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COMPETITIVE PERFORMANCE IN AN APPLE BERRY POLYCULTURE

DISSERTATION

Presented in Partial Fulfillment of the Requirements for

the Degree Doctor of Philosophy in the Graduate

School of The Ohio State University

By

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*****

The Ohio State University
2002

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ABSTRACT

The purpose of this study was to compare the competitive ability of four understory berry crops to an apple overstory. 'Goldrush' apple trees on M.7 rootstock were intercropped with either blackberry (Rubus spp., cv. 'Navaho'), honeyberry (Lonicera caerulea, cvs. 'Blue Belle' and 'Blue Velvet'), jostaberry (Ribes nidigrolaria) or lingonberry (Vaccinium vitis-idaea, cvs. 'Red Pearl' and Koralle'). Both blackberry and jostaberry appeared to be stronger competitors than was apple, as both species negatively affected the growth, bloom and fruit set of the apple trees. Blackberry and jostaberry exhibited high growth rates and the ability to proliferate within zones of soil nutrient enrichment, while apple did not demonstrate a consistent ability to proliferate its roots in zones of nutrient enrichment. The observed negative effects on the apple tree were primarily attributed to competition for nitrogen, as the apple trees intercropped with blackberry or jostaberry were deficient in leaf nitrogen concentration. For both blackberry and jostaberry, intraplant competition had a much greater negative impact on growth than did interplant competition with apple. However, the yield of both species was reduced when planted under apple trees, primarily due to competition for light. Jostaberry appeared to be particularly sensitive to shaded conditions as its photosynthetic capacity was greatly reduced and it failed to flower even under lightly, artificially imposed shaded conditions. Blackberry was also negatively affected by
shade, but to a lesser degree than jostaberry. Of all the intercrops examined, the apple-
honeyberry combination was the only one that showed promise as a viable system. The
apparent success of the combination primarily stemmed from the weakness of
honeyberry as a competitor. While honeyberry allocated more of its biomass below-
ground than any of the other plant species, its extensive root system did not exhibit the
plasticity required to take advantage of regions of nutrient enrichment. Honeyberry had
a low growth rate and it seemed to prefer both crowded and shaded conditions. While
lingonberry was also a weak competitor with respect to apple, the apple-lingonberry
polyculture was not recommended because of the inherent differences between the two
species in their soil pH requirements.
This dissertation is dedicated to my parents, Michael and Connie Rivera,
who instilled in me a love of learning and have always supported
me in all my life’s endeavors.
ACKNOWLEDGMENTS

I wish to express my sincere appreciation to committee members Dr. Donald Eckert, Dr. Dave Ferree, Dr. Martin Quigley, and especially Dr. Joseph Scheerens, who not only provided advice and encouragement, but who also spent countless hours helping me in the field in the freezing cold and sweltering heat. I also extend my gratitude to members of the OARDC staff who helped with various aspects of the field study, from planting and maintenance to data collection including, John Elliott, Bruce Williams, Eric Chanay, John Schmid, and David Scurlock.

I would also like to acknowledge the invaluable help I received from Diana Hardy and Stacie Reid. I doubt there have ever been two more conscientious and loyal student employees at the OARDC than they. I would like to thank the greenhouse staff for their care and assistance of my greenhouse studies, including Lee Duncan, Kim Hershberger and Glen Cassidy.

I would like to express my thanks to Dr. Ray Miller and Jean Flickinger for their help with the subculturing of mycorrhizal slants. Kathy Demchak of Pennsylvania State University and Dr. Sarah Hambleton of the Eastern Cereal and Oilseed Research Centre, Ontario deserve recognition for their guidance and assistance they provided with
respect to the staining and counting of ericoid mycorrhizae. Finally I extend an extra special thanks to the OARDC for the financial support of this study and my graduate training.
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CHAPTER 1

INTRODUCTION

Polyculture refers to the practice of growing two or more crops on the same field simultaneously. There are many reported advantages to intercropping systems: they yield more per unit area of land, have fewer pest outbreaks, use available resources more efficiently, are more sustainable, and protect against economic risk. Ultimately though, the success of an intercrop is dependent on the extent of competition for resources between the species under culture.

Since intercropping involves the planting of two or more crops in the same field simultaneously, competition between plants may inhibit the growth of either or both. It is generally accepted that if the niche requirements of two sympatric species are sufficiently similar, one or the other will be extirpated given enough time. Conversely, if the two species have similar but distinct requirements, they may both persist indefinitely in the same environment (Vandermeer, 1990). When two plants are grown together, basic physiologic principles dictate that they will almost always compete. However, the extent of the competition is often such that both plants are able to remain productive. In fact, despite decades of experimental field evidence that demonstrates the existence of competition, there is still much debate over both the importance of
competition and those plant attributes that make some plant species successful competitors under different environmental conditions (Goldberg, 1990).

This study compares the competitive ability of four different understory crops to an apple overstory. 'Goldrush' apple on M.7 rootstock was intercropped with either lingonberry (*Vaccinium vitis-idaea*, cvs. ‘Red Pearl’ and ‘Koralle’), honeyberry (*Lonicera caerulea*, cvs. ‘Blue Belle’ and ‘Blue Velvet’), jostaberry (*Ribes nidigrolaria*) or blackberry (*Rubus* spp., cv. ‘Navaho’).

This study seeks to correlate certain plant physiological characteristics with competitive ability. If characteristics such as nutrient uptake capacity, root proliferation, shade tolerance, and photosynthetic capacity can be correlated with plant performance in the field, the success of future intercropping systems can be predicted for different species combinations prior to planting.

The entire study is comprised of one field component and several greenhouse and laboratory experiments. Due to the inequality in size of the apple trees and berry shrubs, both above and below-ground, we hypothesize that the berry species with the most shade tolerance, greatest nutrient uptake capacity, and greatest root proliferation ability will be the most suitable for an apple intercropping system. These are the characteristics that we believe will impart superior competitive ability and will allow smaller berry species to successfully coexist with apples in the relatively fertile soils of managed orchards.
Objectives:

1. To compare the performance by measuring above ground growth, flowering, fruit set, fruit yield, and the spatial distribution of root systems of four potential polyculture systems in which all component species are woody perennials.

2. To determine if there are differences in the timing and extent of root proliferation and nutrient uptake between the component apple and berry species.

3. To determine the dependence of each of the five component species on mycorrhizal symbiosis and to determine the contribution to plant uptake of phosphorus, nitrogen and potassium provided by the associated mycorrhizal complexes.

4. To determine the effect of mycorrhizal associations on interspecific competition between each apple x berry combination in terms of growth and infection rate.

5. To determine the effect of shade on growth and nutrient uptake of each component berry species.
CHAPTER 2

REVIEW OF LITERATURE

Polyculture

Polyculture or intercropping is a traditional farming strategy that is designed to promote diet diversity, income generation, production stability, minimization of risk, reduced insect and disease incidence, efficient use of labor, intensification of production with limited resources and maximization of returns under low levels of technology (Altieri, 1987). Polyculture is the planting of two or more crops in the same field simultaneously. Prior to the advent of mechanized and industrialized agriculture, the practice was common even in temperate North America. For example, 57% of the soybean acreage in Ohio was grown in combination with maize in 1923 (Vandermeer, 1990). Although the practice has all but disappeared in countries with industrialized agriculture, it remains common in underdeveloped countries.

Agroforestry is a type of polyculture in which trees are combined spatially and temporally with agricultural crops and/or animals. The term agroforestry can be subclassified depending on the structure of the particular agroforestry practice. Agrisilviculture refers to a system in which crops, including tree/shrub crops, are grown
in combination with trees. Silvopastoral systems combine trees with pasture/animals. Agrosilvopastoral systems combine trees with agricultural crops and pasture/animals.

Trees can improve the productivity of a given agroecosystem by influencing soil characteristics, hydrology, and microclimate (Farrell, 1987). Trees can potentially affect the nutrient status of the soil by exploiting deeper mineral reserves or capturing leached nutrients. Through the deposition of their leaf litter, these minerals are returned to the soil as organic matter. Increased organic matter improves soil structure and increases the soil humus content, cation exchange capacity, and microorganism activity.

In a study to evaluate the effect of trees on soil fertility, Farrell (1987) found that available phosphorus increased up to sevenfold under capulin (*Prunus capuli*) and sabina (*Juniperus deppeana*). Both trees are utilized in traditional farming systems in central Mexico. In addition, total carbon and potassium increased two- to threefold, nitrogen, calcium and magnesium increased one-and-a-half- to threefold, and cation exchange capacity increased one-and-a-half- to twofold.

Trees also alter the microclimate by reducing wind speed and moderating temperature changes and relative humidity under the canopy. In general, tree canopies result in lower maximum and higher minimum temperatures under the canopy as compared to those in open areas (Farrell, 1987). In addition, there is evidence that trees can also bring water from deeper in the soil profile to the soil surface where it can be taken up by understory crops (Dawson, 1993; Caldwell et al., 1998; Horton and Hart, 1998).
The trees used in agroforestry systems are also directly productive. Such trees are used to produce wood, food, forage, oil, medicinal products or other by-products. The black locust (*Robinia pseudoacacia*), in addition to fixing nitrogen, is an important honey plant and source of durable wood for fenceposts (Farrell, 1987). Another nitrogen-fixing tree, *Acacia albida*, is valued as a source of forage and wood, but also is leafless during the rainy season when sorghum and millet are being grown and thus, competition for light between the tree and crops is greatly reduced. Other tree species such as chestnut (*Castanea*), carob (*Ceratonia*) and honey locust (*Gleditsia*) are used to supplement the human diet since they have higher values of proteins, carbohydrates, and fats than most grains (Smith, 1953).

Despite the extensive use of trees in polyculture systems throughout the world, competitive interactions between tree and crop can be significant. The component plant species in agroforestry systems usually differ greatly in size. Smaller understory species may be inhibited by shading and possibly by competition for water and nutrients.

When water and nutrients are freely available, light is usually the primary limiting factor to growth and fruiting. This problem can be alleviated by choosing shade-requiring understory species. For example, black pepper, cacao, pineapple, and vanilla are often grown successfully under coconuts (Ong et al., 1996). In fact, in non-mechanized tropical systems, coffee, tea, and cacao are often grown under one or two strata of shade trees (Farrell, 1987). In such systems, water or nutrient availability rather than light is the primary limiting factor.
When resources are not limiting, densely planted monocultures usually provide the most efficient resource capture system (Ong et al., 1996). For an agroforestry system to be more productive than corresponding monocultures, the mixture must be able to capture more of the available resources or to use them more efficiently. Under such circumstances, the combination usually provides a greater yield than yields of its component crops when grown in monoculture. Such yield advantages have been widely reported for intercrops and are often expressed in terms of Land Equivalent Ratio (LER). LER is the ratio of the area under sole cropping to the area under intercropping, at the same level of management, that gives an equal amount of yield (Ong, 1996). For example, Natarajan and Willey (1980) found that 0.94 hectares of sorghum monoculture and 0.68 hectares of pigeonpea monoculture were needed to produce the same quantities of sorghum and pigeonpea that were harvested from a 1.0 hectare polyculture. The LER of the polyculture was thus 1.62. Although the yield of each crop species in the mixture was reduced by competition, the total yield of the polyculture on an area basis was 62% greater than for the monocultures.

In a polyculture system where one component species is a tree and the other is an annual crop, the tree species has a considerable advantage in sequestering both above- and below-ground resources since the tree is usually well-established before the crop is ever sown. Corlett et al. (1992a, 1992b) found that the gain in resource capture of a *Leucaena leucocephala*/pearl millet (*Pennisetum typhoides*) alley-cropping system was insufficient to offset the reduced light capture by the pearl millet. This problem is less
insufficient to offset the reduced light capture by the pearl millet. This problem is less serious if the tree component is also used to produce high value crops, such as fruit, that could offset the loss in yield of the annual crop component.

That successful agroforestry systems exist is not in question. However, current research in the area of agroforestry is centered on understanding resource capture principles to understand the mechanisms involved in tree-crop interactions (Ong et al., 1996). Spatial sharing of below ground resources is another area of continuing research in agroforestry. Thus far, very little research has been done in agroforestry systems that include woody understory species in addition to the tree species.

**Competition and competitive success**

It is generally accepted that if the niche requirements of two species are sufficiently similar, one or the other will be suppressed or locally eliminated given enough time. Conversely, if the two species have similar but distinct requirements, they may both persist indefinitely in the same environment (Vandermeer, 1990). When two plants are grown together, basic physiologic principles dictate that they will almost always compete. However, the extent of the competition is often such that both plants are able to remain productive. In fact, despite decades of experimental field evidence that demonstrates the existence of interspecific competition, there is still much debate over both the importance of competition and those plant attributes that make some plant species successful competitors under different environmental conditions (Goldberg, 1990).
An important aspect of the debate is the disagreement over the role of plant traits in competitive success (Aerts et al., 1991; Campbell et al., 1991b; Grace, 1991). Although ecologists are in general agreement that plasticity in growth and allocation is important for resource capture among competing plants, there are different hypotheses on how plasticity might contribute to competitive success. The resource-ratio hypothesis (Huston and Smith 1987; Tilman, 1987, 1988) asserts that there is an inverse relationship between above and below ground competitive abilities. This inverse relationship is proposed to occur because allocation of a resource to one structure precludes allocation to another. Plants that allocate more biomass to shoots will be better competitors for light. Those that favor allocation to roots will be better competitors for water and nutrients. This hypothesis predicts that along a gradient of decreasing fertility there will be a transition from above ground to below ground competitive ability as allocation is switched in favor of roots. Thus, there is a negative correlation between above and below ground competitive abilities.

An alternative theory (Grime 1973, 1974, 1977, 1979: Grime and Hodgson, 1987) suggests that the ability to capture resources above and below ground are interdependent and that both of these abilities will reach a maximum in rapidly growing, perennial communities in fertile soils. This theory suggests that along a gradient of increasing fertility, members of the plant community will show an increased capacity for high growth rate, high morphological plasticity and foraging both above and below ground. Conversely, the benefits of these characteristics should be reduced as soil
these circumstances, plants with low growth rates, long-lived and relatively undynamic root systems, low tissue turnover rates, and the ability to accumulate nutrients in plant tissue (thereby uncoupling nutrient uptake from growth) will be more successful (Grime, 1979, 1988).

Relatively few studies of competition have been conducted in such a way as to be useful in comparing Tilman’s and Grime’s theories. This is because few studies have been able to adequately distinguish between competition for light or for nutrients. Aerts et al. (1991) designed an experiment in which the relation between competitive ability and biomass allocation for three plant species was determined in a factorial combination in which the different types of competition were separated. They found that contrary to Tilman’s theory, the allocation patterns of the three species studied indicated no apparent trade-off between their competitive abilities for above and below ground resources. In a similar study, Campbell et al. (1991a) also found no evidence that differential biomass allocation patterns existed between plants from low-fertility environments as opposed to high-fertility environments.

Despite the evidence refuting Tilman’s theory, the controversy between the theories of Grime and Tilman is ongoing. In fact, it has been argued that the differences in the two theories are mostly the result of differing definitions of competition and are otherwise largely compatible (Grace, 1990, 1991).

In an extensive review of the importance of competition, Wilson (1988) found that below ground competition usually affected the balance of competing species more than above ground competition. In addition, the effects of competition were found to be
more severe at high levels of resource availability. Unfortunately, competition for below ground resources is recognized more by its manifestations than by its mechanisms (Caldwell, 1987). However, below ground competitive ability has been correlated with such attributes as root density, surface area, and plasticity either in root growth or in the properties of enzymes involved in nutrient uptake (Casper and Jackson, 1997).

**Below-ground competition**

Below ground competition occurs when plants reduce the growth or survival of their neighbors by reducing soil resources. In contrast to above ground competition which involves competition for only one primary resource, light, below-ground competition involves a broad range of soil resources including water and at least twenty essential mineral nutrients (Casper and Jackson, 1997). In fact, much of the competition that occurs between plants happens below ground, and the effects of such competition often affect the plant more than those of above ground competition. In a review of forty-seven journal articles on competition, Wilson (1988) found that thirty-three (>70%) of the experiments concluded that root competition had a greater effect on growth than shoot competition.

Soil resources reach the root surface by one of three processes: root interception, mass flow or diffusion. Root interception generally accounts for less than 10% of resource uptake by roots (Marschner, 1995). Mass flow of water and nutrients is driven by transpiration and is a function of water movement to the root and the concentration of dissolved nutrients. Diffusion occurs when uptake exceeds supply by mass flow,
forming zones of localized concentration gradients. Given these methods by which plants acquire soil resources, several plant traits that might influence below ground competitive ability can be determined.

Perhaps the most important plant attribute of competitive success below ground is the ability to exploit a large soil volume. This ability depends on several root characteristics such as rooting depth, density, growth rate, and total surface area. However, despite numerous studies, a direct correlation between root density and the outcome of below ground competition is still lacking. Casper and Jackson (1997) suggest several possible explanations for this discrepancy. First, competition for resources may occur between roots of the same plant, so the return per investment in new root growth may decline at higher densities. Second, the location of plant roots and their ability to exploit nutrient-rich patches may be just as important as rooting density. Third, the role of mycorrhizae in nutrient acquisition is both important and frequently overlooked in nutrient competition studies, and fourth, physiological uptake capacities may also be crucial to competitive ability.

**Root proliferation**

Since nutrient availability in the soil can vary considerably over distances of only a few centimeters (Snaydon, 1962), the ability of plants to rapidly exploit nutrient-rich patches is likely an important mechanism of effective competition (Tilman, 1988). In fact, in some environments, a significant portion of nutrient uptake by plants comes from temporary patches of nutrient-rich soil (Chapin, 1980).
Numerous studies have demonstrated root proliferation in nutrient rich environments. Drew and Saker (1975, 1978) demonstrated root proliferation in barley seedlings in localized zones of increased nutrient supply. Granato and Raper (1989) demonstrated a similar response in maize roots. Passioura and Wetselaar (1972) used plexiglass boxes to show that wheat roots proliferate near banded applications of nitrogen. Crick and Grime (1987) showed that the roots of plants grown in partitioned pots proliferated in the compartments with the highest nutrient concentrations. Eissenstat and Caldwell (1988) used a root periscope to observe root proliferation in the field after localized applications of nutrient solutions.

