budworm. Oecologia. 81: 341-344.

Campbell, Robert W.; Torgersen, Torolf R.; Hosman, Kevin P.; Srivastava, Nilima. 1983. Sex Ratios of the Western Spruce Budworm (Lepidoptera:Tortricidae). Can. Ent. 115: 1059-1063.

Carlson, C.E. 1989. Influence of habitat types on forest pests of the northern forest pests of the northern Rocky Mountains. In: Proceedings--Land classifications based on vegetation: applications for resource management; November 17-19, 1987, Moscow, ID; U.S. Department of Agriculture, Forest Service, Intermountain Research Station GTR-INT-257; Ogden, UT; pp. 186-192.

Cates, R.G.; Redak, R.; Henderson, C.B. 1983a. Natural product defensive chemistry of Douglas-fir, western spruce budworm success, and forest management practices. Z. Ang. Ent. 96: 173-182.

Cates, R.G.; Redak, R.; Henderson, C.B. 1983b. Patterns in defensive natural product chemistry: Douglas-fir and western spruce budworm interactions: 3-19. In: Hedin, P.A. ed., Plant Resistance to Insects. Amer. Chem. Soc., Wash., D.C.

Cates, R.G.; Redak, R.A. 1988. Variation in the terpene chemistry of Douglas-fir and its relationship to western spruce budworm success. In: Spencer, K.C., ed. Chemical Mediation of Coevelution: San Diego, CA. Acad. Press: 317-344.

Chapin, F. Stuart III. 1991. Integrated responses of plants to stress: A centralized system of physiological responses. Bio Science. 41 (1): 29-36.

Cheo, P.C. 1982. Effects of tannic acid on rhizomorph production by Armillaria mellea. Phytopathology. 72: 676- 679.

Clancy, K.M.; Wagner, M.R.; Tinus, R.W. 1988. Variations in nutrient levels as a defense: Identifying key nutritional traits of host plants of the western spruce budworm, p. 203-213. In: Mattson, W.J.; Levieux, J.; and Bernard-Dagan, C., eds. Mechanisms of Woody Plant Defenses Against Insects: Search for Pattern. New York: Springer-Verlag. 416 p.

Clancy, Karen M.; Itami, Joanne K.; Huebner, Daniel P. 1993. Douglas-fir nutrients and terpenes: potential resistance factors to western spruce budworm defoliation. Forest Science 39(1): 78-94.

Cleary, B.D.; Zaerr, J.B. 1980. Pressure chamber techniques for monitoring and evaluating seedling water status. New Zealand Journal of Forestry Science. 10(1): 133-141

Cobbinah, J. R.; Morgan, F.D.; Douglas, T.J. 1982. Feeding responses of the gum leaf skeletonizer Uraba lugens (Walter) to sugars, amino acids, lipids, sterols, salts, vitamins and cerain extracts of eucalyptus leaves. J. Aust. Entomol. Soc. 21: 225-236.

Cochran, P.H. 1979. Gross yields for even-aged stands of Douglas-fir and white or grand fir east of the Cascades in Oregon and Washington. Gen. Tech. Rep. PNW-263. Portland, OR: US Department of Agriculture, Forest Service, Pacific Northwest Research Station. 17 p.

Cochran, William G.; Cox, Gertrude M. [1957]. Experimental Designs, second edition. New York: Wiley. 611 p. Cook, A.G. 1977. Nutrient chemicals as phagostimulants for Locusta migratoria (L.). Ecol. Entomol. 2: 113-121.

Cook, J.L.; Houseweart, M.W.; Kulman, H.M.; and Thompson, L.C. 1979. Foliar mineral differences related to sawfly defoliation of white spruce. Environ. Entomol. 7: 780-781.

Crist, C.R.; Schoeneneiss, D.F. 1975. The influence of controlled stresses on the susceptibility of European white birch stems to attack by Botryosphaeria dothidea. Phytopathology. 65: 369-73.

Cyr, D.R.; Buxton, G.F.; Webb, D.P. Dumbroff, E.B. 1990. Accumulation of free amino acids in the shoots and roots of three northern conifers during drought. Tree Physiology. 6: 293-303.

Cuddy, P. 1982. Defoliation and conifer physiology, growth, and survival. Logan, UT: Utah State University; 61 p. M.F. thesis.

Dina, S.J.; Klikoff, L.G. 1973. Effect of plant moisture stress on carbohydrate and nitrogen content of big sagebrush. J. Range Manag. 26: 207-209.

Dunbar, D.M.; Stephens, G.R. 1975. Association of two-lined chestnut borer and shoestring fungus with mortality of defoliated oaks in Connecticut. For. Sci. 21(2): 169-174.

Eaton, F.M.; Ergle, D.R. 1948. Carbohydrate accumulation in the cotton plant at low moisture levels. Plant Physiol. 23: 169-187.

Ehrlich, J. 1939. A preliminary study of root diseases in western white pine. Sta. Pap. No. 1. Missoula, MT: U.S. Department of Agriculture, Forest Service, Northern Rocky Mountain Forest and Range Experiment Station. 10 p.

Entry, J.A.; Cromack, K. Jr. 1989. Phenolic compounds inhibit Armillaria growth in vitro. In: Proceedings of the Seventh International Conference on Root and Butt rots of Forest Trees. D.J. Morrison, ed.; Vernon and Victoria B. C. Canada. 1988 August 9-16: 632-640 p.

Entry, J.A.; Cromack, K., Jr.; Hansen, E.; Waring, R.H. 1991. Response of western coniferous seedlings to infection by Armillaria ostoyae under limited light and nitrogen. Phyt. pathology. 81: 89-94.

Entry, J.A.; Martin, N.E.; Cromack, K., Jr.; (and others). 1986. Light and nutrient limitation in Pinus monticola: seedling susceptibility to Armillaria infection. Forest Ecology and Management. 17: 189-198.

Feeny, P. 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. Ecology 51: 565-581.

Feiler, Von Sonja; Tesche, M.; Zentsch, W.; Schmidt, P.A.; Bellman, Christa. 1992. Untersuchungen zum Wasserhaushalt der Fichte bei Befall durch Armillaria spp. Eur. J. For. Path. 22: 329-336. Parey, V.P., Hamburg and Berlin. ISSN; 0300-1237. (ABSTRACT)

Filip, G.M.; Schmitt, C.L.; Hosman, K.P. 1992. Effects of harvest season and stump size on incidence of Annosus root disease of true fir. Western Journal of Applied Forestry. 7(2): 54-57.

Filip, G.M.; 1989. Interactions among root diseases and agents of defoliation. In: Morrison, D.J., ed.; Proceedings of the 7th International Conference on Root and Butt Rots; 1988 August 9-16; Vernon and Victoria, B.C; International Union of Forestry Research Organizations. 149-155.

Filip, G.M.; Goheen, D.J. 1984. Root diseases cause severe mortality in white and grand fir stands of the Pacific Northwest. For. Sci. 30: 138-142.

Foiles, Marvin W. 1965. Grand fir, Abies grandis (Dougl.) Lindl. In: Silvics of forest trees of the United States. p. 19-24. Fowells, H.A.; US Department of Agriculture, Agriculture Handbook 271. Washington, DC.

Foiles, M.W.; Graham, R.T.; Olsen, D.F., Jr. 1990. Grand fir, Abies grandis (Dougl. ex D. don) Lindl. In: Burns, R.M. and Honkala, B.H., eds. Silvics of North America. Vol 1, Conifers. US Department of Agriculture, Agricultural Handbook 654. Washington, DC. 52-59 p.

Garraway, M.O. 1970. Rhizomorph initiation and growth in Armillaria mellea promoted by o-aminobenzoic and p-aminobenzoic acids. Phytopathology. 60: 861-865.

Garraway, M.O. 1975. Stimulation of Armillaria mellea growth by plant hormones in relation to the concentration and type of carbohydrate. European Journal of Forest Pathology. 5: 35-43.

Garraway, M.; Hütterman A.; Wargo, P. 1991. Ontogeny and Physiology. In: Shaw, C.G.; Kile, G.A., eds., Armillaria Root Disease. Handbook No. 691. Washington, D.C.: U.S. Department of Agriculture: 21-46.

Garrett, S.D. 1956. Rhizomorph behavior in Armillaria mellea (Vahl) Quel., II. Logistics of infection. Annals of Botany. 20: 193-209.

Gershenzon, J. 1984. Changes in the levels of plant secondary metabolites under water and nutrient stress. Recent Adv. Phyochem. 18: 273-320.

Gershenzon, J.; Lincoln, D.E.; Langenheim, J.H. 1978. The effect of moisture stress on monoterpenoid yield and composition in Satureja douglassii. Biochem. Syst. Ecol. 6: 33-34.

Graham, S.A. 1939. Forest insect populations. Ecol. Monogr. 9: 301-310.

Greenbank, D.O. 1956. The role of climate and dispersal in the initiation of spruce budworm in New Brunswick. I. The role of climate. Can J. Zool. 34: 453-456.

Greenbank, D.O. 1963. Climate and the spruce budworm. Mem. Entomol. Soc. Can. 31: 174-180.

Grimalsky, V.I. 1961. The causes of the resistance of pine stands to needle-eating pests. Zool. Zh. 40: 1656-1664.

Haack, R.A.; Slansky, F. Jr. 1987. Nutritional ecology of wood-feeding Coleoptera, Lepidoptera, and Hymenoptera. In: Slansky, F. Jr., Rodriguez, J.G., eds. Nutritional Ecology of Insects, Mites, and Spiders. New York: Wiley: 449-486.

Hagen, R.H.; Chabot, J.F. 1986. Leaf anatomy of maples (Acer) and host use by Lepidoptera larvae. Oikos. 47: 335-345.

Haig, Irvine T. 1932. Second-growth yield, stand, and volume tables for the western white pine type. Tech. Bull. 323. Washington, DC.: U.S. Department of Agriculture: 68 p.

Hanson, K.R.; Havir, E.A. 1981. Phenylalanine ammonia-layase. In: Conn, E.E., ed. The Biochemistry of Plants vol. 7. Secondary Plant Products. New York: Academic Press, Inc. 575-626.

Hard, J.; Tunnock, S.; Eder, R. 1980. Western spruce budworm defoliation trend relative to weather in the northern region, 1969-1979. U.S. Department of Agriculture, Forest Service, Northeast Region, State and Private Forestry.

Hardy, Y.; Lafond, A.; Hamel, A. 1983. Epidemiology of the current spruce budworm outbreak in Quebec. Forest Science. 29: 715-725.

Hartly, S.D. 1988. The inhibition of phenolic biosynthesis in damaged and undamaged birch foliage and its effect on insect herbivores. Oecologia. Berlin 76: 65-70.

Harvey, G.T. 1974. Nutritional studies of eastern spruce budworm (Lepidoptera: Tortricidae) I. Soluable sugars. Can. Entomol. 106(4): 353-366.

Harvey, G.T. 1975. Nutritional studies of eastern spruce budworm (Lepidoptera:Tortricidae) II. Starches. Can. Entomol. 107: 717-728.

Haukioja, E.; Niemela, P. 1979. Birch leaves as a resource for herbivory: Seasonal occurrence of increased resistance in foliage after mechanical damage of adjacent leaves. Oecologia. 39: 157-159.

Helvey, J.D.; Tiedemann, A.R. 1978. Effects of defoliation by Douglas-fir tussock moth on timing and quantity of streamflow. Research Note PNW-326. Portland, OR: U.S. Department of Agriculture, Forest Service: 13 p.

Heron, R.J. 1965. The role of chemotactic stimuli in the feeding behavior of spruce budworm larva of white spruce. Can. J. Zool. 43: 247-269.

House, H.L. 1974. Nutrition. In: Physiology of Insecta. Rockstein, ed. New York: Academic Press, Inc. 1-62.

Houston, D.R. 1981. Some dieback and decline diseases of northeastern forest trees: forest management considerations. In: Proceedings of the annual silviculture workshop; 1981 1-5 June; Roanoke, VA. Washington, DC: U.S. Department of Agriculture, Forest Service: 248-265 p.