Although the phenomenon of root proliferation has been well documented, the timing of the proliferation has not been adequately researched. Only one study has sought to measure the timing of proliferation. Jackson and Caldwell (1989) found that the roots of the native tussock grass, *Agropyron desertorum*, rapidly proliferated within one day of the initial nutrient solution injection. However, the roots of an introduced tussock grass, *Agropyron spicatum*, failed to proliferate at any time during the two-week experiment. Thus, different species (even those in the same genus) vary in their capacity to make plastic adjustments to the size and distribution of their root systems.

Simulation models have shown that under many soil conditions, the root characteristic that most influences nutrient uptake is total rooting density, especially for the uptake of immobile elements like phosphorus (Barber, 1984). Thus, it follows that rapid root proliferation in localized zones of nutrient enrichment is likely an important mechanism of effective competition.
However, the ability of a plant to rapidly exploit nutrient-rich patches via root proliferation is not necessarily correlated with the nutrient uptake ability of competing root systems. Caldwell et al. (1991b) showed that root density alone could not explain relative nutrient uptake among three species in a sagebrush steppe. The native tussock grass *A. desertorum* had 8-10 times more roots in enriched nutrient patches as did the sagebrush, *Artemesia tridentata*, one week after the nutrients were applied, and 4-6 times more roots after three weeks. Despite this difference, both species were able to acquire similar amounts of phosphate from the nutrient patches. In addition, the sagebrush was able to acquire 6-8 times more phosphate than the native grass, *Pseudoroegneria spicata*, despite greater root densities for the grass.

In an earlier study, Caldwell et al. (1985) found that when in competition, *A. tridentata* obtained much less phosphorus from soil space shared with *A. desertorum* than from space shared with *P. spicatum*. This was true even though the grass/shrub rooting densities in the soil interspaces did not significantly differ between the *A. tridentata/A. desertorum* or *A. tridentata/P. spicatum* combinations. Surprisingly, in a later study Caldwell et al. (1991a) found that when grown together, *P. spicatum* and *A. desertorum* had similar levels of phosphorus uptake from enriched and control patches. Thus, although much is known about the ability of roots to respond to nutrient patches, considerably less is known about how nutrient heterogeneity influences competition.

In an attempt to answer this question, Campbell et al. (1991a) measured the responses of leaf canopies and root systems of eight herbaceous species to standardized resource patches (light or nutrients). To test the predictive value of the result of these
responses, the eight species were grown together and then ranked in order of total shoot biomass. The results showed that dominance of a particular species was not correlated with plasticity. Rather, the capacity for dominance depended more on a high relative growth rate and extensive architecture above and below ground. These attributes allowed for "high scale foraging" of a large volume of canopy and soil space. These attributes can be contrasted with the smaller leaves and finer roots of subordinate plants, which allow for "high precision foraging" of local undepleted patches of canopy and soil space.

To further understand the way in which the responses of plants to resource heterogeneity affect competition between species, more experiments are needed that integrate the resource emphasis of physiological ecology with measurements of plant performance. Processes such as fine-root maintenance/turnover, root absorption capacities, and mycorrhizal symbioses all depend on a continuous energy supply to the roots and plant demand for mineral nutrients (Caldwell et al., 1987). It may be that competition between neighboring root systems is influenced more by root physiological processes than by root morphology and density. For example, Campbell and Grime (1989) concluded that the lower rates of turnover of tissues and the capacity of roots to remain viable under stress were important components of the ability of Festuca ovina to exploit brief pulses of mineral nutrient enrichment.

**Root architecture**

Root architecture refers to the "spatial configuration of the root system, i.e., the explicit geometric deployment of root axes" (Lynch, 1995). In addition to root size, root
architecture is considered to be a major factor in the nutrient uptake efficiency of plants (Fitter, 1991). Root simulation models have shown that the architectural characteristics of roots affect nutrient uptake. Barber and Silberbush (1984) demonstrated that nutrient uptake rate was dependent on root length, radius, and density. Fitter et al. (1991) showed that root architecture affected the volume of soil from which nutrients could be taken up and the exploitation efficiency of the root system as a whole. They concluded that high exploitation efficiency was associated with a herringbone topology (branching predominantly on the main axis) and with long interior and exterior links (vertices that end in internodes or meristems, respectively).

The effect of root architecture on nutrient uptake is a difficult area to study because of the many interactions involved. For example, nutrient uptake varies with species, soil type, water status, root surface area and other physiological/morphological characteristics. However, an application of DFMO (α-DL-difluoromethylornithine), an inhibitor of putrescine synthesis, has been found to cause changes in phenotype development of root systems (Burtin et al., 1991). Bar-Tal et al. (1997) found that DFMO affected the development of excised tomato roots in solution cultures. DFMO could be used as a tool for studying the effect of root architecture on nutrient uptake, since it would allow comparisons of the same species that differ only in architecture of their root systems.

Root architecture can also have an important influence on root interactions with soil biota (Lynch, 1995). For example, Hetrick et al. (1991) found that root fibrousness
was the best single predictor of mycorrhizal dependence. Plant species with highly fibrous root systems developed fewer mycorrhizal symbioses than species with coarse root systems.

Although some of the variation in root architecture among species is under genetic control, there is considerable phenotypic plasticity within many species (Fitter and Strickland, 1991). Architectural plasticity may represent an alternative to biomass plasticity as a response to nutrient heterogeneity for species with coarse roots. It is likely that species with coarse root systems may be poorly adapted to respond to short-term nutrient patchiness and may utilize architectural rather than biomass plasticity, whereas fine-rooted species can effectively exploit such short-lived patches through their ability to rapidly create dense networks of ephemeral roots (Fitter, 1994). Fitter and Strickland (1992) found significant architectural differences between species and within species on different soils and in different years. Thus, they concluded that architectural plasticity in addition to biomass plasticity should be used to help explain the behavior of root systems under different environmental conditions.

Measuring root systems

Although root systems are important to plant function and ecology, the difficulty in obtaining adequate measurements of roots has been a deterrent to their study in the field. However, there are many techniques for assessing root system structure and function.

The only way to examine the entire root system of a plant is by careful excavation of roots from the soil (Caldwell and Virginia, 1989). This method has been
widely used by researchers to describe the depth and width of root systems (Dhyani et al., 1990; Toky and Bisht, 1992; Groot and Soumare, 1995). This method, however, is very labor intensive and only provides information of the root system at one point in time.

Soil coring methods are very commonly used to obtain quantitative information on root system biomass and rooting length. Drew and Saker (1980) examined the relationship between root numbers observed on the face of soil cores and the length and relative distribution of roots extracted from the soil. Caldwell et al. (1987, 1991b, 1996) used soil cores to determine the microscale distributions of roots in the field. However, the accuracy of using soil cores is highly dependent on the method employed to remove the roots from the soil. Caldwell and Fernandez (1975) found that compared to dry sieving, a flotation procedure using an NaCl solution followed by wet sieving (pore size 0.03 mm²) yielded a greater quantity of fine roots by a factor of 2.4. Smucker et al. (1982) developed a hydropneumatic elutriation system for separating roots from soil that they claim provides a rapid and high recovery of roots. The use of many other washing, flotation, and chemical dispersing agents in removing roots from soil profiles are reviewed by Boehm (1979).

Separating roots of different plant species is another difficult task in studying root systems. Hand separation on the basis of color, size, and branching pattern is subjective at best, tedious, and extremely difficult for separating young fine roots. However, simple and rapid methods have been developed for some species combinations. Rumbaugh et al. (1988) used near infrared reflectance spectroscopy to
distinguish between alfalfa and four grass species when grown in binary mixtures. Caldwell et al. (1987) found distinct differences in fluorescence from concentrated extracts of dried roots of *Artemisia* and *Agropyron* species. Several studies have used radio-labeled or stable isotopes to distinguish between the roots of different species in mixed root samples (Caldwell et al., 1985, 1991a; Litav and Harper, 1967; Mamolos et al., 1995).

Since the relationship between root length and surface area and absorptive capacity of root systems is considered to be important, a number of methods have been used to estimate those variables without resorting to complete excavation. Total root length is most commonly estimated by a line-point method (Newman, 1966; Tennant, 1975; Jackson and Caldwell, 1989) in which root length is based on the number of intercepts of random transects with roots spread over a surface. This approach has been mechanized with curvometers, photoelectric counters, scanners and computer programs (Rowse and Phillips, 1974; Richards et al., 1979; Lynch and van Beem, 1993; Nielsen et al., 1994).

Estimates of root production are important in studies of total plant productivity since in most perennial stands, root system production is greater than above ground production (Caldwell, 1987). The most common measurement approach is sequential root biomass sampling. These are usually done by taking soil cores over a period of time (e.g. one year or growing season) and then calculating total root production (Caldwell and Virginia, 1989).
Another method used for estimating root production is the measuring of the ingrowth of roots into root-free soil in mesh bags that are placed in the ground and removed periodically (Fabiao et al., 1985). This method assumes that root growth into the bags is the same as in free soil, and the method has been criticized on the grounds that the assumption is not valid (Shierlaw and Alston, 1984). Other approaches include $^{14}$C-dilution techniques that measure the change in $^{14}$C/$^{12}$C in roots following a $^{14}$CO$_2$ labeling of the shoot system (Caldwell and Camp, 1974), the use of root observation chambers (Boehm, 1979), root periscopes (Eissenstat and Caldwell, 1988), color video cameras (Upchurch and Ritchie, 1984) and other root observation equipment.

Mycorrhizae

Mycorrhizal fungi are ubiquitous in terrestrial plant communities, forming associations with the roots of approximately 90% of the plant species that have been examined. These plant-fungal associations are generally considered mutualistic, whereby the fungus obtains carbon from the plant and the plant receives nutrients that are transported via the hyphal network (Allen and Allen, 1990). However, it has also been demonstrated that infection by mycorrhizal fungi may result in no benefit, or in antagonistic effects, to host plants under certain conditions (Francis and Read, 1995).

In general, mutualism dominates, and the importance of mycorrhizal fungi in nutrient uptake and especially phosphorus acquisition has long been recognized. Since phosphorus is often found at low concentrations in many soils and is generally considered immobile in the soil, mycorrhizal mediated uptake of phosphorus has been the most widely studied aspect of the VAM symbiosis. Numerous pot experiments and
several field studies have shown that mycorrhizal roots are much more efficient at
taking up phosphorus than uninfected roots (George et al., 1992; Jakobsen et al., 1992).
It has also been demonstrated that nitrogen (Bethlenfalvay et al., 1991; Tobar et al.,
1994), zinc (Kothari et al., 1991), and copper (Li et al., 1991) are taken up by and
translocated along mycorrhizal hyphae. Typically, these studies and others like them
have used a two-compartment system, where root growth into the hyphal compartment
was restricted by a fine nylon mesh. Hyphal uptake from the outer compartment could
then be measured as a percentage of total phosphate uptake.

There are three major groups of mycorrhizae, including vesicular-arbuscular
mycorrhizae (VAM or AM), ectomycorrhizae and ericoid mycorrhizae. VAM
mycorrhizae are the most abundant worldwide of the three groups. They form
associations with both woody and herbaceous plants and generally have low host-
specificity (Allen and Allen, 1990). VAM is typically more abundant in pasture land
and deciduous forests or where phosphorus supply is limited. It is also usually the only
form found in crop plants and fruit trees.

VAM live within cortical cells and form internal structures for carbon storage
(vesicles) and nutrient/carbohydrate exchange between fungus and plant (arbuscules).
Infection begins either with soil propagules (spores) or from contact with neighboring
roots. VAM hyphae penetrate the root either through a root hair or between epidermal
cells and spread intercellularly along the cortex and intracellularly upon reaching the
second layer of cortical cells (Bowen, 1987). During the formation of arbuscules,
penetration into the cortical cell begins as a constricted hyphal peg causes the cortical
cell wall to stretch and invaginate. Since cortical cell walls are not ruptured during hyphal penetration, it is thought that a fungal enzyme facilitates penetration by stretching and altering the host cell wall and middle lamella. After penetration, the hypha resumes its normal size and branches several times to form the arbuscule. The arbuscule contains polysaccharide-rich lomasomes that are thought to be important in exchanges of metabolites between the plant and fungus (Bowen, 1987).

The VAM fungi belong to four genera, *Acaulaspora, Gigaspora, Glomus,* and *Sclerocystis* (Marschner, 1995). Different VAM species vary in the extent of spread within the root and in their final balance with the root. In addition to differences in infection among species, environmental conditions can also affect infection and spread of hyphae within roots. Root exudates, noninfecting rhizosphere bacteria, mineral nutrient supply, soil disturbance, moisture, pH and temperature have all been shown to impact VAM infection, spread and survival both positively and negatively (Bowen, 1987; Marschner, 1995).

Ectomycorrhizae (EC) form hyphal structures that are external to the plant cells and form associations with mainly woody plants, especially in Pinaceae, Betulaceae, Fagaceae and Salicaceae (Marschner, 1995). Ectomycorrhizae are characterized by two main features: an interwoven sheath of hyphae surrounding the root surface and hyphae that penetrate the intercellular spaces of the cortex to form a network of mycelium referred to as the Hartig net. The Hartig net almost completely envelops the cortex, increasing the surface area of the fungus-root interface. Ectomycorrhizae are more abundant in boreal and temperate forests and where nitrogen is limited.
Ericoid mycorrhizae are associations of higher fungi that form both internal and external hyphal structures in the roots of the Ericaceae. *Hymenoscyphus ericae* (Read) Korf and Keman, *Oidiodendron griseum* and *Scytalidium vaccinii* are three ericoid species that have been identified as mycorrhizal symbionts (Goulart et al., 1993). The ericoid mycorrhizae are Ascomycetes that lack both the vesicles and arbuscules of the VAM symbionts and the Hartig net of the EC symbionts. Infected cortical cells are invaded only through the outer cell wall and external hyphae are only weakly developed (Goulart et al., 1993). In fact, external hyphae extend into the soil less than 1 cm from the root (Read, 1985). It has been proposed that one reason for the lack of mycelial growth in the soil is because the optimal growth for the fungi occurs between pH 6 and 7 while the optimal pH for the host plants ranges from 4 – 5 (Pearson and Read, 1975). This may suggest that the fungi may be integral to host adaptation to higher pH soils.

Most research on mycorrhizae has focused on nutrient acquisition mediated by arbuscular mycorrhizal fungi (AMF or AM) of individual plants or hyphal connected neighboring plants. In VAM plants, uptake of phosphorus by the fungus is thought to come from the same labile soil pool from which plant roots take up phosphorus (Marschner, 1995). Mycorrhizal hyphae extend from the internal infection out into the surrounding soil, thereby effectively increasing the absorptive surface area of the roots. Phosphorus is taken up by this hyphal network and is translocated as polyphosphates to the arbuscules, where it is hydrolyzed and most likely transported as inorganic phosphate across the plasma membrane of the root cell (Marschner, 1995).
The effectiveness of VAM fungi in providing phosphorus to its host plants depends to a large degree on the VAM species. Jakobsen (1992) found that phosphorus inflow per unit mycorrhizal root length was 2.5-3 times as high with *Acaulospora laevis* as with *Glomus* spp. or *Scutellospora calospora*. Differences in phosphorus uptake has even been shown to occur between ecotypes of the same VAM species (Marschner, 1995).

The uptake and subsequent translocation along mycorrhizal hyphae has also been demonstrated for elements other than phosphorus (Bethlenfalvay et al., 1991; Tobar et al., 1994; Rhodes and Gerdemann, 1978; Kothari et al., 1991; and Li et al., 1991). The uptake and content of copper and zinc have been shown to be higher in mycorrhizal than in nonmycorrhizal roots. Li et al. (1991) demonstrated that the contribution of VAM hyphae to copper uptake was as much as 60% of total uptake in white clover. Kothari et al. (1991) found that hyphal delivery of zinc was 25% of total uptake in clover. Since both zinc and copper are associated with low mobility in the soil, the mechanism by which mycorrhizae enhance uptake of these nutrients is thought to be similar to that of phosphorus, namely that the hyphae provide increased absorptive area. However, Li et al. (1991), by varying the phosphorus supply, found that the ratio of phosphorus to copper transport within the hyphae varied by a factor of 25, indicating that hyphal uptake/transport of both elements were regulated separately.

The importance of mycorrhizae in the transfer of highly mobile nutrients, such as nitrogen, has been assumed to be low. However, given the great demand of plants for nitrogen and its decrease in mobility due to environmental conditions, such as water

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stress, the effect of mycorrhizae on nitrogen uptake may be more relevant than has been previously thought. Tobar et al. (1994) demonstrated that under water-stressed conditions, the $^{15}$N enrichment of lettuce (*Lactuca sativa* L.) was four times higher in mycorrhizal than in nonmycorrhizal plants. George et al. (1992) found that hyphal uptake of nitrogen accounted for 35% of the total nitrogen taken up by mycorrhizal plants. Inoculation with VAM fungi has also been used to increase symbiotic N$_2$ fixation and improved soil nitrogen uptake in bean, *Phaseolus vulgaris* (Redecker et al., 1997).

The importance of mycorrhizae in nitrogen acquisition may be of greater importance in ectomycorrhizal and ericoid mycorrhizal associations than in VAM, since many ecto- and ericoid mycorrhizal systems are primarily nitrogen-limited rather than phosphorus-stressed. Finlay et al. (1988) showed that as much as 50% of shoot free amino acids of *Pinus sylvestris* were $^{15}$N-labeled, indicating direct mycelial transport. Inoculation of *Calluna vulgaris* and *Vaccinium macrocarpon* with the ericoid species *Hymenoscyphus ericae* resulted in increased nitrogen concentration in the shoot, increased total nitrogen and increased shoot growth (Read and Stribley, 1973; Stribley and Read, 1974). Powell (1982) found that inoculation of blueberry (*Vaccinium corymbosum* L.) seedlings with *H. ericae* stimulated shoot growth and dry matter production, and increased shoot nitrogen, sulfur and calcium concentrations. In another study, Powell and Bates (1981) found that mycorrhizal inoculation of blueberry increased fruit yields as much as 92%, varying by the cultivar.
Evidence suggests that both ectomycorrhizae and ericoid mycorrhizae are capable of producing enzymes that allow them to access complex organic forms of both nitrogen and phosphorus (Dighton, 1991). It has also been demonstrated that ericoid mycorrhizae can assimilate proteins and amino acids from the soil and transfer those sources of nitrogen to the host plants (Stribley and Read, 1980; Bajwa and Read, 1986).