Houston, D.R.; Kuntz, J.E. 1964. Studies of the maple blight. Part III. Pathogens associated with maple blight. University of Wisconsin Res. Bull. 250: 59-79.

Hsiao, T.C. 1973. Plant responses to water stress. Ann. Rev. Plant Physiol. 24: 519-570.

Hsiao, T.C.; Acevedo, E.; Fereres, E.; Henderson, D.W. 1976. Stress metabolism. Water stress, growth, and osmotic adjustment. Philos. Trans. R. Soc. London, Ser.B 273, 479-500.

Huang, P.; Fuhrer, E. 1979. As to food quality of spruce needles for forest damaging insects. 12. Variation in epidermis and hypodermis structure. Z. Ang. Ent. 88: 231-245.

Jackson, M.L. 1958. Soil Chemical Analysis. Englewood Cliffs, N.J.: Prentice Hall. 158 p.

Jennings, D.T.; Crawford, H.S. 1984. Effects of bird predation on spruce budworm: a pilot study. In: Recent Advances in Spruce Budworm Research: Proceedings of CANUSA Spruce Budworm Research Symposium. Bangor, Maine. Sept. 16-20, Ottawa, Ontario: CANUSA. 98-99 p.

Jennings, Daniel T.; Houseweart, Mark W. 1978. Sexing spruce budworm pupae. Forest Service Research Note NE-255. Broomall, PA: U.S. Department of Agriculture.

Josyln, Mayard. 1970. Methods in Food Analysis: Physical, chemical and instrumental methods in analysis. 2nd ed. New York: Academic Press, Inc. 845 p.

Karasevicz, D.; Merrill, W. 1986. Succession of biodeterioration fungi in oaks killed following gypsy moth defoliation in Pennsylvania. Annual Meeting of the American Phytopathological Society, Potomac Division, 1986 2-4, April. Phytopathology. 76(5): 564.

Kegg, J.D. 1971. The impact of gypsy moth: repeated defoliation of oak in New Jersey. Journal of Forestry. 69: 852-854.

Kegg, J.D. 1973. Oak mortality caused by repeated gypsy moth defoliation of oak in New Jersey. Journal of Economic Entomology. 66: 639-641.

Kemp, William P.; Everson, Dale O.; Wellington, W.G. 1985. Regional Climatic Patterns and Western Spruce Budworm Outbreaks. Tech. Bull. 1693. Washington, DC: U.S. Department of Agriculture, Forest Service, Canada/United States Spruce Budworms Program: 31 p.

Kemp, W.P.; Moody, V.L. 1984. Relationships between regional soils and foliage characteristics and western spruce budworm (Lepidoptera:Tortricidae) outbreak frequency. Environmental Entomology. 13: 1291-1297.

Kolomiets, N.G.; Stadnitskii, G.V.; Vorontzov, A.I. 1979. The European Pine Sawfly. New Delhi: Amerind Publ. Co., Pvt. Ltd., (U.S. Dep. Comm. Note, Tech. Inf. Serv., Springfield, Virginia).

Kozlowski, Theodore T.; Kramer, Paul J.; Pallardy, Stephen G. 1991. The Physiological Ecology of Woody Plants. San Diego, Ca.: Academic Press, Inc. 657 p.

Kramer, P.J., 1983. Water Relations of Plants. New York: Academic Press.

Landis, W.R.; Hart, J.H. 1967. Cankers of ornamental crabapples associated with Physalospora obtusa and other microorganisms. Plant Dis. Reptr. 51: 230-34.

Larson, S.; Tenow, O. 1984. Areal distribution of a Neodiprion sertifer (Hymenoptera:Diprionidae) outbreak on Scots pine as related to stand conditions. Holarctic Ecol. 7: 81-90.

Lawrence, Robert Kent, 1990. Phenological variation in the susceptibility of White Spruce to the spruce budworm. Lansing, MI: Michigan State University, Ph.D. dissertation. 133 p.

Lindberg, M.; Johansson, M. 1992. Resistance of Picea abies seedlings to infection by Heterobasidion annosum in relation to drought stress. Eur. J. For. Path. 22: 115-124.

Ma, W.C. 1977. Electrophysiological evidence for chemosensitivity to adenosine, adenine and sugars in Spodoptera exempta and related species. Experientia 33:356-358.

Martinat, P.J. 1987. The role of climatic variation and weather in forest insect outbreaks. In: Barbosa, P.; Schultz, J.C. eds. Insect Outbreaks. New York: Academic Press, Inc.: 241-268.

Mason, R.R.; Tigner, T.C. 1972. Forest-site relationships within an outbreak of lodgepole needle miner in central Oregon. Research Paper PNW-146. Portland OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.

Mattson, W.J. 1980. Herbivory in relation to plant nitrogen content. Ann. Rev. Ecol. Syst. 11: 119-161.

Mattson, W.J.; Addy, N.D. 1975. Phytophagous insects as regulators of forest primary production. Science 190: 515-522.

Mattson, W.J.; Haack, R.A. 1987a. Role of drought stress in provoking outbreaks. In: Barbosa, P.; Schultz, J.C., eds. Insect Outbreaks. New York: Academic Press, Inc.: 365-407.

Mattson, W.J.; Haack, R.A. 1987b. The role of drought in outbreaks of plant-eating insects. BioScience. 37: 110-118.

Mattson, W.J.; Scriber, J.M. 1987. Nutritional ecology of insect folivores of woody plants: Nitrogen, water, fiber, and mineral considerations. In: Slansky, F. Jr.; Rodriguez, J.G. eds., Nutritional Ecology of Insects, Mites, Spiders, and Related Invertebrates. New York: John Wiley & Sons. 105-146 p.

Mattson, W.J.; Slocum, S.S.; Koller, C.N. 1983. Spruce budworm (Choristorneura fumiferana) performance in relation to foliar chemistry of its host plants. In: Talerico, R.L.; Montgomery, M. eds. Forest Defoliator -- Host Interactions: A Comparison Between Gypsy Moth and Spruce Budworms. General Technical Report NE-85. U.S. Department of Agriculture, Forest Service. 55-65 p.

McDonald, G.E.; Martin, N.E.; Harvey, A.E. 1988. Occurrence of Armillaria spp. in forests of the Northern Rocky Mountains. USDA Intermountain Research Paper, INT. 385. Intermountain Forest and Research Experiment Station. Moscow, ID 83843.

Miller, C.A. 1957. A technique for estimating the fecundity of natural populations of the spruce budworm. Can. J. Zool. 35: 1-13.

Miller, C.A. 1977. The feeding impact of spruce budworm on balsam fir. Can. J. For. Research. 7(1): 76-84.

Mooney, H.A.; Chu, C. 1974. Seasonal allocation in Heteromeles arbutifolia, a California evergreen shrub. Oecologia. 14: 295-306.

Mooney, H.A.; Gulmon, S.L; Johnson, N.D. 1983. Physiological constraints on plant chemical defenses. In: Hedin, P. ed., Plant Resistance to Insects. American Chemical Society Symposium Series 208. Washington, D.C.: American Chemical Society: 21-36.

Morrison, D.J. 1981. Armillaria root disease: A guide to disease diagnosis, development and management in British Columbia. Can. For. Serv./Pac. For. Res. Ctr. Victoria, B.C. BC-X-203. 15 pp.

Morrison, D.J. 1991. Identity of Armillari isolates used in studies of Rhizomorph behavior and pathogenicity. Mycological Research 95; pp. 1437-1438.

Muzika, R.M. 1989. Carbon allocation and secondary metabolites in Abies grandis as influenced by nitrogen fertilization and seed source. Lansing, MI: Michigan State University. 153 p. Ph.D. dissertation.

Muzika, Rose-Marie; Engle, Judith; Parks, Catherine; Wickman, Boyd. 1993. Variation in phenology and monoterpene patterns of defoliated and nondefoliated Douglas-fir (Pseudotsuga menziesii var. glauca). Res. Pap. PNW-RP-459. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 10 p.

Nylund, J. 1988. The regulation of mycorrhiza formation--carbohydrate and hormone theories reviewed. Scand. J. For. Res. 3: 465-479.

Otto, D. 1970. Zur Bedeutung des Zuckergehaltes der Nahrung für die Entwicklung nadelfressender Dieferninskten. Arch. Forstwes. 19: 135-150. (ABSTRACT)

Ouellet, M.J.; Lailamme, M.; Perron, J.M. 1983. Effects des sucres sur le comportement alimentaire de Lambdina fiscellaria. Entomol. Exp. Appl. 34: 139-142. (ABSTRACT)

Parker, J. 1970. Effects of defoliation and drought on root food reserves in sugar maple seedlings. Res. Pap. NE-169. Broomall, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 8 p.

Parker, J.; Houston, D.R. 1971. Effects of repeated defoliation on root and root collar extractives of sugar maple trees. Forest Science. 7: 91-95.

Parker, J.; Patton, R.L. 1975. Effects of defoliation and root height above a water table on some red oak root metabolites. J. Am. Soc. Hortic. Sci. 104: 417-421.

Pfister, Robert D.; Kovalchik, Bernard L.; Arno, Stephen F.; Presby, Richard C. 1977. Forest habitat types of Montana. General Technical Report INT-34. Ogden, UT: U.S. Department of Agriculture. Forest Service, Intermountain Forest and Range Experiment Station. 174 p.

Pilon, P.G.; Blais, J.R. 1961. Weather and outbreaks of the spruce budworm in the province of Quebec from 1939 to 1956, Can. Entomol. 93: 118-123.

Pitman, M.G. 1981. Ion uptake. In: Paleg, L.G.; Aspinall, D. eds., Physiology and Biochemistry of Drought Resistance in Plants. New York: Academic Press, Inc. 71-96.

Prestidge, P.A.; McNeill, S. 1983. The importance of nitrogen in the ecology of grassland Auchenorrhyncha. Symp Brit. Ecol. Soc. 22: 257-281.

Puritch, G.S.; Mullick, D.G. 1975. Effect of water stress on the rate of non-suberized impervious tissue formation following wounding in Abies grandis. J. Exp. Bot. 26: 903-910.

Raske, A.G.; Sutton, W.J. 1986. Decline and mortality of black spruce caused by spruce budworm defoliation and secondary organisms. Inf. Rep. N-X-236, Newfoundland Forestry Centre, Canadian Forestry Centre. p. 29.

Redfern, D. B. 1970. The ecology of Armillaria mellea: Rhizomorph growth through soil. In: Toussoun, T.A.; Bega, R.V.; Nelson, P.E., eds. Root diseases and soil-borne pathogens: Proceedings of the symposium; 1968 July, London: Imperial College. Berkeley: University of California Press: 147-149.

Redfern, D.B.; Filip, G.M. 1991. Inoculum and infection. In: Shaw, C.G.; Kile, G.A., eds., Armillaria Root Disease. Handbook No. 691. Washington, D.C.: U.S. Department of Agriculture: 48-60.

Rhoades, D.F. 1979. Evolution of plant chemical defense against herbivores. In: G.A. Rosenthal and D. H. Janzen, eds., Herbivores: Their interaction with secondary plant metabolites. New York: Academic Press, Inc.: 3-4 p.

Richards, B.N.; Wilson, G.L. 1963. Nutrient supply and mycorrhiza development in Caribbean pine. Forest Science 9: 405-412.

Risbeth, J. 1978. Effects of soil temperature and atmosphere on growth of Armillaria rhizomorphs. Transactions of the British Ecological Society. 70: 213-220.

Ritter, G.; Pontor, G. 1969. Root development of young Scots pine as a factor in resistance to attack by Armillaria mellea. Archiv für Forstwesen. 18: 1037-1042.

Rose, R.; Rose, C.L.; Omi, S.K.; Forry, K.R.; Durrall, D.M.; Bigg, W.L. 1991. Starch determination by perchloric acid vs enzymes: evaluating the accuracy and precision of six colorimetric methods. J. Agric. Food Chem. 39(1): 2-11.