Little is known about the role of mycorrhizae in the uptake of other nutrients such as potassium, calcium and magnesium. George et al. (1992) found no increase in potassium uptake by mycorrhizal compared to nonmycorrhizal roots of *Agropyron repens*. Hyphal transport of sulfur, potassium and calcium has been demonstrated but the importance of such transport is unknown (Marschner, 1995).

In addition to mycorrhizal mediated nutrient acquisition, recent studies have demonstrated that mycorrhizae may influence the outcome of competitive interactions among plant species. For mycorrhizae to change the competitive outcome of neighboring plants, they must have different physiological effects on those plants. Indeed, it has been demonstrated by many researchers that plants exhibit different degrees of mycotrophy. Generally, plants have been divided into three groups based on their dependence on mycorrhizae, including nonmycotrophic, facultatively mycotrophic and obligately mycotrophic. It has become increasingly realized that although some plant species respond mutualistically to VA fungi, others may be antagonized, showing reduction in yield and survivorship (Francis and Read, 1995). Thus, mycorrhizal fungi may play a defining role in determining plant competitive relationships and ultimately community structure.
Several possible mechanisms for mycorrhizal mediation of plant species composition have been proposed in recent years. Grime et al. (1987) suggested that mycorrhizae mediated interplant transfer of resources from dominant to subordinate species may increase the abundance of the latter and thereby increase plant species diversity. Bergelson and Crawley (1988) suggested that mycorrhizae may increase plant species diversity by allowing competitive release of subordinate species from dominant species that are more weakly mycotrophic. Hartnett and Wilson (1999) have also considered that alterations in resource distribution between neighboring plants via hyphal connections could affect plant species composition.

In their study with three calcareous grassland plant species and four AMF species, van der Heijden et al. (1998a, 1998b) concluded that AMF communities have the potential to determine plant community structure. This conclusion was based on three key pieces of evidence. First, the three plant species differed in their dependence on AMF. Second, specific AMF species and AMF mixtures had significantly different effects on several plant growth variables and these effects varied among plant species. Third, the amount of variation in the growth response of a plant species to four AMF species and to the mixture of AMF species differed among the plant species.

Hartnett and Wilson (1999) found similar results in a grassland ecosystem in northern Kansas. They attributed the dominance of C4 grasses to the differential host species response to fungal colonization. This conclusion was based on the experimental
observation that the suppression of native mycorrhizae resulted in decreases in abundances of the dominant, obligately mycotrophic $C_4$ tall grasses and compensatory increases of many subordinate facultatively mycotrophic $C_3$ grasses and forbs.

Grime et al. (1987) found a similar shift in community structure in a microcosm study of pasture species. They demonstrated that the addition of mycorrhizae to a mixture of grasses and forbs shifted the community to a greater proportion of forbs.

The impact of mycorrhizal symbiosis on competition between *Andropogon gerardii* (big bluestem) and *Koeleria pyranidata* (junegrass) has also been demonstrated experimentally (Hetrick et al., 1989, 1994). *A. gerardii* was 98% dependent on the symbiosis, whereas *K. pyranidata* was less than 0.02% dependent. When competing in pairs, *A. gerardii* dominated when the mycorrhizal symbiosis was present and *K. pyranidata* dominated when it was not present. Thus, the competitive dominance of big bluestem in tallgrass prairies is strongly related to mycorrhizal status.

In another study, Hetrick et al. (1991) compared 23 prairie forbs with mycorrhizal symbioses to determine if flowering phenology or root morphology were important factors in predicting mycorrhizal dependence. The results of their study revealed that the best single predictor of mycorrhizal dependence was root fibrosity. Plants with relatively coarse root systems displayed high levels of mycorrhizal dependence, while those with highly fibrous root systems had low levels of dependence. The use of root morphology to predict mycorrhizal dependence was also affected by
phosphorus supply in the soil. Phosphorus dependence of nonmycorrhizal plants was found to be an important predictor at low P levels and root diameter was a significant predictor of dependence at higher P levels.

It is apparent from these data that mycorrhizae can cause shifts in plant community composition. Other studies have shown that mycorrhizae had no greater influence on plant competition than other biotic (herbivory) and abiotic (temperature, soil moisture) factors (Allen and Allen, 1990). Thus, the importance of mycorrhizae to competition will vary between plants and ecosystems. Given their potential importance to plant competition and species diversity, however, their incorporation in studies of plant competition may help to determine mechanisms of competition previously unexplained.

**Jostaberry**

The jostaberry (*Ribes nidigrolaria*) is classified in the *Ribes* genus of the Saxifragaceae family and is a cross between a black currant and a gooseberry (Bauer, 1986). Unlike its black currant parent, the jostaberry is resistant to white pine blister rust. In addition, it is mildew, rust, and gall-mite resistant.

Jostaberries are deciduous shrubs with alternate, simple, palmately veined and often clustered leaves. Stems are generally smooth but may have a few thorns at the nodes. Vegetatively propagated plants have a fibrous, adventitious, shallow root system (Harmat et al., 1990). Buds are located on one-year old shoots and are long, pointed, and light brown in color. Flower buds are usually located laterally along one-year old
shoots and fruit is mostly borne on one or two-year old wood. From the terminal flower buds, short internode fruiting structures (called strigs) form, each of which contain 1-3 flowers. Flowers are self-fertile and are insect pollinated.

Jostaberrties are planted in early spring or fall in rows 2-3 m apart and 1.5 m apart in the row. Pruning should be done during the dormant season to allow light penetration into the canopy and to balance growth. Since jostaberrties fruit on one-year old wood, pruning should maintain an abundance of strong one-year old wood and strong 2 or 3-year old wood with one-year old branches. A well maintained bush should have 8-10 canes, with about half being one-year old canes. The tips of branches should not be headed back (Harmat et al., 1990).

Lingonberry

A member of the Ericaceae, the lingonberry (Vaccinium vitis-idaea L.) is a woody, evergreen dwarf shrub distributed worldwide in northern temperate and subarctic areas (Stang et al., 1988). In Sweden, lingonberry bushes are frequently found in Scotch pine forests on average to poor quality sites, and coverage does not vary much in relation to the density of tree cover (Kardell, 1980). In Alaska, lingonberries have a diverse habitat from dry roadside slopes to acid-peat bogs, and from mature forests to fully exposed alpine tundra (Holloway, 1984). However, throughout its range, lingonberries appear to be most prevalent in forests with moist, acid soils with a well-developed organic matter layer and moderate shade.

Lingonberry fruit is an important berry crop that is harvested from the wild. Uses for the berry include sauce, preserves, candy, jelly, syrup, ice-cream, wine, and
liqueurs. Holloway (1981) noted at least 25 common names for *V. vitis-idaea* including lingonberry, cowberry, alpine cranberry, moss cranberry, mountain cranberry, partridgeberry, red whortleberry and lingon.

Plant stems of the lingonberry are semi-woody, each bearing numerous shoots 1-2 mm in diameter. The leaves are simple, evergreen, leathery, obovate and alternate in a spiral. Plants reproduce by seed and rhizomes. Roots consist of tap roots and adventitious roots at nodes along rhizomes and creeping stems. Flowers are produced in terminal racemes with four sepals, a bell-shaped corolla, eight stamens and four locules per ovary. Stang et al. (1993) found that flower initiation occurred at 8-12 hour daylengths in Wisconsin with a minimum of eight weeks photoperiod required for maximum floral induction. Berries are globose, red when ripe, and up to 1 cm in diameter (Stang et al., 1988). The fruit has a high tannin content, is very acid (pH of 2.5), and has a tart flavor (Penney et al., 1997).

**Blackberry**

Blackberries belong to the Rosaceae family and are classified as members of the genus *Rubus*, subgenus *Eubatus*, which comprises a widely variable group of plants. In general, *Rubus* species have perennial root systems with shoots that are biennial. These shoots, or canes, do not flower during the first year and are referred to as primocanes. In their second year, the canes flower and fruit and are termed floricanes. After fruiting, the floricanes die and must be pruned from the shrub.

American blackberry cultivars are classified as erect thorny, western trailing, semierect thornless, and erect thornless (Moore and Skirvin, 1990). The cultivar
'Navaho' is an erect, genetically thornless blackberry released by the University of Arkansas in 1988. It has vigorous, smooth canes, large fruit clusters, and ripens late in the season.

Floral initiation is believed to be triggered by low temperatures, short daylengths, genotype and environment (Moore and Skirvin, 1990). Inflorescences form at the terminals of the floricanes and the number of flowers per inflorescence varies greatly with genotype. Flowers consist of many pistils located above a succulent receptacle and surrounded by whorls of stamens. Each pistil develops into a single drupelet with a single seed. The fruit that is eaten is actually composed of many drupelets that share a common receptacle and is referred to as an aggregate fruit. Individual fruits may weigh up to 10g each, but most are between 5 and 8g (Moore and Caldwell, 1983).

Blackberries are usually planted in the spring in rows spaced 10-12 ft apart and 4 ft apart within the row. Erect blackberries must be pruned both in the summer and winter. In the summer, primocanes are cut back to 36 to 48 inches. Since primocanes emerge all summer long, pruning must be done throughout the summer. After fruiting, floricanes must be removed before the following spring. During dormant pruning, laterals are cut back to 12–18 inches and weak, damaged or dead canes are removed (Goulart et al., 1996).

**Honeyberry**

Native to eastern Siberia and the Kurile Islands, the honeyberry (*Lonicera caerulea*) is a member of the honeysuckle family, Caprifoliaceae. The taxonomy of this
polymorphic species is complex due to its extremely wide geographic, ecological, and morphological variation. Significant variations have been observed in growth habit, leaf pubescence and fruit flavor (Kuklina, 1985). It is virtually unknown as a horticultural crop in the United States. The plant is reportedly shade tolerant, but unlike many other honeysuckle species, it is not invasive. Small, white, fragrant flowers are produced in March or April and berries ripen in June. The berry is blue and looks like an elongated blueberry.

All members of the Caeruleae subsection of the genus are considered to be self-sterile, as stamens ripen 20-28 hours later than the pistil. In a comparison of 45 varieties of edible *Lonicera*, Plekhanova (1982) found that fruit set was only 0.6-8.7% when naturally self-pollinated, 2.5-8.7% when artificially self-pollinated, and 30-50% under natural pollination (mixture of pollen) conditions. As a result, at least two cultivars are required for pollination and fruit set.

**Apple**

The domestic apple (*Malus domestica* Borkh.) is thought to have originated in the Caucasus region of southeastern Europe and possibly southwestern Siberia (Westwood, 1993). The genus consists of approximately 15 primary species, including 4 from North America, 2 from Europe and the rest from Asia. Most of the domestic cultivars grown in the United States are derived from *Malus pumila* Mill., the common apple of Europe.

Although some apple species are non-hardy, the apple is one of the hardiest temperate-zone fruit, requiring 1000-1600 winter chilling hours for most commercial
cultivars. The time required to mature the fruit can be as short as 70 days or more than 180 days. Although there are several hundred named cultivars of apples, about 90% of U.S. production comes from only 13 varieties of which 5 account for more than 2/3 of all production (Westwood, 1993).

Apple is a deciduous tree with ovoid, imbricate scaled buds and simple, entire leaves that are serrate or lobed. Flowers are white to pink in color with 15-50 stamens, yellow anthers and an inferior ovary. The inflorescence is determinate with 5 or sometimes 6 flowers. Flower buds are usually formed on terminal shoots or short spurs. Floral bud initiation occurs in early summer for the following year’s fruit. The fruit is a pome and the color is variable depending on variety from deep red to bright red, yellow, green/red bicolors, green, and yellows/greens with a pink to reddish blush.

In apple, fruit set does not occur with every flower; only 2-8% of flowers set fruit (Westwood, 1993). However, under orchard conditions, apple will still set more fruit than is needed for a full crop of large-sized fruits. Thus, fruit thinning is routinely done in apple orchards to increase fruit size, reduce limb breakage, improve color and quality and to stimulate floral initiation for the following year’s crop. Three different methods of fruit thinning that are typically used in apple orchards include hand-picking, mechanical, and chemical.

Roots of apple trees will generally spread 2 to 3 times as far as the branches and will spread downward until further growth is prevented by an impervious layer of subsoil or water table (Epstein, 1973). Commercial apples are grafted onto several types of rootstocks, which significantly affects the performance of the scion: yield
efficiency, yield per tree, resistance to pests and diseases, hardiness, tree size, fruit quality, precocity, root suckering, anchorage, and ease of propagation (Ferree and Carlson, 1987). Although choice of rootstock affects tree size, the ultimate size of a mature tree on a given rootstock also depends on soil, climate, culture and choice of scion, since the inherent vigor of a variety will carry through regardless of the rootstock (Westwood, 1993).

Various measurements of plant growth have been used to approximate total above ground growth of apple trees. Such measurements include shoot length, tree height, fresh or dry weight, leaf area index, leaf efficiency, trunk, stem or limb diameter, plant volume, fruit size, and yield. The abundance of measurements has developed out of the need to quantify plant efficiency without destructively harvesting the tree, especially since full apple production and maturity does not occur until several years after planting.

Trunk diameter has been used as a simple estimate for total tree size since the 1920’s; C.D. Murray reported a predictable correlation between the volume of the shoot system and the cross-sectional area of the tree trunk (Westwood, 1993). Trunk cross-sectional area has a linear relationship to total above ground weight and allows for the calculation of yield efficiency, regardless of tree size. However the relationship between trunk cross-sectional area and above ground weight is best when used for measuring young, widely spaced trees that have not been severely pruned.

There is a paucity of information regarding the use of apple trees as a component of a polyculture or agroforestry system. The influence of different ground cover systems
on the growth of young apple trees has, however, been an area of limited research in the apple literature. Although ground covers are essential in orchards to control erosion, many of the species used are vigorous grasses that compete with the trees for water and nutrients. Shribbs and Skroch (1986) evaluated 12 different cover systems to determine their influence on apple tree growth. Their study compared mulch, bare ground, cultivated ground, blackberry (*Rubus* spp.), Korean lespedeza (*Lespedeza stipulaciea* Maxim.), red sorrel (*Rumex acetosella* L.), tall broadleaf complex, wheat (*Triticum aestiyum* L.), nimblewill (*Muhlenbergia schreberii* J.F. Gmel.), Kentucky bluegrass (*Poa pratensis* L.), orchardgrass (*Dactylis glomerata* L.), and tall fescue (*Festuca arundinacea* L.). After four years of growth, they found that the blackberry, red sorrel, wheat, and nimblewill covers did not inhibit tree growth, as compared to the management systems without living plants. Trees in tall broadleaf, Kentucky bluegrass, orchardgrass, and tall fescue covers were smaller than those in all the other treatments.

In a greenhouse study, Shribbs et al. (1986) compared two grass (orchardgrass, Kentucky bluegrass) and two broadleaf species (red sorrel, Korean lespedeza) at four densities and fertility levels on the growth of apple seedlings. The results of their experiments indicated that apples and groundcovers competed for nitrogen when balanced nutrients were available and that although nitrogen deficiencies could be overcome by the addition of nitrogen, growth inhibition was only partially overcome. They found that orchardgrass and red sorrel inhibited tree growth more than Kentucky bluegrass and they attributed this to differences in biomass production.
CHAPTER 3

GROWTH AND FRUITING OF FIVE COMPONENT PLANT SPECIES OF AN APPLE POLYCULTURE IN THE FIELD

INTRODUCTION

Polyculture is a traditional farming strategy designed to promote diet diversity, income generation, production stability, minimization of risk, reduced insect and disease incidence, efficient use of labor, intensification of production with limited resources and land area, and maximization of returns under low levels of technology (Altieri, 1987).

Agroforestry is a type of polyculture in which trees are combined spatially and temporally with agricultural crops and/or animals.

Trees can improve the productivity of a given agroecosystem by influencing soil characteristics, hydrology, and microclimate (Farrell, 1987). Trees can potentially affect the nutrient status of the soil by exploiting deeper mineral reserves or capturing leached nutrients. Through the deposition of their leaf litter, these minerals are returned to the soil as organic matter. Increased organic matter improves soil structure and increases the soil humus content, cation exchange capacity, and microorganism activity.

In a study to evaluate the effect of trees on soil fertility, Farrell (1987) found that available phosphorus increased up to sevenfold under capulin \( (Prunus capuli) \) and sabina \( (Juniperus deppeana) \). Both trees are utilized in traditional farming systems in
central Mexico. In addition, total carbon and potassium increased two- to threefold, nitrogen, calcium and magnesium increased one-and-a-half- to threefold, and cation exchange capacity increased one-and-a-half- to twofold in such systems.

Trees also alter the microclimate by reducing wind speed, and moderating temperature changes and relative humidity under the canopy. In general, tree canopies result in lower maximum and higher minimum temperatures under the canopy as compared to in open areas (Farrell, 1987). In addition, there is evidence that trees can also bring water from deeper in the soil profile to the soil surface where it can be taken up by understory crops (Dawson, 1993; Caldwell et al., 1998; Horton and Hart, 1998).

Despite the extensive use of trees in polyculture systems throughout the world, competitive interactions between tree and crop can be significant. The component plant species in agroforestry systems usually differ greatly in size, and the smaller understory species may be inhibited by shading and possibly by competition for water and nutrients.

When water and nutrients are freely available, light is usually the primary limiting factor to growth and reproduction. When resources are not limiting, densely planted monocultures usually provide the most efficient resource capture system (Ong et al., 1996). For an agroforestry system to be more productive than its corresponding sole crops, the combination must be able to capture more of the available resources or to use them more efficiently. Under such circumstances, the combination usually provides a greater yield than yields of its component crops when in grown in monoculture. Such yield advantages have been widely reported for intercrops and are often expressed in
terms of Land Equivalent Ratio (LER). LER is the ratio of the area under sole cropping to the area under intercropping, at the same level of management, that gives an equal amount of yield (Ong, 1996). For example, Natarajan and Willey (1981) found that 0.94 hectares of sorghum monoculture and 0.68 hectares of pigeonpea monoculture were needed to produce the same quantities of sorghum and pigeonpea that were harvested from a 1.0 hectare polyculture. The LER of the polyculture was thus 1.62. Although the yield of each crop species in the combination was reduced by competition, the total yield of the polyculture on an area basis was 62% greater than for the monocultures.