Ross, Darrell W.; Berisford, C. Wayne. 1990. Nantucket pine tip moth response to water and nutrient status of Loblolly pine. Forest Science, 36(3): 719-733.

Rykowski, K. 1976. Recherche sur la nutrition azotée de plusieurs souches de l'Armillaria mellea I. L'influence de différentes concentrations du carbone et de l'azote (C:N). European Journal of Forest Pathology. 6: 264-274. (ABSTRACT)

Rykowski, K. 1984. Niektóre troficzne unwarunkowania patogeniczności Armillaria mellea (Vahl) Quél. W uprawach sosnowych. Prace Instytutu Badawczego Leśnictwa. 640: 1-140. (ABSTRACT)

Salisbury, F.B.; Marinos, N.G. 1985. The ecological role of plant growth substances. In: Pharis, R.P.; Reid, D.M. eds., Enclyclopedia of Plant Physiology. vol. 11. New York: Springer-Verlag.

Salisbury, F.B.; Ross, C.W. 1985. Plant Physiology. third edition. Belmont, California: Wadsworth Publishing Company.

SAS Institute, Inc. 1982. SAS User's Guide to Statistics. Cary, N.C.: SAS Institute, Inc.

Saunier, R.E.; Hull, H.M.; Ehrenreich, J.H. 1968. Aspects of the drought tolerance in creosotebush (Larrea divaricata). Plant Physiol. 43: 401-404.

Schoeneweiss, Donald F. 1975. Predisposition, stress, and plant disease. Ann. Rev. Phytopathol. 13: 193-211.

Schoeneweiss, Donald F. 1981. The role of environmental stress in diseases of woody plants. Plant Disease. 4: 308-314.

Schoeneweiss, Donald F. 1983. Drought predisposition to Cytospora canker in blue spruce. Plant Disease. 67: 383-385.

Scriber, J.M. 1984. Host plant suitability. In: Bell, W.J.; Carde, R.T. eds., Chemical Ecology of Insects. Sunderland, Massachusetts: Sinauer Assoc.: 159-202.

Secrest, H.C.; MacAloney, J.; Lorenz, R.C. 1941. Causes of the decadence of hemlock at the Menominee Indian Reservation, Wisconsin. Journal of Forestry. 31: 3-12.

Shaw, C.G. III. 1975. Epidemiological insights into Armillaria mellea root rot in a managed ponderosa pine forest. Corvallis, OR: Oregon State University. 201 p. Ph.D. dissertation.

Shaw, C.G. III. 1977. Armillaria isolates for pine and hardwoods differ in pathogenicity to pine seedlings. Plant Disease Reporter. 61: 416-418.

Shaw, C.G. III. 1980. Characteristics of Armillaria mellea on pine root systems in expanding centers of root rot. NW Science. 54: 137-145.

Shaw, C.G., III. 1985. In vitro responses of different Armillaria taxa to gallic acid, tannic acid, and ethanol. Plant Pathology. 34: 594-602.

Shepherd, Roy F. 1983. A techique to study phenological interactions between Douglas-fir and emerging second instar western spruce budworm. In: Talerico, Robert L.; Montgomery, Michael, eds. Proceedings of the 1983, Forest defoliator host interactions: a comparison between gypsy moth and spruce budworm: Proceedings of a symposium; 1983 April 5-7; New Haven, CT. Gen. Tech. Rep. NE-85. Radnor PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest and Range Experiment Station: 17-20.

Shields, W.J., Jr.; Hobbs, S.D. 1979. Soil nutrient levels and pH associated with Armillariella mellea on conifers in northern Idaho. Canadian Journal of Forest Research. 9: 45-48.

Singh, D. 1970. Armillaria root rot in a coniferous plantation in Newfoundland. Ottawa, Canada: Department of Fisheries and Forestry. Bi-monthly Research Notes. 26(1): 5-6.

Singh, P. 1983. Armillaria Root rot: Influence of soil nutrients and pH on the susceptibility of conifer species to the disease. European Journal of Forest Pathology. 13: 92-101.

Singleton, V.L.; Rossi, J.A. 1965. Colorimetry of total phenolics with phosphomolybdic-phosphotungstic acid reagents. American Journal of Enology and Viticulture 16: 144-158.

Solo Statistical System. 1991. Los Angeles: BMDP Statistical Software, Inc.

Steele, R.; Torrie, J. 1960. Principles and Procedures of Statistics. New York: McGraw-Hill Company. 481 p.

Steinhoff, R.J. 1978. Early growth of grand fir seedlings in northern Idaho. In: Proceedings of the IUFRO joint meeting of working parties, vol. 2: Lodgepole pine, Sitka spruce and Abies provenances. B.C. Ministry of Forests, Vancouver, B.C. 359-365 p.

Sterner, T.E. 1970. Butt decay in balsam fir defoliated by the spruce budworm. Can. Dept. Fish. Forest Bi. Mon. Res. Notes 26(4): 38-39.

Stoszek, K.J.; Mika, P.G.; Moore, J.A.; Osborne, H.L. 1981. Relationships of Douglas-fir tussock moth defoliation to site and stand characteristics in northern Idaho. For. Sci. 27: 431-442.

Tabatabai, M.A.; Bremmer, J.M. 1970. A simple turbidimetrio method of determining total sulfur in plant materials. Agron. J. 62(6): 805-806.

Temple, Alice S. 1981. Field studies of the relationship between herbivore damage and tannin concentration in bracken (Pteridium aquilinum Kuhn). Oecologia 51: 97-106.

Thompson, A.J.; Harris, J.W.E.; Shepherd, R.F.; Silversides, R.H. 1984. Relating weather to outbreaks of western spruce budworm. Can. Entomol. 116: 375-381.

Thorsteinson, A.J. 1960. Host selection in phytophagous insects. Ann. Rev. Entomol. 5: 193-218.

Towers, B.; Stambaugh, W.J. 1968. The Influence of induced soil moisture stress upon Fomes annosus root rot of loblolly pine. Phytopathology. 58: 269-272.