In a polyculture system where one component species is a tree and the other is an annual crop, the tree species has a considerable advantage in sequestering both above- and below-ground resources since the tree is usually well-established before the crop is ever sown. Corlett et al. (1992a, 1992b) found that the gain in resource capture of a *Leucaena leucocephala* / pearl millet (*Pennisetum typhoides*) alley-cropping system was insufficient to offset the reduced light capture by the pearl millet. This problem is less serious if the tree component is also used to produce high value crops, such as fruit, that could offset the loss in yield of the crop component.

That successful agroforestry systems exist is not in question. However, current research in the area of agroforestry is centered on understanding resource capture principles to understand the mechanisms involved in tree-crop interactions (Ong et al.,
1996). Spatial sharing of below ground resources is another area of continuing research in agroforestry. Thus far, very little research has been done in agroforestry systems that include woody understory species combined with tree species.

The objective of this study was to compare four potential agroforestry systems in which all component species are woody perennials that produce a valued fruit crop. ‘Goldrush’ apple (*Malus* Mill.) on M.7 rootstock were intercropped with either lingonberry (*Vaccinium vitis-idaea*, cv. ‘Red Pearl’ and ‘Koralle’), honeyberry (*Lonicera kamchatika*, cv. ‘Bluebelle’ and ‘Blue Velvet’), jostaberry (*Ribes nidigrolaria*) or blackberry (*Rubus* spp., cv. ‘Navaho’). Plant performance was evaluated based on measurements of above-ground growth, flowering, fruit set and fruit yield. A second objective was to compare the distribution of root systems between the tree and each understory species.

**MATERIALS AND METHODS**

An apple/berry polyculture was designed and planted in May and June 1999 at the Ohio Agricultural Research and Development Center (OARDC) in Wooster, Ohio. The soil type was a Wooster silt loam (fine-loamy, mixed mesic Typic Fragiudalf). Apples were planted on May 20 and the berries were planted on June 18, 21, and 23, 1999. There were 17 treatments, eight of which consisted of an apple/berry polyculture at two different distances from the tree. The remaining treatments included monoculture controls for the first eight treatments and an apple control. Each treatment was replicated five times in a randomized complete block design.
Distances from the apple tree were based on the recommended between-row distances for each of the berry crops. For each berry, two treatments consisted of berries planted at one-half the recommended distance, while the remaining two treatments were planted at the recommended distance. On this basis, lingonberries were planted alone and in combination with apple in rows that were either 0.6 or 1.2m apart and 0.3m apart within the row. Honeyberries and jostaberies were planted in rows that were either 0.9 or 1.8m apart and 1.2m apart within the row. Blackberries were planted in rows that were either 1.2 or 2.4m apart and 1.2m apart within the row. In all cases, apple trees were planted in the center of the plot. Berries were planted in rows on the east and west sides of the tree.

Planting holes were amended with 1:1 v/v of peat and native soil. Plots were covered with landscape fabric for weed control (entire plot plus a 61cm border around the plots) and pesticides were sprayed as needed. Hand-weeding around the base of the plants was done as needed. On May 3, 2000 a 2-4cm deep layer of wood-chip mulch was placed around the base of each plant to further suppress weeds. A fresh layer of mulch was applied in April 2001.

Plant performance was determined by measuring above-ground growth for each species at the end of each growing season. Flowering, percent fruit set and fruit yield were also measured in 2000 and 2001.

The diameter of the apple trunks 30cm above the graft union was measured on a yearly basis: July 1, 1999; November 11, 1999; October 11, 2000; October 15, 2001. Diameter measurements were then converted to trunk cross-sectional area. The total
number of flowers on each tree were counted on April 24, 2000 and April 24, 2001. Apples were harvested on October 10, 2000 and October 17, 2001. For each year, the percentage of fruit set was calculated.

In 1999, for each of the four berry species, growth was estimated by measuring the height of the longest shoot and spread in two directions. All berries were measured initially on July 21, 1999. Year-end measurements were taken for all berries except honeyberry on November 11, 1999. Honeyberry plants were not measured because they had dropped their leaves within one month of planting. These measurements were then converted to total above-ground volume.

In June and July 2000, 23 additional plants of each berry species were manipulated to determine the growth variables that provided the best estimate of above-ground dry weight. Several variables were measured for each plant species and multiple regression analyses were performed to determine which variables provided the best estimate of dry weight. For lingonberry, those variables were the same as those measured in 1999: length of the longest shoot, depth and width (P<0.0001, r²=0.86). Blackberry growth was estimated by measuring the total number of canes, the total number of laterals, the length of the first and third longest shoots (P<0.0001, r²=0.72). In addition, pruned blackberry canes taken during the year were separated by age of the wood, bagged, oven-dried, and weighed. Jostaberry growth was estimated by measuring the diameter of the largest trunk 5-cm above the ground, the length of first and second longest shoots, the total number of trunks, the total number of laterals, the width and the depth of the plant (P<0.03, r²=0.55). The two different honeyberry cultivars had to be
measured using different variables due to the difference in their growth habits. ‘Blue Velvet’ growth was estimated by measuring the total number of trunks, the total number of laterals, and the length of the longest shoot (P<0.001, r²=0.91). ‘Blue Belle’ growth was estimated by measuring the diameter of the largest trunk 4-cm above the ground, the total number of trunks, the length of the first and third longest shoots, the width and the depth of the plant (P<0.03, r²=0.89). Subsequent growth measurements for all four berry species were taken on October 11, 2000 and October 20, 2001.

Bloom, fruit set, and fruit yield were measured for all berry species in 2000 and 2001. In 2000, fruit yield could not be measured for honeyberry because flowering of the two cultivars was phenologically separated and fruit was not produced. ‘Blue Velvet’ bloom was measured on April 28, 2000 as were floral remnants on ‘Blue Belle’. In 2001, the two cultivars were only one week apart in their bloom times. Flowers were counted on April 13, 2001 for ‘Blue Belle’ and on April 19, 2001 for ‘Blue Velvet’. Fruit was harvested on May 25 and 29, 2001. Lingonberry bloom was not measured in 2000 or 2001, but berries were harvested on August 29 and October 10, 2000 and October 2, 2001. Jostaberry bloom was measured April 28, 2000 and berries were harvested on June 30 and July 17. In 2001, jostaberry bloom was measured on April 24 and fruit was harvested on June 28, July 5, July 13, and July 19. In 2000, blackberry bloom was measured on two canes per plant on June 2 and berries were harvested on July 17, August 2, 11, 24, September 1, 7, 20, 27, October 3, 10. In 2001, blackberry bloom was measured on two laterals per plant on June 7 and berries were harvested on July 19, 22, 27, August 2, 8, 14, 21, 28, September 5, 11, 18, and 25.
Soil cores were taken from all the plots containing apple, blackberry, and/or jostaberry in the fall of 2001. Four subsamples were taken from each plot at an equidistant location from the center of the plot (the center of the soil area shared by the apple and berry). Soil cores were 12.7 cm in diameter and were taken at two different depths: 0-20 cm and 21-40 cm. Roots within the cores were washed free of soil, separated by species and root diameter (0-1 mm, 1-4, and >4), oven-dried and weighed. The root lengths of randomly chosen core samples were also measured by species using the root-intersect method (Newman, 1966).

The closely spaced polyculture treatments were replicated in a second location under four year old 'Golden Delicious' trees on M.9 rootstock on May 10, 2000. The purpose of this replication was to determine if there were differences in the growth and fruiting behavior of the understory berry crops when placed under already established apple trees as compared to planting under newly planted whips. The berries planted under the older trees were of the same physiological age as those planted under the apple whips the previous year. The same growth and fruiting parameters were measured for all the berry species.

RESULTS

Apple Growth and Yield Parameters

Apple shoot length per year and trunk cross-sectional area were generally smaller in the polyculture treatments beginning in 2000 and continuing into 2001 (Table 3.1). While the reduction in growth was not significantly different from the monoculture in the honeyberry and lingonberry treatments, both growth variables were
<table>
<thead>
<tr>
<th>Treatment</th>
<th>1999</th>
<th>2000</th>
<th>2001</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Total Shoot Length (m)</td>
<td>Cross-sectional Area (cm²)</td>
<td>Total Shoot Length (m)</td>
</tr>
<tr>
<td>Apple</td>
<td>0.59 ab ¹</td>
<td>277.3 ab</td>
<td>2.46 a</td>
</tr>
<tr>
<td>+ Blackberry (R)</td>
<td>0.63 a</td>
<td>301.1 ab</td>
<td>1.85 bc</td>
</tr>
<tr>
<td>+ Blackberry (C)</td>
<td>0.45 ab</td>
<td>245.7 b</td>
<td>1.38 cd</td>
</tr>
<tr>
<td>+ Honeyberry (R)</td>
<td>0.43 ab</td>
<td>232.9 b</td>
<td>2.12 ab</td>
</tr>
<tr>
<td>+ Honeyberry (C)</td>
<td>0.58 ab</td>
<td>272.1 ab</td>
<td>2.16 ab</td>
</tr>
<tr>
<td>+ Jostaberry (R)</td>
<td>0.59 ab</td>
<td>326.2 a</td>
<td>1.73 bc</td>
</tr>
<tr>
<td>+ Jostaberry (C)</td>
<td>0.42 b</td>
<td>230.0 b</td>
<td>0.97 d</td>
</tr>
<tr>
<td>+ Lingonberry (R)</td>
<td>0.47 ab</td>
<td>263.7 ab</td>
<td>2.23 ab</td>
</tr>
<tr>
<td>+ Lingonberry (C)</td>
<td>0.57 ab</td>
<td>273.0 ab</td>
<td>2.26 ab</td>
</tr>
</tbody>
</table>

¹ Treatments followed by (R) stand for apple + berry at the recommended spacing for the berry, while those followed by (C) stand for apple + berry at close spacing for the berry.

² Treatment means were separated using Duncan’s Multiple Range Test (P<0.05). Means followed by the same letter are not significantly different.

Table 3.1: Mean shoot length and trunk cross-sectional area of ‘Goldrush’ apple as influenced by four understory berry species at two spacings.
Figure 3.1: Mean apple shoot length per year when grown in monoculture (A) and when grown in combination with blackberry (B) or jostaberry (J) at recommended (rec) or at close spacing for the berry

significantly affected by the blackberry and jostaberry treatments. The negative effect on apple growth in the blackberry and jostaberry treatments was compounded by close spacing (C) of the berries, but this further reduction in apple growth did not differ from the recommended spacing (R) of berries. A jostaberry understory appeared to have a greater negative effect on apple growth than did blackberry, as the apples in the jostaberry (R) treatment were nearly equal in size as the apples in the blackberry (C) treatment (Table 3.1). This trend was especially apparent for apple shoot length by the end of 2001 (Figure 3.1).

In 2001, apple yield was significantly reduced (P<0.0001) by all polyculture treatments (Table 3.2). Other yield parameters, including bloom, apple size, and percent...
fruit set were not affected by a lingonberry (R, C) understory. Other than a reduction in bloom in the honeyberry (C) treatment, a honeyberry understory did not affect the remainder of the yield parameters. The blackberry and jostaberry treatments significantly reduced all yield parameters examined regardless of berry spacing. Yield was so reduced in these treatments that apple size could not be calculated for either jostaberry treatment or for the blackberry (C) treatment, since a sufficient sample of apples was not available.

Apple yield parameters followed a similar trend as the growth parameters, as a jostaberry understory seemed to have a greater negative effect than blackberry (R), while the honeyberry and lingonberry treatments had little effect on the apple.

**Berry Growth and Yield Parameters**

Blackberry plant size, in terms of estimated dry weight, was significantly affected by both the spacing of the berries and the presence of an apple overstory. The blackberries in the polyculture (C) treatment were already significantly smaller by the end of 2000, than the blackberries in all other treatments (Table 3.3). By the end of 2001, the blackberries in the closely spaced treatments were smaller than those in the treatments with recommended spacing, but there were no differences between those berries with respect to the presence or absence of an apple tree. However, at recommended spacing, the presence of an apple tree did significantly reduce blackberry plant size.

Throughout the three seasons of growth, the blackberry monoculture (R) treatment had the most canes removed through the normal pruning process (Table 3.3).
Table 3.2: Mean apple bloom, yield, apple size and percent fruit set in 2000 and 2001 when grown in monoculture and when grown in polyculture with a berry understory.
<table>
<thead>
<tr>
<th>Treatment</th>
<th>Estimated Dry Weight (g)</th>
<th>Weight of Pruned Canes (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2000</td>
<td>2001</td>
</tr>
<tr>
<td>Blackberry (R)</td>
<td>102.58 a</td>
<td>140.96 a</td>
</tr>
<tr>
<td>Blackberry (C)</td>
<td>95.66 a</td>
<td>108.62 bc</td>
</tr>
<tr>
<td>+ Apple (R)</td>
<td>99.05 a</td>
<td>118.75 b</td>
</tr>
<tr>
<td>+ Apple (C)</td>
<td>85.43 b</td>
<td>104.32 c</td>
</tr>
</tbody>
</table>

1 Total above ground dry weight estimated by measuring the total number of canes, the total number of laterals, and the length of the first and third longest shoots ($P \leq 0.0001$, $r^2 = 0.72$).
2 First, Second and Third refer to the three seasons of growth evaluated in this study.
3 (R) refers to monoculture or polyculture (+ Apple) treatments grown at a recommended between row spacing of 2.4m.
4 (C) refers to monoculture or polyculture (+ Apple) treatments grown at a close spacing of 1.2m between rows.
5 Treatment means were separated using Duncan’s Multiple Range Test ($P \leq 0.05$). Means followed by the same letter are not significantly different.

Table 3.3: Estimated dry weight of individual blackberry plants when grown at two different spacings in either a monoculture or when grown below an apple overstory.

The weight of these canes also served as a measure of plant productivity and as early as the 1999 growing season, differences between the treatments were observed. In all three seasons, the spacing of the blackberries affected pruned cane weight more than did the presence of an apple tree. While the polyculture treatments did reduce cane weight, the effect was most pronounced when the blackberries were already spaced closely. In fact, there was not a significant difference in the total weight of pruned canes between the blackberry (R) treatment and the apple + blackberry (R) treatment.
Blackberry fruit size and percent fruit set were largely unaffected by the treatments in 2000 and 2001 (Table 3.4). Although yield was also unaffected by the treatments in 2000, by 2001, yield was significantly reduced in the polyculture treatments as compared to the monoculture treatments. Unlike its effect on plant size, blackberry spacing had no effect on yield (Figure 3.2).

There were no differences among treatments with respect to plant size of 'Blue Belle' honeyberry plants in any of the three years measured (Table 3.5). As early as one year after planting, 'Blue Velvet' plants were significantly smaller when planted in a monoculture at the recommended spacing than in any of the other treatments.

There was an observed difference in the growth habits of the two cultivars. 'Blue Belle' had an upright habit while 'Blue Velvet' was much more spreading. 'Blue Belle' also leafed out and flowered earlier in the spring and lost its leaves earlier in the autumn than did 'Blue Velvet.'

There were no differences in bloom of 'Blue Belle' or 'Blue Velvet' in 2000 (Table 3.6). Because 'Blue Belle' flowered two weeks earlier than 'Blue Velvet,' bloom was the only yield parameter measured in 2000. Although 'Blue Belle' still bloomed earlier than 'Blue Velvet' in 2001, there was enough of an overlap in bloom times for pollination to occur and yield and percent fruit set were measured in addition to bloom. While 'Blue Belle' bloom was unaffected by treatment, yield and percent fruit set were lower in both monoculture treatments than in the polycultures (Table 3.6). This same trend was observed in the measured yield parameters of 'Blue Velvet.' Bloom, yield, and
<table>
<thead>
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<th>Treatment</th>
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<th>2001</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Plot Yield (g)</td>
<td>Berry Size (g)</td>
</tr>
<tr>
<td>Blackberry (R) ¹</td>
<td>5891 a³</td>
<td>3.99 b</td>
</tr>
<tr>
<td>Blackberry (C) ²</td>
<td>4629 a</td>
<td>3.87 b</td>
</tr>
<tr>
<td>+ Apple (R)</td>
<td>6455 a</td>
<td>4.62 a</td>
</tr>
<tr>
<td>+ Apple (C)</td>
<td>5392 a</td>
<td>4.31 ab</td>
</tr>
</tbody>
</table>

¹ (R) refers to monoculture or polyculture (+ Apple) treatments grown at a recommended between row spacing of 2.4m.
² (C) refers to monoculture or polyculture (+ Apple) treatments grown at a close spacing of 1.2m between rows.
³ Treatment means were separated using Duncan's Multiple Range Test ($P \leq 0.05$). Means followed by the same letter are not significantly different.

Table 3.4: Blackberry yield, fruit size, and percent fruit set when grown at two different spacings in either a monoculture or under an apple overstory.
Figure 3.2: Mean blackberry yield per plot when grown in monoculture (B) or in combination with apple (A+B) at the recommended (rec) between row spacing of 2.4m and at a close spacing of 1.2m between rows.

percent fruit set of 'Blue Velvet' was also lowest in the monoculture (R) treatment than in all other treatments. Although there were no differences in bloom or yield between the remaining three treatments, percent fruit set was significantly higher in the monoculture (C) treatment.

In addition to the difference in bloom times between 'Blue Belle' and 'Blue Velvet', there were significant differences in the fruiting parameters of the two cultivars (Table 3.7). Despite equivalent yields, the two cultivars differed in bloom, fruit size, and percent fruit set. Bloom, as measured by the number of flowers per plant, was more than
<table>
<thead>
<tr>
<th>Treatment</th>
<th>Blue Belle Estimated Dry Weight (g)</th>
<th></th>
<th>Blue Velvet Estimated Dry Weight (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2000</td>
<td>2001</td>
<td></td>
</tr>
<tr>
<td>Honeyberry (R)</td>
<td>211.23 a</td>
<td>287.30 a</td>
<td>153.93 b</td>
</tr>
<tr>
<td>Honeyberry (C)</td>
<td>189.23 a</td>
<td>271.19 a</td>
<td>194.72 a</td>
</tr>
<tr>
<td>+ Apple (R)</td>
<td>200.86 a</td>
<td>285.14 a</td>
<td>200.94 a</td>
</tr>
<tr>
<td>+ Apple (C)</td>
<td>219.97 a</td>
<td>304.27 a</td>
<td>192.70 a</td>
</tr>
</tbody>
</table>

1 Total above ground dry weight estimated by measuring the diameter of the largest trunk 4cm above the ground, the total number of trunks, the length of the first and third longest shoots, the width and the depth of the plant ($P \leq 0.03$, $r^2 = 0.89$).