Tunnock, S.; Denton, R.E.; Carlson, C.C. 1969. Larch casebearer and other factors involved with deterioration of western larch stands in northern Idaho. US Department of Agriculture. For. Serv. Res. Pap. INT-68, Ogden, Utah. p 10.

Tuomi, Juha. 1992. Toward Integration of Plant Defence Theories. Trends in Ecology and Evolution 7(11): 365-367.

Tuomi, Juha; Niemela, Pekka; Haukioja, Erkki; Seija, Siren; Neuvonen, Seppo. 1984. Nutrient stress: an explanation for plant anti-herbivore responses to defoliation. Oecologia. 61: 208-210.

Twardus, D.B. 1980. Evaluation of weather patterns in relation to western spruce budworm outbreak in northcentral Washington, 1970-1980. Forest Insect and Disease Management. U.S. Forest Service. Pacific Northwest Reg., Mimeo. Rep. 1980.

Twarowski, Z.; Twarowska, I. 1959. Studia i obserwacje miodowg Armillaria mellea (Vahl) Quél. jako przyczyn masowego zamierania drzewostanów. Prace Instytutu Badawczego Leśnictwa. 192: 3-63. (ABSTRACT)

Tyree, M.T.; Jarvis, P.G. 1982. Water in tissues and cells. Encycl. Plant Physiol., New Ser. 12B., 35-77.

Vaadia, Y.; Roney, F.C; Hagen, R.M. 1961. Plant water deficits and physiological processes. Annu. Rev. Plant Physiol. 12: 293-326.

Van Sickle, G.A. 1987. Host Response. In: Brookes, M.H.; Campbell, R.W.; Colbert, J.J.; Mitchell, R.G.; Stark, R.W., eds., Western Spruce Budworm. Tech. Bull. No. 1694. U.S. Department of Agriculture, 57-70 p.

Viets, F.G., Jr. 1972. Water deficits and nutrient availability. In: Kozlowski, T.T., ed., Water Deficits and Plant Growth vol. 3, New York: Academic Press, Inc. 217-239 p.

Wagner, M.R.; Blake, E.A. 1983. Western spruce budworm consumption -- Effects of host species and foliage chemistry. In: Talerico, R.L.; Montgomery, M. eds., Forest Defoliator -- Host Interactions: A Comparison Between Gypsy Moth and Spruce Budworms. Gen. Tech. Rept. NE-85. U.S. Department of Agriculture, Forest Service. 49-54 p.

Wagner, M.R.; Evans, P.D. 1985. Defoliation increases nutritional quality and allelochemics of pine seedlings. Oecologia. 67: 235-237.

Wahlstrom, Kjell T. 1992. Infection Biology of Armillaria Species: in vitro pectinolytic activity, infection strategy field distribution and host responses. Swedish University of Agricultural Sciences, Department of Forest Mycology and Pathology. Ph.D. Dissertation.

Wargo, P.M. 1972. Defoliation-induced chemical changes in sugar maple roots stimulate growth of Armillaria mellea. Phytopathology. 62: 1278-1283.

Wargo, P.M. 1977. Armillariella mellea and Agrilus bilineatus and mortality of defoliated oak trees. Forest Science. 23(4): 485-492.

Wargo, P.M. 1984. How stress predisposes trees to attack by Armillaria mellea -- a hypothesis. In: Kile, G.A., ed., Proceedings of the 6th international conference on root and butt rots of forest trees.; 1983 August 25-31; Melbourne, Victoria, and Gympie, Queensland, Australia. Melbourne: International Union of Forestry Research Organizations: 115-121.

Wargo, P.; Harrington, T. 1991. Host stress and susceptibility. In: Shaw, C.G.; Kile, G.A., eds., Armillaria Root Disease. Handbook No. 691. Washington D.C.: U.S. Department of Agriculture: 88-101.

Wargo, P.M.; Houston, D.R. 1974. Infection of defoliated sugar maple trees by Armillaria mellea Phytopathology. 64: 817-822.

Wargo, P.M.; Montgomery, M.E. 1983. Colonization by Armillaria mellea and Agrilus bilineatus of oaks infected with ethanol. Forest Science. 29: 848-857.

Wargo, P.M.; Shaw, C.G., III. 1985. Armillari root rot: The puzzle is being solved. Plant Disease 69(10): 826-832.

Waring, R.H. 1983. Estimating forest growth and efficiency in relation to canopy leaf area. Adv. Ecol. Res. 13: 327-354.

Waring, Gwendolyn; Cobb, Neil 1992. The impact of plant stress on herbivore population dynamics. In: Bernays, E. ed., Insect-Plant Interactions. Vol. IV. Boca Raton: CRC Press. 167-226.

Webb, W.L. 1980. Starch content of conifers defoliated by the Douglas-fir tussock moth. Can. J. For. Res. 10: 535-540.

Webb, W.L. 1981. Relation of starch content to conifer mortality and growth loss after defoliation by the Douglas-fir tussock moth. Forest Science. 27: 224-232.

Wellington, W.G. 1954. Weather and climate in forest entomology. Meteorol. Monogr. 2: 11-18.

Wellington, W.G.; Fettes, J.J.; Turner, K.B.; Belyea, R.M. 1950. Physical and biological indicators of the development of outbreaks of the spruce budworm, Choristoneura fumiferana (Clem.) (Lepidoptera:Toricidae). Can. J. Res., Sect. D 28: 308-331.

White, T.C.R. 1969. An index to measure weather-induced stress of trees associated with outbreaks of psyllids in Australia. Ecology 50: 905-909.

White, T.C.R. 1974. A hypothesis to explain outbreaks of looper caterpillars, with special reference to populations of Selidosema suavis in a plantation of Pinus radiata in New Zealand. Oecologia. 16: 279-301.

White, T.C.R. 1976. Weather, food, and plagues of locusts. Oecologia. 22: 119-134.

White, T.C.R. 1984. The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. Oecologia 63: 90-105.

Whitmore, F.W.; Zahner, R. 1966. Development of the xylem ring in stems of young red pine trees. Forest Science. 12, 198.