2 Total above ground dry weight estimated by measuring the total number of trunks, the total number of laterals and the length of the longest shoot ($P \leq 0.001$, $r^2 = 0.91$).

3 (R) refers to monoculture or polyculture (+ Apple) treatments grown at the recommended between row spacing of 1.8m.

4 (C) refers to monoculture or polyculture (+ Apple) treatments grown at a close spacing of 0.9m between rows.

5 Treatment means were separated using Duncan’s Multiple Range Test ($P \leq 0.05$). Means followed by the same letter are not significantly different.

Table 3.5: Estimated dry weight of honeyberry cultivars ‘Blue Belle’ and ‘Blue Velvet’ when grown at two different spacing in either a monoculture or under an apple overstory.
<table>
<thead>
<tr>
<th>Treatment</th>
<th>2000</th>
<th>2001</th>
<th>2000</th>
<th>2001</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Blue Belle</td>
<td>Blue Velvet</td>
<td>Blue Belle</td>
<td>Blue Velvet</td>
</tr>
<tr>
<td>Flowers Per Plant</td>
<td>Flowers Per Plant</td>
<td>Flowers Per Plant</td>
<td>Flowers Per Plant</td>
<td>Fruit Set (%)</td>
</tr>
<tr>
<td>Honeyberry (R)¹</td>
<td>36.0 a³</td>
<td>95.1 a</td>
<td>12.93 b</td>
<td>210.6 b</td>
</tr>
<tr>
<td>Honeyberry (C)²</td>
<td>56.2 a</td>
<td>107.8 a</td>
<td>21.73 ab</td>
<td>261.0 ab</td>
</tr>
<tr>
<td>+ Apple (R)</td>
<td>61.9 a</td>
<td>119.7 a</td>
<td>28.57 a</td>
<td>310.0 a</td>
</tr>
<tr>
<td>+ Apple (C)</td>
<td>56.2 a</td>
<td>120.8 a</td>
<td>34.93 a</td>
<td>282.2 ab</td>
</tr>
</tbody>
</table>

¹ (R) refers to monoculture or polyculture (+ Apple) treatments grown at the recommended between row spacing of 1.8m.
² (C) refers to monoculture or polyculture (+ Apple) treatments grown at a close spacing of 0.9m between rows.
³ Treatment means were separated using Duncan's Multiple Range Test (P ≤ 0.05). Means followed by the same letter are not significantly different.

Table 3.6: Bloom, yield and percent fruit set of two honeyberry cultivars, 'Blue Belle' and 'Blue Velvet' when grown at two different spacings in either a monoculture or under an apple overstory.
<table>
<thead>
<tr>
<th>Cultivar</th>
<th>No. of Flowers</th>
<th>Yield (g)</th>
<th>Fruit Size (g)</th>
<th>Fruit Set (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Blue Belle</td>
<td>110.85 b</td>
<td>24.54 a</td>
<td>0.40 b</td>
<td>51.1 a</td>
</tr>
<tr>
<td>Blue Velvet</td>
<td>265.98 a</td>
<td>20.81 a</td>
<td>0.73 a</td>
<td>11.6 b</td>
</tr>
</tbody>
</table>

1 Treatment means were separated using Duncan's Multiple Range Test ($P \leq 0.05$). Means followed by the same letter are not significantly different.

Table 3.7: Cultivar differences between 'Blue Belle' and 'Blue Velvet' with respect to bloom, yield, fruit size, and percent fruit set.

twice as great in 'Blue Velvet' as in 'Blue Belle.' Fruit size of 'Blue Velvet' was also nearly twice that of 'Blue Belle.' Percent fruit set, however, was nearly five times higher in 'Blue Belle' than in 'Blue Velvet.'

After three seasons of growth, jostaberry plant size was significantly affected by the treatments (Table 3.8). Both plant volume and estimated dry weight were greatest in the monoculture (R) treatment in 2000 and 2001. By 2001, the addition of an apple tree significantly reduced both parameters but not to as large a degree as decreasing the the spacing between rows of jostaberry plants. In fact, the plants in the monoculture (C) treatment were significantly smaller than those in the polyculture (R) but no different in size than those in the polyculture (C) treatment.

Yield parameters including bloom, yield, and percent fruit set of jostaberry were unaffected by the treatments in 2000 (Table 3.9). By 2001, bloom was reduced in the polyculture treatments but the reduction was not significantly lower than the monoculture (C) treatment. Although yield was also reduced by the addition of an apple...
### Table 3.8: Estimated plant volume and dry weight of jostaberry when grown at two different spacings in either a monoculture or under an apple overstory.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Plant Volume (m³)</th>
<th>Estimated Dry Weight (g)</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1999</td>
<td>2000</td>
<td>2001</td>
</tr>
<tr>
<td>Jostaberry (R)²</td>
<td>0.29  a⁴</td>
<td>1.51  a</td>
<td>2.74  a</td>
</tr>
<tr>
<td>Jostaberry (C)³</td>
<td>0.31  a</td>
<td>1.24  b</td>
<td>1.46  c</td>
</tr>
<tr>
<td>+ Apple (R)</td>
<td>0.25  a</td>
<td>1.29  ab</td>
<td>2.10  b</td>
</tr>
<tr>
<td>+ Apple (C)</td>
<td>0.31  a</td>
<td>1.18  b</td>
<td>1.40  c</td>
</tr>
</tbody>
</table>

1 Total above ground dry weight estimated by measuring the diameter of the largest trunk 5cm above ground, the length of the first and second longest shoots, the total number of trunks, the total number of laterals, and the width and depth of the plant (P ≤ 0.03, r² = 0.55).

² (R) refers to monoculture or polyculture (+ Apple) treatments grown at the recommended between row spacing of 1.8m.

³ (C) refers to monoculture or polyculture (+ Apple) treatments grown at a close spacing of 0.9m between rows.

⁴ Treatment means were separated using Duncan’s Multiple Range Test (P ≤ 0.05). Means followed by the same letter are not significantly different.

Tree, the difference was not significant from the monoculture treatments. Percent fruit set was higher when the jostaberry plants were closely spaced, with or without the presence of an apple tree, but again this difference was not significant from jostaberry set when the plants were at the recommended spacing.

Lingonberries were unaffected by the treatments in terms of plant size and yield in each of the three seasons of growth (data not shown). Although each plot initially contained one row of ‘Koralle’ and one row of ‘Red Pearl,’ by the end of 2000 nearly all of the ‘Koralle’ plants had died, leaving only one row of ‘Red Pearl’ per plot.
<table>
<thead>
<tr>
<th>Treatment</th>
<th>2000</th>
<th>2001</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No. of Flowers</td>
<td>Yield (g)</td>
</tr>
<tr>
<td>Jostaberry (R) ¹</td>
<td>37.90 a³</td>
<td>23.73 a</td>
</tr>
<tr>
<td>Jostaberry (C) ²</td>
<td>37.15 a</td>
<td>18.20 a</td>
</tr>
<tr>
<td>+ Apple (R)</td>
<td>28.75 a</td>
<td>12.13 a</td>
</tr>
<tr>
<td>+ Apple (C)</td>
<td>32.20 a</td>
<td>16.71 a</td>
</tr>
</tbody>
</table>

¹ (R) refers to monoculture or polyculture (+ Apple) treatments grown at the recommended between row spacing of 1.8m.
² (C) refers to monoculture or polyculture (+ Apple) treatments grown at a close spacing of 0.9m between rows.
³ Treatment means were separated using Duncan’s Multiple Range Test (P ≤ 0.05). Means followed by the same letter are not significantly different.

Table 3.9: Jostaberry bloom, yield, and percent fruit set when grown at two different spacings in either a monoculture or under an apple overstory.

**Root Growth Parameters**

Apple root length and mass were largely unaffected by treatment at both the 0-20cm (P1) and 20-40cm (P2) soil depths (Table 3.10). The percentage of apple roots from the total roots collected within each soil core sample from P1 was reduced from 100% in the apple monoculture to 47% in the jostaberry (C), 36% in the jostaberry (R), 35% in the blackberry (R), and 33% in the blackberry (C) treatment. However, there were no differences in the percentage of apple roots between the blackberry (R, C) and jostaberry (R, C) treatments. The percentage of apple roots in P2 soil cores followed the same trend as that of the shallow soil profile. The proportion of apple roots was
<table>
<thead>
<tr>
<th>Treatments</th>
<th>Root Length (cm) 0-20 cm</th>
<th>Root Length (cm) 20-40 cm</th>
<th>Feeder Root Mass (&lt;1 mm) 0-20 cm</th>
<th>Feeder Root Mass (&lt;1 mm) 20-40 cm</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Apple</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Apple</td>
<td>1589.8 a ³</td>
<td>1242.8 a</td>
<td>81.1 b</td>
<td>99.7 a</td>
</tr>
<tr>
<td>+ Blackberry (R)</td>
<td>960.4 a</td>
<td>558.0 a</td>
<td>124.2 ab</td>
<td>103.9 a</td>
</tr>
<tr>
<td>+ Blackberry (C)</td>
<td>1364.9 a</td>
<td>1227.7 a</td>
<td>132.4 ab</td>
<td>97.5 a</td>
</tr>
<tr>
<td>+ Jostaberry (R)</td>
<td>1386.8 a</td>
<td>1513.2 a</td>
<td>214.8 a</td>
<td>91.8 a</td>
</tr>
<tr>
<td>+ Jostaberry (C)</td>
<td>1515.4 a</td>
<td>986.2 a</td>
<td>199.7 a</td>
<td>154.0 a</td>
</tr>
<tr>
<td><strong>Blackberry</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Blackberry (R)</td>
<td>4346.3 a</td>
<td>908.1 a</td>
<td>195.7 b</td>
<td>61.8 b</td>
</tr>
<tr>
<td>Blackberry (C)</td>
<td>3060.6 a</td>
<td>1360.0 a</td>
<td>280.7 ab</td>
<td>185.1 a</td>
</tr>
<tr>
<td>+ Apple (R)</td>
<td>2674.3 a</td>
<td>1572.1 a</td>
<td>282.9 ab</td>
<td>116.6 ab</td>
</tr>
<tr>
<td>+ Apple (C)</td>
<td>3773.0 a</td>
<td>1374.8 a</td>
<td>402.3 a</td>
<td>142.8 ab</td>
</tr>
<tr>
<td><strong>Jostaberry</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jostaberry (R)</td>
<td>2328.6 b</td>
<td>1611.1 a</td>
<td>324.9 b</td>
<td>213.6 a</td>
</tr>
<tr>
<td>Jostaberry (C)</td>
<td>3733.9 ab</td>
<td>1658.8 a</td>
<td>453.6 ab</td>
<td>192.3 a</td>
</tr>
<tr>
<td>+ Apple (R)</td>
<td>2759.9 b</td>
<td>1517.1 a</td>
<td>453.5 ab</td>
<td>165.7 a</td>
</tr>
<tr>
<td>+ Apple (C)</td>
<td>4375.8 a</td>
<td>1618.9 a</td>
<td>557.6 a</td>
<td>164.7 a</td>
</tr>
</tbody>
</table>

1 (R) refers to monoculture or polyculture (+ Apple) treatments grown at the recommended between row spacing of 2.4 m for blackberry and 1.8 m for jostaberry.

2 (C) refers to monoculture or polyculture (+ Apple) treatments grown at a close spacing of 1.2 m or 0.9 m between rows for blackberry or jostaberry, respectively.

3 Treatment means were separated using Duncan’s Multiple Range Test (P ≤ 0.05). Means followed by the same letter are not significantly different.

Table 3.10: Mean apple, blackberry, or jostaberry root length and feeder root mass harvested from four soil cores taken per treatment at two soil depths.

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reduced from 100% in the apple monoculture to 51% in the jostaberry (C), 42% in the
jostaberry (R), 42% in the blackberry (R), and 36% in the blackberry (C) treatment.
There were no differences in the proportion of apple roots among these polyculture
treatments.

Blackberry root length was unaffected by treatment at both soil depths (Table 3.10). Although total root mass was also unaffected by treatment, the mass of feeder
roots (<1.0mm diameter) was significantly affected both in P1 (P<0.0307) and P2
(P<0.0319). In P1, blackberry feeder root mass was significantly lower in the
monoculture (R) as compared to the polyculture (C) treatment. The remaining two
treatments were intermediary with respect to feeder root mass and were not significantly
different from each other or the two aforementioned treatments. Blackberry feeder root
mass followed the same trend in the 20-40cm soil profile. Feeder root mass was again
significantly lower in the monoculture (R) treatment than in the monoculture (C)
treatment. Root mass in the two polyculture treatments were not different from each
other or from the monoculture treatments.

Jostaberry root length in P1 was significantly affected by the spacing within the
treatments and not by the presence of an apple overstory (P<0.0234). The closely
spaced treatments, especially the polyculture, had greater root lengths than either of the
treatments planted at the recommended spacing (Table 3.10). However, within each
spacing, there was not a difference in root length with respect to monoculture or
polyculture. Although total root mass was unaffected by treatment, there was a
difference in feeder root mass in P1 with respect to treatment (P<0.0500). The
polyculture (C) treatment had a greater root mass than did the monoculture (R). The remaining two treatments were intermediary with respect to feeder root mass and were not significantly different from each other or the two aforementioned treatments. There were no differences in jostaberry root length or mass in the 20–40cm soil profile.

Although the treatments generally did not have a large impact on the rooting behavior of apple, blackberry, and jostaberry, there were significant differences with respect to the rooting patterns between these species. Both berry species demonstrated greater root length and root mass in the 0–20cm soil profile as compared to the 20–40cm profile (Figs. 3.3 and 3.4). Apple root length followed the same trend for root mass but apple roots were determined to be of equal length in P1 and P2. In P1, apple root length and apple feeder root mass were always significantly less than those of its berry companion (Figs 3.5 and 3.6). However, this pattern was generally not evident in P2.

Nutrient Parameters

Percent nitrogen of apple leaf tissue was highest in the monoculture, honeyberry and lingonberry treatments and significantly lower in the blackberry and jostaberry polycultures (Table 3.11). Conversely, the concentrations of phosphorus and potassium in apple leaves were significantly higher in the blackberry, jostaberry and honeyberry (C) treatments than all other treatments. Percent nitrogen was positively correlated with apple yield, while concentrations of phosphorus and potassium were negatively correlated with yield (Figure 3.7). Percent nitrogen was also positively correlated with total shoot length (P<0.0391, r²=0.48), bloom (P<0.0047, r²=0.70), and fruit set.
Figure 3.3: Mean root length of apple, blackberry and jostaberry in the 0-20cm soil profile (P1) as compared to the 20-40cm soil profile (P2)

Figure 3.4: Mean mass of feeder roots (<1mm diameter) of apple, blackberry, and jostaberry in the 0-20cm soil profile (P1) and the 20-40cm profile (P2)
Figure 3.5: Mean root length differences between apple, blackberry and jostaberry in the 0-20cm soil profile (P1) and in the 20-40cm profile (P2)

Figure 3.6: Mean feeder root mass (<1mm diameter) differences between apple, blackberry and jostaberry in the 0-20cm soil profile (P1) and the 20-40cm profile (P2)
<table>
<thead>
<tr>
<th>Treatment</th>
<th>Nitrogen (%)</th>
<th>Phosphorus (µg/g)</th>
<th>Potassium (µg/g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Apple</td>
<td>2.06 a²</td>
<td>2658.3 bc</td>
<td>12470 d</td>
</tr>
<tr>
<td>+ Blackberry (R)</td>
<td>1.62 cde</td>
<td>6233.3 a</td>
<td>20332 a</td>
</tr>
<tr>
<td>+ Blackberry (C)</td>
<td>1.71 bcd</td>
<td>6481.3 a</td>
<td>20432 a</td>
</tr>
<tr>
<td>+ Honeyberry (R)</td>
<td>2.02 a</td>
<td>2277.7 c</td>
<td>15053 cd</td>
</tr>
<tr>
<td>+ Honeyberry (C)</td>
<td>1.97 ab</td>
<td>4579.0 ab</td>
<td>17484 abc</td>
</tr>
<tr>
<td>+ Jostaberry (R)</td>
<td>1.41 e</td>
<td>4549.0 ab</td>
<td>18957 ab</td>
</tr>
<tr>
<td>+ Jostaberry (C)</td>
<td>1.59 de</td>
<td>6556.7 a</td>
<td>20539 a</td>
</tr>
<tr>
<td>+ Lingonberry (R)</td>
<td>1.89 abc</td>
<td>3478.0 bc</td>
<td>16368 bc</td>
</tr>
<tr>
<td>+ Lingonberry (C)</td>
<td>1.79 abcde</td>
<td>3881.0 bc</td>
<td>17526 abc</td>
</tr>
</tbody>
</table>

1 Treatments followed by (R) stand for apple + berry at the recommended spacing for the berry while those followed by (C) stand for apple + berry at close spacing for the berry.

2 Treatment means were separated using Duncan's Multiple Range Test ($P \leq 0.05$). Means followed by the same letter are not significantly different.

Table 3.11: Apple leaf tissue nutrient concentrations of nitrogen, phosphorus and potassium when grown in monoculture and when grown in polyculture with a berry understory.
Figure 3.7: Relationship between apple yield and apple leaf concentrations of nitrogen, phosphorus and potassium

(P<0.0003, $r^2=0.86$). Phosphorus concentration was negatively correlated with total shoot length (P<0.0067, $r^2=0.67$), trunk cross-sectional area (P<0.0294, $r^2=0.52$), bloom (P<0.0017, $r^2=0.78$), and fruit set (P<0.0052, $r^2=0.70$). Potassium concentration was negatively correlated with total shoot length (P<0.0089, $r^2=0.65$), trunk cross-sectional area (P<0.0399, $r^2=0.47$), bloom (P<0.0018, $r^2=0.77$), and fruit set (P<0.0033, $r^2=0.73$).