Wickman, B.E., Mason, R.R., Paul, H.G. 1992. Thinning and nitrogen fertilization in a grand fir stand infested with western spruce budworm. Part II: Tree growth response. Forest Science, 38(2): 252-264.

Witter, J.A.; Wisanen, L.A. 1978. The effect of differential flushing times among trembling aspen clones on Tortricid caterpillar populations. Environmental Entomology. 7: 139-143.

Woodhams, D.H.; Kozlowski, T.T. 1954. Effects of soil moisture stress on carbohydrate development and growth in plants. Am. J. Bot. 41: 316-320.

Yemm, E.; Willis, A. 1954. The estimation of carbohydrates in plant extracts by anthrone. Biochem. J. 57: 508-514.

Zahner, R. 1968. Water Deficits and Growth of Trees. In: Kozlowski, T.T. ed., Water Deficits and Plant Growth. vol. 2. Plant Water Consumption and Response. New York: Academic Press, Inc.

APPENDICES

Appendix 1a. Results of Analysis of Variance of Western Spruce Budworm - Group I.

Response	Source of Variation	df	SS	MS	F	P
Total Pupae (survival)	Inoculation	1	.125	.125	0.06	NS
	Water	1	55.125	55.125	25.94	.0070
	I x W	1	.125	.125	0.06	NS
	Error	4	8.5	2.1		
	Total	7	63.8			
Wt. Females	Inoculation	1	8.45E-07	8.45E-07	0.11	NS
	Water	1	2.48E-04	2.48E-04	31.00	.0051
	I x W	1	6.84E-06	6.84E-06	.85	NS
	Error	4	3.20E-05	8.02E-06		
	Total	7	2.88E-04			
Wt. Males	Inoculation	1	8.201E-06	8.201E-06	2.23	NS
	Water	1	1.891E-05	1.891E-05	5.13	.0861
	I x W	1	5.951E-06	5.951E-06	1.62	NS
	Error	4	1.473E-05	3.683E-06		
	Total	7	4.779E-05			
Female:Male	Inoculation	1	.6412	.6412	1.08	NS
	Water	1	.59024	.5902	.99	NS
	I x W	1	.4925	.4925	.83	NS
	Error	4	2.3740	.5935		
	Total	7	4.098			

Appendix 1b. Results of Analysis of Variance of Western Spruce Budworm - Group II.

Response	Source of Variation	df	SS	MS	F	P
Development rate	Sex	1	231.6	231.6	5.64	.019
	Water	1	1362.2	1362.2	33.13	.001
	S x W	1	81.3	81.3	1.98	NS
	Error	93	3823.5	41.1		
	Total	96	5298.4			
Female:Male	Water	1	2.829	2.829	14.67	.003
	Error	10	1.92	1.92		
	Total	11	4.757			

Appendix 2. Results of Analysis of Variance of Infection Rates, of Seedlings Inoculated with A. ostoyae.

GROUP I

Response	Source of Variation	df	SS	MS	F	P
Dead infected	Water	1	4.5	4.5	9.00	.0399
	Defoliation	1	12.5	12.5	25.00	.0075
	W x D	1	4.5	4.5	9.00	.0399
	Error	4	2	.5		
	Total	7	23.5			
Live infected	Water	1	.125	.125	1.00	NS
	Defoliation	1	1.125	1.125	9.00	.0399
	W x D	1	.125	.125	1.00	NS
	Error	4	.500	.125		
	Total	7	1.875			
GROUP II						
Dead infected	Water	1	.347	.347	4.76	.032
	Defoliation	3	.930	.310	4.25	.008
	W x D	3	.375	.125	1.71	NS
	Error	64	4.666	.07		
	Total	71	6.319			
Live infected	Water	1	.01	.013	.10	NS
	Defoliation	3	.59	.199	1.47	NS
	W x D	3	.041	.013	.10	NS
	Error	64	8.66	.135		
	Total	71	9.32			

Appendix 3. Results of Analysis of Variance of Group I Seedlings Phenolic Content.

Response	Source of Variation	df	SS	MS	F	P
Foliage Phenolics	Water	1	1.715	1.715	0.14	NS
	Defoliation	1	251.5	251.5	21.01	0.001
	W x D	1	110.1	110.1	9.20	0.006
	Inoculation	1	59.8	59.8	5.00	0.034
	W x I	1	.9	.9	0.08	NS
	D x I	1	6.94	6.9	.58	NS
	W x D x I	1	42.3	42.3	3.53	0.072
	Error	24	287.4	11.9		
	Total	31	760.9			
Root Phenolics	Water	1	83.6	83.6	17.93	.0029
	Defoliation	1	20.9	20.9	4.5	.066
	W x D	1	.07	.07	0.02	NS
	Inoculation	1	6.6	6.6	1.42	NS
	W x I	1	48.7	48.7	10.45	.012
	D x I	1	6.1	6.1	1.31	NS
	W x D x I	1	18.9	18.9	4.06	.07
	Error	8	37.3	4.6		
	Total	15	222.4			

Appendix 4. Results of Analysis of Variance of Group I Seedlings Sugar Content.

Response	Source of Variation	df	SS	MS	F	P
Foliage Sugars	Water	1	2228.1	2228.1	10.59	.011
	Defoliation	1	816.5	816.5	3.88	.084
	W x D	1	444.4	444.4	2.11	NS
	Inoculation	1	29.2	29.2	0.14	NS
	W x I	1	118.7	118.7	0.56	NS
	D x I	1	22.1	22.1	0.10	NS
	W x D x I	1	.3	.3	0.00	NS
	Error	8	1683.8	210.5		
	Total	15	5343.2			
Root Sugars	Water	1	111.1	111.1	31.56	.0005
	Defoliation	1	4.7	4.7	1.34	NS
	W x D	1	11.3	11.3	3.20	NS
	Inoculation	1	.5	.5	0.14	NS
	W x I	1	10.3	10.3	2.94	NS
	D x I	1	10.0	10.0	2.85	NS
	W x D x I	1	.7	.7	0.20	NS
	Error	8	28.1	3.5		
	Total	15	176.8			

Appendix 5. Results of Analysis of Variance of Group I Seedlings Starch Content.