There were no differences with regard to treatment in blackberry leaf concentrations of nitrogen (P>0.1578), phosphorus (P>0.5584) or potassium (P>0.9009). Percent nitrogen ranged from 2.2 to 2.5%, phosphorus concentration ranged from 1601 to 1859 $\mu$g/g tissue and potassium concentration from 11885 to 12299 $\mu$g/g tissue (data not shown).
There were no differences with regard to treatment in honeyberry leaf concentrations of phosphorus (P>0.3453) or potassium (P>0.0946). However, there was a difference among treatments in leaf concentrations of nitrogen (P<0.0099). Plants in the monoculture (R) treatment had significantly higher concentrations of nitrogen than the two polyculture treatments but did not differ from the monoculture (C) treatment. There was no difference in percent nitrogen between either polyculture treatment. Percent nitrogen ranged from 1.4 to 1.7%, phosphorus concentration ranged from 1782 to 2470 \( \mu g/g \) tissue and potassium concentration from 5798 to 8273 \( \mu g/g \) tissue (data not shown).

There were no differences with regard to treatment in jostaberry leaf concentrations of nitrogen (P>0.7831), phosphorus (P>0.1749) or potassium (P>0.1832). Percent nitrogen ranged from 1.5 to 1.7%, phosphorus concentration ranged from 4638 to 5790 \( \mu g/g \) tissue and potassium concentration from 26345 to 28996 \( \mu g/g \) tissue (data not shown).

There were no differences with regard to treatment in lingonberry leaf concentrations of nitrogen (P>0.0821), phosphorus (P>0.2692) or potassium (P>0.1264). Percent nitrogen ranged from 0.9 to 1.1%, phosphorus concentration ranged from 979 to 1151 \( \mu g/g \) tissue and potassium concentration from 5142 to 6005 \( \mu g/g \) tissue (data not shown).

Leaf concentrations of nitrogen, phosphorus and potassium varied widely among the five plant species (Figure 3.8). Blackberry had higher levels of N than all other species and was well within its sufficiency range of 2-3\% (Mills and Jones, 1996), even
Figure 3.8: A comparison of leaf concentrations of phosphorus, potassium, and nitrogen between apple, blackberry, honeyberry, jostaberry, and lingonberry plants.

when placed in an intensive polyculture at close spacing. Although apple had the second highest leaf N content, its levels were below its published sufficiency range of 1.9-2.4% (Cahoon, 1985) when planted with blackberry (1.4-1.6%) and jostaberry (1.4-1.6%). Jostaberry and honeyberry had roughly equal levels of nitrogen. With its range among treatments of 1.5-1.7%, jostaberry was well below the sufficiency range established for Ribes nigrum of 2.0-2.5%. Given the lack of information regarding the optimum nutritional status of honeyberry and lingonberry, it is not possible to determine whether the levels observed in their foliage was adequate for growth and fruiting. Jostaberry and apple had the greatest concentration of phosphorus in their leaves as compared to
the other three plant species (Figure 3.8). For both jostaberry and apple, the observed concentrations of P were much greater than their established sufficiency ranges of 0.22-0.65\% for apple and 0.1-0.3\% for jostaberry. Blackberry leaf levels of P ranged from 0.16-0.19\% and were much lower than the optimum range of 0.25-0.40\%.

Potassium concentrations were much higher in jostaberry leaves than in the leaves of any of the other species (Figure 3.8). Jostaberry leaves had nearly twice the concentration of K than the reported range for leaf levels of 1.4-1.7\%. Apple leaf concentrations of K were between 1.2-2.1\% and were within the sufficiency range of 1.2-1.8\%. At 1.2\%, blackberry leaf concentrations of K were lower than the reported optimum range of 1.5-2.5\%.

**Berry Growth (under 1 year old trees vs. 4 year old trees)**

There were significant differences in the growth (as measured by an estimate of final plant size) and yield of the berries planted under the four year old apple trees as compared to those planted under the one year old whips (Table 3.12). All of the lingonberries planted under the larger trees died within the first few months after planting. With the exception of blackberry plant size and ‘Blue Velvet’ yield, growth and yield of all the berry species was reduced under the larger trees. The yield of jostaberry was reduced by half, while losses in blackberry and ‘Blue Belle’ yields were even greater. Conversely, the yield of ‘Blue Velvet’ was slightly increased under the larger trees, although the difference in the two locations was not a significant one.
<table>
<thead>
<tr>
<th>Tree Age</th>
<th>Yield Per Plant (g)</th>
<th>Estimated Dry Weight (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Blackberry</td>
<td>'Blue Belle'</td>
</tr>
<tr>
<td>1 Year Old</td>
<td>1888.4 a</td>
<td>17.58 a</td>
</tr>
<tr>
<td>4 Year Old</td>
<td>844.7 b</td>
<td>5.0 b</td>
</tr>
</tbody>
</table>

1 Means followed by the same letter are not significantly different. Means reported in the table are the result of individual t-tests with the following p values: blackberry yield, $P \leq 0.0304$; blackberry dry weight, $P \leq 0.2869$; 'Blue Belle' yield, $P \leq 0.0047$; 'Blue Belle' dry weight, $P \leq 0.0539$; 'Blue Velvet' yield, $P \leq 0.3759$; 'Blue Velvet' dry weight, $P \leq 0.4905$; jostaberry yield, $P \leq 0.0228$; and jostaberry dry weight, $P \leq 0.0109$.

Table 3.12: Yield and estimated dry weight of 3 year old blackberry, honeyberry cultivars: 'Blue Belle' and 'Blue Velvet,' and jostaberry when planted under newly planted apple trees and under four year old apple trees.
Jostaberry and 'Blue Belle’ growth was also reduced under 4 year old trees as compared to 1 year old trees. Blackberry and 'Blue Velvet’ growth was nearly equal at both locations.

**Land Equivalent Ratio (LER)**

As a final measure of plant performance, land equivalent ratios (LER) were calculated to evaluate the efficiency of each polyculture system (Table 3.13). Due to the severe reduction in yield of the apple trees when intercropped with blackberry and jostaberry, the calculated LER’s showed a polyculture disadvantage. All four treatments could produce the same level of yield on less area of land when grown as individual monocultures. Conversely, the LER’s for the honeyberry and lingonberry treatments showed an advantage for the polyculture systems as more land would be required in monoculture to achieve the same level of yield.
Table 3.13: Estimated land equivalent ratios (LER) for several types of apple polyculture systems (apple estimates are based on 417 trees/ha, which would be achieved at a spacing of 4m within row and 6m between rows).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>LER</th>
</tr>
</thead>
<tbody>
<tr>
<td>Apple + Blackberry (R)</td>
<td>0.71</td>
</tr>
<tr>
<td>Apple + Blackberry (C)</td>
<td>0.63</td>
</tr>
<tr>
<td>Apple + Honeyberry (R)</td>
<td>2.68</td>
</tr>
<tr>
<td>Apple + Honeyberry (C)</td>
<td>1.58</td>
</tr>
<tr>
<td>Apple + Jostaberry (R)</td>
<td>0.75</td>
</tr>
<tr>
<td>Apple + Jostaberry (C)</td>
<td>0.79</td>
</tr>
<tr>
<td>Apple + Lingonberry (R)</td>
<td>1.35</td>
</tr>
<tr>
<td>Apple + Lingonberry (C)</td>
<td>1.27</td>
</tr>
</tbody>
</table>

1 Treatments followed by (R) stand for apple + berry at the recommended spacing for the berry while those followed by (C) stand for apple + berry at close spacing for the berry.
DISCUSSION

The growth and yield of apple was significantly affected by the plant species with which it was placed in polyculture. Jostaberry and blackberry significantly reduced both the yield and growth of the apple trees. As the apple trees in those treatments were deficient in leaf nitrogen concentration, the observed negative effects on the apple tree were likely due to competition for nitrogen. Although light levels were not monitored, it is unlikely that the apple trees were competing for light with the jostaberry and blackberry understories, as the apple was significantly larger in height and spread than either of the berry species. Competition for water could be another explanation for the observed effects on the apple trees. However, soil moisture was measured frequently throughout each of the three growing seasons and the field was irrigated as necessary. Thus, it is more likely that the apple trees in the blackberry and jostaberry polycultures were unable to take up sufficient amounts of nitrogen. Since only the apple trees in blackberry and jostaberry polycultures were deficient in nitrogen, it appears as though both blackberry and jostaberry were more successful competitors for nitrogen than was apple.

Harvested roots from soil cores in the apple, blackberry, and jostaberry monocultures and polycultures showed that apple root length and apple feeder root mass were always less than that of blackberry or jostaberry. However, apple root length and feeder root mass was largely unaffected by treatment. In fact, apple roots taken from the monoculture control treatment were often of shorter length and mass than those taken from blackberry or jostaberry treatments, the treatments in which the apples were deficient in nitrogen. It seems contradictory that there would be fewer apple roots in the
monoculture where apple leaf nitrogen levels were adequate and more apple roots in the nitrogen deficient apple treatments. Caldwell et al. (1991b) showed that root abundance alone was insufficient to explain tissue nutrient analyses for three sagebrush steppe species. Despite a four- to tenfold greater root mass of the tussock grass, *Agropyron desertorum*, over the sagebrush, *Artemisia tridentata*, the two species acquired the same amount of phosphorus from nutrient rich patches of soil. The shrub also took up six to eight times more phosphate than the grass, *Pseudoroegneria spicata*, despite greater root densities of the grass.

In their review of belowground competition, Casper and Jackson (1997) offered four possible explanations for the lack of direct correlation between root density and the outcome of belowground competition:

"First, competition may also occur among roots on the same plant, so the return per investment in new root growth may decline at higher root densities. Second, where and when roots are deployed may be just as important as average root density. A plant with much root surface in one region of the soil might be poorly represented in a second region or less able to concentrate its roots in localized nutrient patches, or rooting density may vary temporally. Third, mycorrhizae play an important role but are frequently ignored in studies of nutrient acquisition, and fourth, physiological properties related to the rate of uptake are also crucial to competitive ability."

All four of these factors may explain why the apple trees in competition with blackberry and jostaberry were deficient in nitrogen and yet had greater root lengths and mass than the apples in monoculture with sufficient levels of nitrogen. Competition between individual apple roots is probably the least likely explanation since apple root mass was still much lower than that of blackberry or jostaberry, both of which were still able to take
up sufficient amounts of nitrogen. The location of apple roots was highly variable; some soil cores had little to no apple roots while others had a large number of roots. Thus, it is possible that apple roots were not within, or do not have the ability to proliferate within, zones of enrichment. Since nutrient availability in the soil can vary considerably over distances of only a few centimeters (Snaydon, 1962), the ability of plants to rapidly exploit nutrient rich soil patches is likely an important mechanism of effective competition (Tilman, 1988), an attribute that may be lacking in apple. Although given the mobility of nitrogen in the soil, this is probably less important to the uptake of nitrogen than for an immobile nutrient such as phosphorus. Differential nutrient uptake rates between apple, blackberry, and jostaberry may also explain the inconsistency between apple root mass and nitrogen acquisition. While differences in mycorrhizal dependence between the species may also exist, these differences are probably less important for nitrogen uptake than for phosphorus.

Apple leaf potassium and phosphorus concentrations were negatively correlated with growth and yield and were therefore highest in the treatments containing jostaberry and blackberry. This is likely because the apple trees in these treatments were very low in yield. Apples, per 100g edible portion, contain 10mg of phosphorus and 110 mg of potassium (Westwood, 1993). Without fruit acting as a sink for these nutrients, it follows that leaf concentrations of both phosphorus and potassium would be higher in those treatments that most negatively affected yield. It is unlikely that the apples and jostaberry were competing for either potassium or phosphorus, since leaf concentrations were well within each species’ published sufficiency ranges and neither of the species exhibited any
deficiency symptoms. Although blackberry leaf concentrations of both phosphorus and potassium were below the established ranges, none of the blackberry plants exhibited any deficiency symptoms. The leaves were collected while the berries were in production and leaf concentrations may have appeared low because the fruit on the plants were acting as sinks for both P and K. It would have likely been more meaningful to collect the leaf samples early in the spring prior to flowering and fruit production.

While blackberry and jostaberry significantly affected the growth of apple, the inverse was not as significant. Although the presence of an apple tree did reduce the growth of both species, berry spacing itself had a much greater impact. For both blackberry and jostaberry, intraspecific competition had a much greater negative impact on growth than did competition with apple. This supports the classical view that intraspecific competition has a greater effect than interspecific competition through the mechanism of greater similarity of resource use. However, in their literature review of field competition experiments in natural communities, Goldberg and Barton (1992) concluded that conspecifics do not usually compete more strongly than heterospecifics. This finding was further used to support the hypothesis that resource partitioning is not an important mechanism of coexistence in plants (Goldberg and Werner, 1983). Since leaf nutrient analyses were not compared among individual plants within treatments, this study is not equipped to determine whether resource partitioning for soil nutrients was the mechanism by which growth was reduced by closer berry
spacings. The fact that there were no significant differences among treatments in nutrient accumulation in the blackberry or jostaberry leaves suggests that the reduction in berry growth may be due to something other than competition for nutrients.

If a resource depletion zone exists around each plant, and the zones of neighboring plants overlap, then it follows that competition will occur within the overlap. If the plants in question are of the same size and neither has a competitive advantage, then competition will be two-sided and the resources will be shared equally (Firbank and Watkinson, 1990). Since the berries were planted at the same time, were of the same physiological age, were approximately equal in size and of the same species, it should be safe to assume that none of the four berry plants in each plot had a competitive advantage. If resources were being shared and differences in soil nutrient accumulation do not explain the reduction in growth, then the resources remaining in the overlap zone include water and light. Since soil moisture was monitored and irrigation was applied as necessary, it is unlikely that differences in water uptake are responsible for the reduction in growth.

Light could very well have been a factor in reducing the growth of the berry plants at close spacing. Being of relatively equal size and spread, the canopy of the berries overlapped throughout the 2001 growing season. It is possible that shading from neighboring berries could have been significant enough to reduce growth. Since light levels and photosynthesis were not measured during the course of the experiment, it is not
possible to state definitively whether competition for light reduced the growth of berries when closely spaced. However, the theory that light was limiting enough to reduce growth could explain the patterns in growth and yield observed in the experiment.

Growth of both blackberry (R) and jostaberry (R) was reduced by the addition of an apple tree. Nutrient analyses showed that both berry species were likely better competitors for nitrogen than was apple and that neither berry was deficient in nitrogen. Although not an effective competitor for nitrogen, the apple, by virtue of its stature, may have been a better competitor for light. The shading of the berries by the apple could have led to the observed reduction in growth. When blackberry and jostaberry were planted closely, the reduction in growth was even greater than when planted with apple (R). With four plants of nearly equal size and overlapping canopies, shading could have been even greater than that produced by one apple tree. Finally, when the blackberry and jostaberry were planted closely under an apple tree, the reduction in growth was the most severe. The shading of individual plants in this treatment would be affected by the overlapping canopies of the four berry plants and by the apple overstory.

That yields in both blackberry and jostaberry, and jostaberry bloom were reduced when planted under an apple tree further supports the theory that competition for light was a significant component in the interactions between these plants. Shading has been shown to reduce the yield and/or fruit set of many fruit crops including strawberry (Garrison et al., 1991), thornless blackberry (Swartz et al., 1984), red raspberry (Waister et al., 1977; Wright and Waister, 1984), black raspberry (Warmund et al., 1995), cranberry (Roper et al., 1995), French American hybrid grape cultivars ‘Chambourcin’

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and ‘Seyval’ (Ferree et al., 2001), apple (Ferree, 1980; Doud and Ferree, 1980), sour cherry (Flore and Layne, 1990), and pear (Kappel and Brownlee, 2001). The reduction in yield of both blackberry and jostaberry and the reduction in growth of jostaberry under 4 year old trees as compared to 1 year old trees indicate the growing impact that competition for light will have on the apple-blackberry and apple-jostaberry polycultures. Both berry species seem to be sensitive to light and the observed yields under 1 year old trees will likely decrease as the plants mature. Even if apple yields were to increase in future years, the increase would likely occur with a simultaneous decrease in berry yield and the LER values would probably remain low. Clearly the apple-blackberry and apple-jostaberry polycultures are unsuitable for production of either crop component.

Apple had little to no effect on the growth or yield of lingonberry. For these ericaceous plants, soil pH was probably the single greatest factor affecting the growth of these plants and was likely the reason for the decline and death of ‘Koralle.’ This cultivar is apparently less tolerant of the soil in this experiment, which had a pH of 6.2. Although ‘Red Pearl’ managed to survive and fruit during the experiment, its growth was slow and it is uncertain whether it would continue to exist under the conditions in which it was placed. Since all of the lingonberries died within the first year of planting under 4 year old trees, it is uncertain what effect future shading would have on the plants under 1 year old trees as those trees mature. In their work with cranberry, Roper et al. (1995) found a significant reduction in yield by postbloom shading with either 72% or 93% shadecloth. As a close taxonomic relative, it is likely that lingonberry would respond similarly to
shaded conditions. Thus, despite its positive LER value, a polyculture of apple and lingonberry is not advisable primarily due to the inherent differences in soil requirements between the species.

The presence of an apple tree seemed to improve both the growth and yield of ‘Blue Belle’ and ‘Blue Velvet’. This plant species performed better when planted closely and when slightly shaded than when planted alone at the recommended spacing. However, if the data from the plants under the 4 year old apple trees is any indication, shading by the apple tree will become an increasing problem for honeyberry as growth and yield will likely be reduced. Although it is uncertain whether the positive LER value in the apple-honeyberry polyculture would be maintained as the trees mature, the system would likely remain feasible for several more years. The greatest impact on the success of the system would likely be the choice of cultivar. Clearly ‘Blue Belle’ and ‘Blue Velvet’ are unsuited for one another as pollen sources since the bloom times of the two cultivars are so variable. It is possible that these two cultivars are either different subspecies of *Lonicera caerulea* or different species altogether. The taxonomy of this polymorphic species is complex due to its extremely wide geographic, ecological, and morphological variation. In the Russian literature, forms of *L. caerulea* like that of ‘Blue Belle’ have been called *L. caerulea* subsp. *edulis*, while those like that of ‘Blue Velvet’ have been called *L. emphylocalyx*, *L. caerulea* subsp. *emphylocalyx*, or *L. caerulea* subsp. *kamtschatica* (Maxine Thompsom, personal communication). Until the taxonomical problems associated with the species have been resolved, any future plantings should include cultivars with similar morphological habits, as it is more likely...
that they will be of the same species and subspecies and will be better sources of pollen for one another. If two such suitable cultivars can be located, then an apple-honeyberry polyculture would be both feasible and productive during apple establishment. It is likely that the system would remain productive even as the apple matures if the plants are spaced at the recommended between row spacing, so as to be further from the tree and less subject to shaded conditions from the apple canopy.

Other authors have argued that spatial and temporal variations in competition may be more important mechanisms of coexistence than is resource partitioning (Shmida and Ellner, 1984). However, the results of this study suggest that resource partitioning for nitrogen and for light were significant mechanisms of competition between the component species of the apple-blackberry and apple-jostaberry polyculture systems. Perhaps if these plants were followed for several more years and viewed as a population, spatial/temporal variation in competition might become more important in explaining the coexistence of these plants. This is because over time, the patterns of resource partitioning observed in this experiment are likely to remain constant in that each species will either compete for and acquire adequate resources for their survival or they will perish. Spatial or temporal variation in competition for those resources may better serve as a mechanistic explanation for the coexistence of the plants that survive.
CHAPTER 4

THE TIMING AND DEGREE OF ROOT PROLIFERATION
OF FIVE FRUIT CROPS

INTRODUCTION

Nutrient-rich patches in soil have been considered to be important sources of mineral nutrients for plants even though they represent a small fraction of the total soil volume exposed to the plants' roots. It has been shown by many researchers that when plant roots encounter these fertile sites, they respond by branching and proliferation to increase local root length in the patch (reviewed by Robinson, 1994). It has also been shown that the physiological uptake capacity of roots increases in local fertile areas (Jackson et al., 1990). These studies suggest that the ability of plants to rapidly exploit nutrient-rich patches and to elevate uptake kinetics in fertile microsites are likely important mechanisms of effective competition (Tilman, 1988).

Numerous studies have demonstrated root proliferation in nutrient rich environments. Drew and Saker (1975, 1978) demonstrated root proliferation in barley seedlings in localized zones of increased nutrient supply. Granato and Raper (1989) demonstrated a similar response in maize roots. Passioura and Wetselaar (1972) used plexiglass boxes to show that wheat roots proliferate near banded applications of nitrogen. Crick and Grime (1987) showed that the roots of plants grown in partitioned
pots proliferated in the compartments with the highest nutrient concentrations. Eissenstat
and Caldwell (1988) used a root periscope to observe root proliferation in the field after
localized applications of nutrient solutions. Jackson and Caldwell (1989) found that the
roots of the native tussock grass, *Agropyron desertorum* rapidly proliferated within one
day of the initial nutrient solution injection. However, the roots of the introduced tussock
grass, *Agropyron spicatum* failed to proliferate at any time during the two-week
experiment.

Thus, different species (even those of the same genus) differ in their capacity to
make plastic adjustments to the size and distribution of their root systems. The objective
of this study was to determine if there are differences in the timing and extent of root
proliferation between the apple and the same berry species used in chapter 3 of this
dissertation.

**MATERIALS AND METHODS**

A greenhouse study was conducted with potted plants in the spring and summer of
2001 at the Ohio Agricultural Research and Development Center (OARDC) in Wooster,
Ohio. Rooted cuttings of each berry plant were potted in 1 gallon tree pots (10cm wide,
35cm deep) filled with a 2:1 mixture of coarse sand and Wooster silt loam. Apple M.7
rootstocks were used for the apple treatment. Four 5-cm square windows were cut in
each pot; the top of each window was approximately 8-cm below the surface of the soil.
The pots were lined with a transparent film, allowing root growth to be viewed through
the window. The windowed pots were then inserted into empty pots to exclude light from
reaching the root systems through the windows.

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Each plant was subjected to three different fertilization treatments: 20ml of a 1200mg/L solution 20-20-20, 20ml of a 6000mg/L solution 20-20-20, or 20ml deionized water. To limit the size of the patches created within the pots, treatments were administered in 10-ml doses over two consecutive days. The solutions were injected through the centers of the windows with a syringe. One window in each pot was left unused to allow for the disqualification of a window if it had too few or too many roots present when the experiment began. There were 8 replicates per plant species.

Prior to the solution injection, roots visible through the windows were traced onto transparencies to establish root length prior to treatment. Subsequent mapping of root growth was made on the same transparencies beginning after the initial 10-ml injection on days 2, 6, 10, and 14. Root lengths from each individual mapping day were measured with the use of a multi-scale digital plan measure (Scale Master® II v2.0, Calculated Industries) and converted to relative growth rates, RGR, (mm³/day⁻¹):

\[
RGR = \frac{\log(L_{2}) - \log(L_{1})}{(t_{2} - t_{1})}
\]

where \(L\) is the root length at either time 1 \((t_{1})\) or time 2 \((t_{2})\).

After 14 days, the transparent windows were cut open and the soil (and roots) from each window were removed to a depth of 3cm. The roots were then sieved from the soil, dried and weighed. The root dry weight from each window was calculated as a percentage of total root mass. The entire experiment was replicated so that there were two trials in total.
RESULTS

There were no differences in the root dry weights from each treatment window when calculated as a percentage of total root mass for apple, blackberry, honeyberry or jostaberry in either Trial 1 or Trial 2 of the experiment (Table 4.1). However, there was a difference in the percentage of lingonberry roots collected from the high-enrichment windows as compared to the control windows. There was also a general trend among apple, blackberry and jostaberry for increased percentages in the high-enrichment vs. the low-enrichment vs. the control windows. Conversely, the percentage of honeyberry roots in fertilized patches decreased in comparison to the control patches.

Overall, there were differences in the inherent allocation patterns of the species with regard to shoot mass, root mass and shoot:root ratio (Table 4.2). Jostaberry and apple had the greatest shoot mass, while blackberry and lingonberry had the lowest and honeyberry was intermediate between the species. With respect to root mass, jostaberry and honeyberry displayed the greatest mass, while lingonberry had the lowest and apple and blackberry were similar in their root dry weights. The shoot:root ratio was significantly greater in apple and lingonberry than in the other species. Blackberry, honeyberry and jostaberry all had shoot:root ratios of less than 1.0 and of those, honeyberry and jostaberry ratios were the lowest.

The roots of jostaberry and blackberry proliferated within 6 days of initial injection, and to a greater extent than all other species (Figures 4.1, 4.2). The response by both species was greater in the high-strength enrichment as compared to the low-strength
Table 4.1: Apple, blackberry, honeyberry, jostaberry or lingonberry root mass from soil patches that received either a high-enrichment or low-enrichment fertilization dose or control patches that received deionized water, expressed as a percentage of total root mass.

and in the first trial as compared to the second. In the first trial, proliferation by both species was of a similar magnitude in the high-strength and low-strength enrichment patches, but the low-strength patches failed to elicit a similar response from jostaberry in the second trial.

Apple failed to proliferate during the two weeks of the experiment in Trial 1 (Figure 4.1). However, apple did display a slight amount of proliferation as early as 2 days after injection in the second trial (Figure 4.2). Apple was the only species to show
<table>
<thead>
<tr>
<th>Plant</th>
<th>Shoot Dry Weight (g)</th>
<th>Root Dry Weight (g)</th>
<th>Shoot:root Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>Apple</td>
<td>6.54 ab</td>
<td>4.28 bc</td>
<td>1.80 a</td>
</tr>
<tr>
<td>Blackberry</td>
<td>3.93 c</td>
<td>5.81 b</td>
<td>0.79 b</td>
</tr>
<tr>
<td>Honeyberry</td>
<td>5.69 b</td>
<td>10.77 a</td>
<td>0.63 c</td>
</tr>
<tr>
<td>Jostaberry</td>
<td>7.32 a</td>
<td>10.52 a</td>
<td>0.74 c</td>
</tr>
<tr>
<td>Lingonberry</td>
<td>3.70 c</td>
<td>2.63 c</td>
<td>1.41 a</td>
</tr>
</tbody>
</table>

Table 4.2: Mean shoot mass, root mass, and shoot:root ratios of apple, blackberry, honeyberry, jostaberry and lingonberry, averaged over trial, when grown individually in 10cm x 35cm tree pots and had portions of their root systems exposed to either patches of high-enrichment or low-enrichment fertilization doses or to control patches of deionized water.

such an early response. Apple root proliferation was slightly greater in the high-strength patch than in the low-strength treatment. However, the degree of apple root proliferation in the low-strength treatment was greater than that of jostaberry, despite the impressive response of the latter in the first trial. Apple also continued to proliferate as late as 14 days after treatment, by which time both blackberry and jostaberry ceased to respond.

Honeyberry failed to proliferate in the first trial but showed a low degree of proliferation in the low-strength treatment of the second trial at days 10 and 14 (Figures 4.1, 4.2). The high-strength treatment failed to illicit any proliferation from honeyberry roots in either trial.
Figure 4.1: Trial 1 mean relative growth rates (RGR) of apple, blackberry, honeyberry, jostaberry and lingonberry control roots (top) and the ratios of mean RGR for roots in low-enrichment soil patches or high-enrichment soil patches and control patches (middle or bottom, respectively). An RGR ratio of 1.0 means that roots in the treated patches grew no faster than those of the same plant in the control patches.
Table 4.2: Trial 2 mean relative growth rates (RGR) of apple, blackberry, honeyberry, jostaberry and lingonberry control roots (top) and the ratios of mean RGR for roots in low-enrichment soil patches or high-enrichment soil patches and control patches (middle or bottom, respectively). An RGR ratio of 1.0 means that roots in the treated patches grew no faster than those of the same plant in the control patches.
Due to the slow growth of lingonberry, only the first trial could be completed during the course of the growing season. In this trial, lingonberry failed to proliferate in either the high- or low-strength enrichment patches (Figure 4.1).

Repeated measures analysis of both trials failed to show a significant effect with regard to fertilization treatment (Tables 4.3, 4.4). While the date and species x date interaction were significant in both trials, the main effect of species was only significant in the first trial. However, the use of the contrast procedure revealed a significant response with regard to treatment on day 6 of both trials as compared to any of the other days in the trials. An analysis of variance of the sixth day data also showed a significant effect of treatment for Trial 1 ($P \leq 0.0095$) and for Trial 2 ($P \leq 0.0184$). A similar analysis of variance by species showed a significant effect of treatment for jostaberry on day 6 ($P \leq 0.0429$) in Trial 1, for apple on day 6 ($P \leq 0.0368$) on day 6 in Trial 2 and for blackberry on day 6 of both trials ($P \leq 0.0172$, $P \leq 0.0502$, respectively). While a non-repeated measures analysis was possibly not the most appropriate test, the magnitude of the one day responses by these species was apparent.
Table 4.3: Trial 1 repeated-measures analysis of variance for relative growth rates (mm/day) of apple, blackberry, honeyberry, jostaberry or lingonberry roots that were exposed to either patches of high-enrichment or low-enrichment fertilization doses or to control patches of deionized water and had those roots measured on days 2, 6, 10 and 14 after the initial treatment injection.
Table 4.4: Trial 2 repeated-measures analysis of variance for relative growth rates (mm/day) of apple, blackberry, honeyberry, jostaberry or lingonberry roots that were exposed to either patches of high-enrichment or low-enrichment fertilization doses or to control patches of deionized water and had those roots measured on days 2, 6, 10 and 14 after the initial treatment injection.
DISCUSSION

This study revealed differences among the plant species in their ability to proliferate roots in patches of nutrient-enriched soil. This ability was most apparent in jostaberry and blackberry roots and to a lesser, more variable degree in apple roots, while the roots of honeyberry and lingonberry failed to proliferate at all. Despite a lack of measurable proliferation in lingonberry roots, it was the only species that displayed a significant difference in the percentage of total root mass found in nutrient-enriched patches as compared to control patches. This suggests that lingonberry does possess a certain degree of precision in its resource foraging ability.

There was a significant difference in the response of the species to nutrient-enrichment in the two trials of the experiment. As these trials were separated by a six-week time-frame, with the second trial initiated later in the summer, differences in ambient or soil temperatures might explain the slower root growth rates of the species in Trial 2 as opposed to Trial 1. Sattelmacher et al. (1990a,b) showed a decrease in the root mass and morphology of potato seedlings at soil temperatures that were either at sub- or supraoptimal levels.

The nutritional history of a plant has been shown to alter its nutrient uptake rates (Drew et al., 1984; Jackson et al., 1976). Since the plants were not fertilized prior to the injection of enriched patches, it is possible that the plants in the second trial were more nutrient deprived than those in the first trial. This might explain the differences in the responses of the plants in the two trials. Apple may only demonstrate enhanced root proliferation when already nutrient starved. This might explain why apple root...
proliferation was only observed in the second trial, assuming that the apples were more nutrient stressed. Conversely, blackberry and jostaberry may have a reduced ability to proliferate when nutrient stressed or they may have been able to regulate their kinetic responses in such a way that enhanced uptake before root proliferation took place, resulting in an apparent reduction in response from the first to the second trial. Drew and Saker (1978) found that localized P enrichment resulted in enhanced P uptake in P-starved barley roots before proliferation occurred. A similar response may have occurred in blackberry and jostaberry.

Despite the different proliferation responses of the species between trials, there was no difference in the shoot or root growths between the trials, other than a small increase in the root dry weight of all species except for blackberry (and lingonberry, which was absent from the second trial). With the exception of blackberry, shoot:root ratio was significantly reduced for all species in the second trial. The typical plant response to decreased nutrient supply is to increase root biomass at the expense of shoot biomass (Marschner, 1995). As this response was observed in apple, honeyberry and jostaberry of the second relative to the first trial, it is likely that the plants in Trial 2 were more nutrient stressed than those in the first.

The atypical response of blackberry suggests that either there was no difference in the nutritional status of the blackberries from one trial to the next or that the difference was not significant enough to alter blackberry resource allocation patterns between the root and shoot. The decrease in its root biomass and proliferation response in the second trial may be due to factors other than nutrition, such as temperature, moisture or inherent
seasonal fluctuations in the root growth patterns of the species. Another possibility is that
blackberry may change its allocation to particular parts within the root (or shoot) as
opposed to a change in the dry matter partitioning between the root and shoot. While not
significant, the percentage dry weight of blackberry roots was 7 times greater in the high-
enrichment patches as compared to the control (Trial 1) and 1.5 times greater in Trial 2.

Root proliferation in fertile soil microsites may be an important mechanism of
below-ground competition for nutrients among plants. The results of this study suggest
that blackberry and jostaberry might have a competitive advantage over apple in
heterogeneous soils due to their ability to proliferate within patches of nutrient
enrichment. However, the ability to rapidly exploit nutrient-rich patches via root
proliferation is not necessarily correlated with the nutrient uptake ability of competing
root systems (Caldwell et al., 1991b). A study that compares the species in their nutrient
uptake rates and tissue nutrient accumulations is necessary to determine whether the
proliferation ability of blackberry or jostaberry correlates with greater nutrient
sequestration as compared to that of apple.
CHAPTER 5

THE INFLUENCE OF MYCORRHIZAL INFECTION ON COMPETITION BETWEEN APPLE TREES AND FOUR UNDERSTORY BERRY CROPS

INTRODUCTION

Mycorrhizal fungi are ubiquitous in terrestrial plant communities, forming associations with the roots of approximately 90% of the plant species that have been examined. These plant-fungal associations are generally considered mutualistic, whereby the fungus obtains carbon from the plant and the plant receives nutrients that are transported via the hyphal network (Allen and Allen, 1990). However, it has also been demonstrated that infection by mycorrhizal fungi may result in no benefit or antagonistic effects to host plants under certain conditions (Francis and Read, 1995). In general, mutualism dominates, and the importance of mycorrhizal fungi in nutrient uptake and especially phosphorus acquisition has long been recognized.

Most research on mycorrhizae has focused on nutrient acquisition mediated by vesicular-arbuscular mycorrhizal fungi (VAM) or arbuscular mycorrhizal fungi (AMF or AM) of individual plants or hyphally connected neighboring plants. Recent studies, however, have demonstrated that AM may influence the outcome of competitive interactions among plant species. For mycorrhizae to change the competitive outcome of neighboring plants of differing species, they must have different physiological effects on
those plants. Indeed, it has been demonstrated that plants exhibit different degrees of mycotrophy. It has become increasingly recognized that although some plant species respond positively to VA fungi, others may be antagonized, showing reduction in yield and survivorship (Francis and Read, 1995). Thus, mycorrhizal fungi may play a defining role in determining plant competitive relationships and, ultimately, community structure.

Several possible mechanisms for mycorrhizal mediation of plant species composition have been proposed in recent years. Grime et al. (1987) suggested that mycorrhizae mediated interplant transfer of resources from dominant to subordinate species may increase the abundance of the latter and thereby increase plant species diversity. Bergelson and Crawley (1988) suggested that mycorrhizae may increase plant species diversity by allowing competitive release of subordinate species from dominant species that are more weakly mycotrophic. Hartnett and Wilson (1999) have also considered that alterations in resource distribution between neighboring plants via hyphal connections could affect plant community composition.

In their study with three calcareous grassland plant species and four AMF species, van der Heijden et al. (1998a, 1998b) concluded that AMF communities have the potential to determine plant community structure. This conclusion was based on three key pieces of evidence. First, the three plant species differed in their dependence on AMF. Second, specific AMF species and AMF mixtures had significantly different effects on several plant growth variables and these effects varied among plant species. Third, the amount of variation in the growth response of a plant species to four AMF species and to the combination of AMF species differed among the plant species.
Hartnett and Wilson (1999) found similar relationships in a grassland ecosystem in northern Kansas. They attributed the dominance of C₄ grasses to the differential host species response to fungal colonization. This conclusion was based on the experimental observation that the suppression of native mycorrhizae resulted in decreased abundance of the dominant, obligately mycotrophic C₄ tall grasses and compensatory increases of many subordinate facultatively mycotrophic C₃ grasses and forbs.

Grime et al. (1987) found a similar shift in community structure in a microcosm study of pasture species. They demonstrated that the addition of mycorrhizae to a combination of grasses and forbs shifted the community to a greater proportion of forbs.

The impact of mycorrhizal symbiosis on plant competition between *Andropogon gerardii* (big bluestem) and *Koeleria pyranidata* (junegrass) has also been demonstrated experimentally (Hetrick et al., 1989). *A. gerardii* was 98% dependent on the symbiosis, whereas *K. pyranidata* was less than 0.02% dependent. When competing in pairs, *A. gerardii* dominated when the mycorrhizal symbiosis was present and *K. pyranidata* dominated when it was not present.