Response	Source of Variation	df	SS	MS	F	P
Foliage Starch	Water	1	8.3	8.3	5.63	0.045
	Defoliation	1	3.4	3.4	2.35	NS
	W x D	1	3.9	3.9	2.68	NS
	Inoculation	1	.003	.003	0.00	NS
	W x I	1	3.4	3.4	.16	NS
	D x I	1	1.6	1.6	1.12	NS
	W x D x I	1	4.9	4.9	3.35	NS
	Error	8	11.8	1.5		
	Total	15	37.7			
Root Starch	Water	1	73.1	73.1	20.83	.001
	Defoliation	1	39.6	39.6	11.27	.010
	W x D	1	72.4	72.4	20.62	.001
	Inoculation	1	.002	.002	0.02	NS
	W x I	1	.1	.1	0.03	NS
	D x I	1	.9	.9	0.27	NS
	W x D x I	1	2.1	2.1	.60	NS
	Error	8	28.0	3.5		
	Total	15	216.4			

Appendix 6. Results of Analysis of Variance for Foliage N, P, and S Content of Seedlings.

Response	Source of Variation	df	SS	MS	F	P
Total Nitrogen	Defoliation level	3	.190	.06	2.78	.051
	Error	25	.569	.02		
	Total	28	.759			
Total Phosphorus	Water	1	.0141512	.0141512	23.33	0.0029
	Defoliation level	3	1.158E-02	3.862E-03	6.37	0.0270
	W x D	3	.0123277	4.109E-03	6.78	0.0236
	Error	6	.003639	.0006065		
	Total	13	3.165E-02			
Total Sulfur	Water	1	1.26E-02	4.22E-03	3.36	.050
	Defoliation level	3	1.18E-03	1.182E-03	0.94	NS
	W x D	3	7.39E-04	2.46E-04	0.20	NS
	Inoculation	1	9.20E-05	9.20E-05	0.07	NS
	W x I	1	5.19E-03	1.73E-03	1.38	NS
	D x I	3	7.37E-06	7.37E-06	0.01	NS
	W x D x I	3	1.85E-03	6.19E-04	0.49	NS
	Error	13	1.63E-02	1.25E-03		
	Total	28	4.16E-02			

Appendix 7. Results of Analysis of Variance for Root N, P, and K Content of Seedlings.

Response	Source of Variation	df	SS	MS	F	P
Total Nitrogen	Defoliation level	3	.121	4.04E-02	6.67	.001
	Error	28	.170	6.071E-03		
	Total	31	.291			
Total Phosphorus	Water	1	1.05E-02	1.05E-02	4.91	.017
	Defoliation level	3	2.90E-02	9.68E-03	4.52	.041
	W x D	3	3.22E-04	1.07E-04	0.05	NS
	Inoculation	1	4.65E-03	4.69E-03	2.17	NS
	W x I	1	3.13E-05	3.13E-05	0.01	NS
	D x I	3	5.42E-04	1.80E-04	0.08	NS
	W x D x I	3	2.71E-03	9.03E-04	0.42	NS
	Error	16	3.42E-02	2.14E-03		
	Total	31	.0809			
Total Potassium	Water	1	.110	.110	13.93	.0018
	Defoliation level	3	3.21E-02	.010	1.35	NS
	W x D	3	8.93E-02	2.97E-03	1.35	NS
	Inoculation	1	1.28E-02	1.28E-02	1.62	NS
	W x I	1	1.03E-02	1.03E-02	1.31	NS
	D x I	3	6.81E-02	2.27E-03	0.29	NS
	W x D x I	3	2.60E-02	8.67E-03	1.10	NS
	Error	16	.126	7.92E-03		
	Total	31	.302			

Appendix 8. Results of Analysis of Variance of Seedlings Phenology.

Response	Source of Variation	df	SS	MS	F	P
% of total buds flushed on March 22	Water	1	12063.3	12063.3	71.18	.0001
	Defoliation	1	2224.6	2224.6	13.13	.0004
	W x D	1	1508.0	1508.0	8.90	.0034
	Inoculation	1	860.4	860.4	5.08	.0258
	W x I	1	245.4	245.4	1.45	NS
	D x I	1	160.4	160.4	.95	NS
	W x D x I	1	5.4	5.4	.03	NS
	Error	136	23049.4	169.4		
	Total	143	40117.3			
Total number of buds that flushed	Water	1	9280.1	9280.1	70.20	.0001
	Defoliation	1	5600.0	5600.0	42.36	.0001
	W x D	1	513.7	513.7	3.89	.050
	Inoculation	1	81.0	81.0	.61	NS
	W x I	1	367.3	367.3	2.78	.080
	D x I	1	560.1	560.1	4.24	.041
	W x D x I	1	506.2	506.2	3.83	.052
	Error	136	17978.0	132.191		
	Total	143	34886.6			

Appendix 9. Results of Analysis of Variance of Group II Seedling Biomass.

Response	Source of Variation	df	SS	MS	F	P
Shoot Biomass	Water	1	41.9	41.9	4.86	.029
	Defoliation level	3	666.6	222.2	25.78	.000
	W x D	3	228.5	76.1	8.84	.000
	Error	136	1172.1	8.6		
	Total	143	2109.2			
Root Biomass	Water	1	42.8	42.8	4.53	.035
	Defoliation level	3	1043.3	347.7	36.74	.000
	W x D	3	28.9	9.6	1.02	NS
	Inoculation	1	24.9	24.9	2.64	NS
	W x I	1	19.5	19.5	2.06	NS
	D x I	3	8.6	2.8	.030	NS
	W x D x I	3	19.7	6.5	0.70	NS
	Error	128	1211.5	9.4		
	Total	143	2399.6			
Root:Shoot	Water	1	.200	.200	3.19	.0763
	Defoliation level	3	.868	.289	4.62	.004
	W x D	3	1.232	.410	6.55	.0004
	Error	136	8.524	.062		
	Total	143	10.825			