It is apparent from these data that mycorrhizae can cause shifts in plant community composition. Other studies have shown that mycorrhizae had no greater influence on plant competition than did other biotic (herbivory) and abiotic (temperature, soil moisture) factors (Allen and Allen, 1990). Thus, the importance of mycorrhizae to vascular plant competition will vary among plants and ecosystems. Given their potential...
importance to plant competition and species diversity, however, their incorporation in studies of plant competition may help to determine mechanisms of competition previously unexplained.

Most studies on mycorrhizal-mediated competition have involved a relatively small number of prairie or agricultural species and have only involved interactions between herbaceous plants. This study will be one of the first to compare mycorrhizal infection between woody perennials in an agricultural setting and between species with VAM and ericoid mycorrhizal associations, with an emphasis on the impact of mycorrhizal infection on competitive ability. The plant species used in both experiments of this study were M.7 apple rootstock (as a representative of apple as a species), lingonberry (*Vaccinium vitis-idaea*, cv. ‘Red Pearl’), honeyberry (*Lonicera kamchatika*, cv. ‘Bluebelle’), jostaberry (*Ribes nidigrolaria*) and blackberry (*Rubus* spp., cv. ‘Navaho’).

**MATERIALS AND METHODS**

**Experiment 1.** The objective of this study was to determine the ability of the ericoidal and VA mycorrhizal species to take up and translocate phosphorus, nitrogen and potassium. Since association of mycorrhiza with a host does not necessarily mean that the mycorrhiza are effective in increasing the growth of that host (Nemec, 1987), the quantification of mycorrhizal-mediated nutrient transfer would help to determine the importance of the symbiosis for each plant species.

To determine the ability of the ericoidal and VA mycorrhizal species to take up and translocate phosphorus, nitrogen and potassium each plant species was grown in pots
similar to that used by George et al. (1992). The pots had two compartments that were separated by a perforated plexi-glass plate and a 450 mesh screen (Newark Wire Cloth Company, NJ). The screen provided a barrier that would allow the penetration of mycorrhizal hyphae but not plant roots. Pots were filled with an autoclaved 2:1 mixture of coarse sand and Wooster silt loam. The resulting soil mixture had a pH of 6.27, 18ug/g P, 27ug/g K, 760ug/g Ca, 101ug/g Mg and 18.1ug/g NO₃-N. Rooted cuttings of each plant species were placed in the inner (root) compartment of each pot. There were two treatments arranged in a randomized complete block design in a greenhouse. The treatments consisted of root compartments that were either inoculated with VAM/ericoid mycorrhizae or not. There were five replications per treatment. The entire experiment was replicated twice. The first experimental trial was planted on June 1, 2001 and harvested 18 weeks later on October 5, 2001. The second trial was begun on July 6, 2001 and harvested 15 weeks later on October 19, 2001. The first trial was fertilized on June 20, 2001. Root compartments received 300mg N, 50mg P and 300mg K per kg of soil. The outer (hyphal) compartments received 334 mg N, 150mg P and 277mg K per kg of soil. This level of fertilization killed all the lingonberry plants and thus fertilization was reduced in trial 2 to 29mg N, 13mg P and 24mg K per kg of soil for each compartment, which was applied on July 25, 2001.

Shoot and root dry weight were determined for each woody plant species. Leaf samples from each plant were analyzed for phosphorus, nitrogen, and potassium. Roots were stained in trypan blue (Phillips and Hayman, 1970) and examined microscopically to assess percentage root colonization by mycorrhizal fungi using a Petri dish scored in
1mm squares (Daniels et al., 1981). Soil samples of root and hyphal compartments were also analyzed. Soil subsamples in the hyphal compartments were used to determine fungal hyphal length (Li et al., 1991).

**Experiment 2.** The objective of this study was to determine the effect of interspecific competition on each apple x berry combination (refer to Chapter 3 of this dissertation). Interspecific competition between each berry species was not considered since the overall purpose of the research was to determine a viable apple-berry intercropping system.

Dormant cuttings were taken from each berry species in the winter of 2000. They were dipped in rooting hormone and placed in a soilless media mix. On June 1, 2001, rooted cuttings of each of the four shrub species were planted in 1:1 combinations with an apple M.7 rootstock in 2 gallon tree pots (41cm deep, 17cm wide). Pots contained an autoclaved 2:1 mixture of coarse sand and Wooster silt loam. The resulting soil mixture had a pH of 6.27, 18ug/g P, 27ug/g K, 760ug/g Ca, 101ug/g Mg and 18.1ug/g NO₃-N. Treatments consisted of each species combination in mycorrhizal inoculated or noninoculated pots that were fertilized with phosphorus or not. There were 4 replications per treatment in a split-plot design.

The roots of each plant species were inoculated with either a mixture of ericoid mycorrhizae (for lingonberry) or VA mycorrhizae (for all remaining woody species) at planting. The VA mycorrhizae inoculum contained a minimum of 50 spores/cc of blended *Glomus brasilianum, G. clarum, G. deserticola, G. intraradices, G. monosporus.*
$G. \ mosseae$, and $Gigaspora \ margarita$ (Bio/Organics $^\text{TM}$). The roots of each of the plant species except the lingonberry were dusted with 3.5g of the inoculum and the soil in the potting hole for each plant received an extra 6g of inoculum.

Ericoid mycorrhizal slants were purchased from the University of Alberta Microfungus Collection. The isolates used were UAMH 8680, UAMH 8871, UAMH 9270, UAMH 8922, and UAMH 9263. The first three isolates were strains of $Hymenoscyphus \ ericae$, while the remaining two were $Oidiodendron \ maius$. The slants were subcultured on plates of Mitchell-Read media and allowed to grow at room temperature for 40 days. After 40 days, 20 agar discs (4mm$^2$) were taken from the leading edge of the colonies and transferred to an Erlenmeyer flask containing 400ml of liquid Mitchell-Read media. These were allowed to grow for 45 days at room temperature. The liquid cultures were then filtered through a Whatman No. 1 filter paper. The fungal slurry from all 5 isolates was combined and macerated in a Waring blender along with 400 ml of distilled water. The roots of each $Vaccinium$ plant was then inoculated with 10 ml of the fungal slurry and the soil in the potting hole received an additional 20ml.

Plants were fertilized every other week with either 80mg 20-20-20 (+ P treatments) or 20-0-20 (-P treatments). After 23 weeks, the plants were harvested and shoot, root, and total dry weight were determined. Root colonization by mycorrhizae was determined as in the first experiment.

For both experiments, mixtures of mycorrhizal species were used rather than individual species. This was because there has been little or no research on specific
mycorrhizal species associated with each fruit species. Given the agricultural setting of the study, it is feasible that orchards could be inoculated with several species of mycorrhizae and that the system could support multiple species of mycorrhizae. In fact, several species of mycorrhizae have been found to co-exist in agricultural landscapes (Marschner, 1995; Nemec, 1987). Thus, the use of mixed mycorrhizal inoculations was considered more realistic to orchard conditions than single species inoculations.

RESULTS

Experiment 1. Unfortunately, the results of this experiment were severely compromised by the penetration of roots into the hyphal compartments of the plant boxes. The penetration by the roots made the objective of the experiment impossible to attain, and therefore, both trials of the experiment were abandoned. It is important to note for future similar experiments that the failure lay in the construction of the box and not in the size of the mesh screen. Roots did not penetrate into the hyphal compartment through the screened barrier; rather they grew around the edges or seams of the barrier. During the construction of the plant boxes, plastic boxes were purchased and a plexiglass barrier was inserted into the box, the edges of which were glued to the sides of the box with a waterproof sealant. It was through the waterproof sealant that the roots were able to penetrate the hyphal compartment. Any future experimental boxes should be constructed by adjoining two separate boxes so that an internal barrier is not necessary.

Experiment 2. Apple shoot growth was significantly affected by companion plant and the application of phosphorus (Table 5.1). Apple root growth was only affected by the companion plant, while apple shoot:root ratios were significantly affected by both
Table 5.1: Probability of F for main and interactive effects of companion plant, phosphorus addition, and mycorrhizal inoculation on the shoot dry weight, root dry weight, shoot:root ratio and mycorrhizal infection of apple.

companion plant and by the application of phosphorus. Although apple roots did become infected, mycorrhizal inoculation did not affect shoot growth, root growth or shoot:root ratios. While mycorrhizal inoculation affected infection rates, the application of phosphorus did not.

The greatest shoot dry weight of apple was achieved when planted in combination with lingonberry, with or without the addition of phosphorus (Table 5.2). When phosphorus was applied, the lowest apple shoot weight was observed when planted with jostaberry, but was not significantly different than that observed when planted in combination with blackberry or honeyberry. When phosphorus was not applied, the lowest apple shoot weight occurred when planted with blackberry but again this was not
<table>
<thead>
<tr>
<th>Apple w/ Companion</th>
<th>Shoot Dry Weight (g)</th>
<th>Root Dry Weight (g)</th>
<th>Shoot:Root Ratio</th>
<th>Mycorrhizal Infection (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>+ P</td>
<td>- P</td>
<td>+ P</td>
<td>- P</td>
</tr>
<tr>
<td>Blackberry</td>
<td>11.79 cd</td>
<td>7.40 e</td>
<td>10.12 cd</td>
<td>8.02 ± d</td>
</tr>
<tr>
<td>Honeyberry</td>
<td>13.13 c</td>
<td>8.66 de</td>
<td>10.45 cd</td>
<td>8.21 ± d</td>
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<tr>
<td>Jostaberry</td>
<td>10.29 cde</td>
<td>9.23 cde</td>
<td>12.19 bc</td>
<td>12.17 bc</td>
</tr>
<tr>
<td>Lingonberry</td>
<td>21.61 a</td>
<td>16.87 b</td>
<td>15.86 a</td>
<td>14.31 ab</td>
</tr>
</tbody>
</table>

1 Treatment means were separated using Duncan’s Multiple Range Test (P<0.05). Means followed by the same letter are not significantly different.

Table 5.2: The effect of phosphorus application, averaged over mycorrhizae treatment, on apple shoot dry weight, root dry weight, shoot:root ratio and mycorrhizal infection rate when the apple was planted in 1:1 combination with either blackberry, honeyberry, jostaberry or lingonberry.
different than when planted with honeyberry or jostaberry. Apple root dry weight followed a trend similar to shoot weight, being greatest when planted with lingonberry and when phosphorus was applied (Table 5.2). However, when planted with jostaberry, apple root growth did not differ with the addition of phosphorus and was similar in dry weight as when planted with lingonberry without the addition of phosphorus. Apple root growth was most reduced when planted with blackberry or honeyberry without the addition of phosphorus.

Apple shoot:root ratio was nearly identical for each companion plant and phosphorus treatment combination (Table 5.2). The notable exception to this observation was when apple was planted with jostaberry, as the shoot:root ratio was significantly lower when phosphorus was applied than when planted with any of the other shrubs.

Although the main effect of mycorrhizal inoculation was not significant, there was a significant interaction between mycorrhizal inoculation and phosphorus application on the shoot:root ratio of apple (Figure 5.1). The presence of mycorrhizae appeared to reduce the shoot:root ratio of apple when phosphorus was not applied, but when phosphorus was applied, mycorrhizal inoculation increased the shoot:root ratio of apple.

The mycorrhizal infection rates of apple roots were highest when the apple was planted with either blackberry or honeyberry than with jostaberry or lingonberry, especially when phosphorus was applied (Table 5.2). Infection of apple roots was 12-21 times lower when the apple was planted with lingonberry than when planted with either blackberry or honeyberry. Infection of apple roots when the apple was planted with jostaberry was similar to that observed with blackberry or honeyberry, but only when
phosphorus was not applied. In fact, there was a significant interaction between companion plant species and mycorrhizal inoculation in the infection rate of apple roots (Figure 5.2). The addition of phosphorus decreased apple root infection nearly 7 times when planted with jostaberry as compared to when phosphorus was absent. For all other companion species, the addition of phosphorus increased apple root infection, although the increase was not significant.

The shoot growth, root growth and shoot:root ratios of blackberry and honeyberry were not affected by either the application of phosphorus or inoculation with mycorrhizae (Table 5.3). The application of phosphorus significantly affected the shoot and root dry weight of jostaberry and the shoot:root ratio and root dry weight of lingonberry.
Figure 5.2: The effects of mycorrhizal inoculation and companion plant on the mycorrhizal infection of apple roots

Inoculation with mycorrhizae had a significant effect on the root weight and shoot:root ratio of jostaberry. The interaction between the application of phosphorus and mycorrhizal inoculation was significant for jostaberry root weight and lingonberry shoot:root ratio. Mycorrhizal infection rates in lingonberry could not be accurately measured due to the presence of some other fungal species contaminant in the lingonberry root samples. Although the roots of the remaining berry species did become infected, the application of phosphorus did not affect those rates.

Jostaberry had the greatest shoot dry weight of any of the berry species, with or without the addition of phosphorus (Table 5.4). Honeyberry and lingonberry had the
<table>
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<tr>
<th>Source of Variation</th>
<th>Shoot Dry Weight (g)</th>
<th>Root Dry Weight (g)</th>
<th>Shoot:Root Ratio</th>
<th>Mycorrhizal Infection (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Blackberry</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Phosphorus</td>
<td>P&gt;0.0778</td>
<td>P&gt;0.8065</td>
<td>P&gt;0.1079</td>
<td>P&gt;0.3404</td>
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<td>Mycorrhizae</td>
<td>P&gt;0.5880</td>
<td>P&gt;0.1049</td>
<td>P&gt;0.4625</td>
<td>P≤0.0018</td>
</tr>
<tr>
<td>P*M</td>
<td>P&gt;0.4680</td>
<td>P&gt;0.5611</td>
<td>P&gt;0.8829</td>
<td>P&gt;0.5335</td>
</tr>
<tr>
<td><strong>Honeyberry</strong></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Phosphorus</td>
<td>P&gt;0.5406</td>
<td>P&gt;0.6345</td>
<td>P&gt;0.6345</td>
<td>P&gt;0.4402</td>
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<td>Mycorrhizae</td>
<td>P&gt;0.7094</td>
<td>P&gt;0.4655</td>
<td>P&gt;0.5906</td>
<td>P≤0.0001</td>
</tr>
<tr>
<td>P*M</td>
<td>P&gt;0.9531</td>
<td>P&gt;0.1264</td>
<td>P&gt;0.2713</td>
<td>P&gt;0.8274</td>
</tr>
<tr>
<td><strong>Jostaberry</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Phosphorus</td>
<td>P≤0.0438</td>
<td>P≤0.0025</td>
<td>P&gt;0.6114</td>
<td>P&gt;0.5580</td>
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<td>Mycorrhizae</td>
<td>P&gt;0.5256</td>
<td>P≤0.0001</td>
<td>P≤0.0083</td>
<td>P≤0.0139</td>
</tr>
<tr>
<td>P*M</td>
<td>P&gt;0.1428</td>
<td>P≤0.0101</td>
<td>P&gt;0.3973</td>
<td>P&gt;0.6157</td>
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<tr>
<td><strong>Lingonberry</strong></td>
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<td></td>
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<tr>
<td>Phosphorus</td>
<td>P&gt;0.1202</td>
<td>P≤0.0055</td>
<td>P≤0.0016</td>
<td>-¹</td>
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<tr>
<td>P*M</td>
<td>P&gt;0.7460</td>
<td>P&gt;0.0627</td>
<td>P≤0.0097</td>
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</table>

¹Missing values due to possible fungal contamination of lingonberry roots

Table 5.3: Probability of F for main and interactive effects of mycorrhizal inoculation and phosphorus addition on shoot dry weight, root dry weight, shoot:root ratio, and mycorrhizal infection of blackberry, honeyberry, jostaberry and lingonberry.
<table>
<thead>
<tr>
<th>Plant</th>
<th>Shoot Dry Weight (g)</th>
<th>Root Dry Weight (g)</th>
<th>Shoot:Root Ratio</th>
<th>Mycorrhizal Infection (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>+ P</td>
<td>- P</td>
<td>+ P</td>
<td>- P</td>
</tr>
<tr>
<td>Blackberry</td>
<td>11.30 b (^1)</td>
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<td>Honeyberry</td>
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<td>6.83 c</td>
<td>6.64 c</td>
</tr>
<tr>
<td>Jostaberry</td>
<td>14.19 a</td>
<td>9.44 bc</td>
<td>16.25 a</td>
<td>12.34 b</td>
</tr>
<tr>
<td>Lingonberry</td>
<td>4.54 d</td>
<td>3.19 d</td>
<td>0.73 d</td>
<td>0.31 d</td>
</tr>
</tbody>
</table>

\(^1\) Treatment means were separated using Duncan’s Multiple Range Test \((P \leq 0.05)\). Means followed by the same letter are not significantly different.

\(^2\) Missing values due to fungal contamination of lingonberry roots

Table 5.4: The effect of phosphorus application, averaged over mycorrhizae treatment, on the shoot dry weight, root dry weight, shoot:root ratio and mycorrhizal infection rates of blackberry, honeyberry, jostaberry or lingonberry when each berry was planted in 1:1 combination with apple.
The shoot:root ratios of blackberry, honeyberry and jostaberry were similar when phosphorus was absent or present, but the ratios of all the species were lower than the shoot:root ratios observed for apple, except when the apple was planted with jostaberry (Table 5.3, 5.4). Lingonberry had the greatest shoot:root ratio of any of the plant species, including apple, but the ratio was significantly reduced when phosphorus was applied. There was also a significant interaction between mycorrhizal inoculation and the application of phosphorus on lingonberry shoot:root ratio (Figure 5.4). The shoot:root
Figure 5.3: The effects of mycorrhizal inoculation and application of phosphorus on the root dry weight of jostaberry

Figure 5.4: The effects of mycorrhizal inoculation and application of phosphorus on the shoot:root ratio of lingonberry

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ratio was significantly decreased in lingonberries grown in phosphorus deficient soils when mycorrhizae were lacking, while the presence of mycorrhizae slightly decreased the shoot:root ratio of lingonberries grown in phosphorus fertilized soils.

Mycorrhizal infection rates of blackberry, honeyberry and jostaberry were similar to each other and were reduced when phosphorus was applied (Table 5.4). Mycorrhizal infection rates in lingonberry could not be accurately measured due to the presence of another fungal species contaminant in the lingonberry root samples.

DISCUSSION

Mycorrhizal inoculation did not alter the competitive interactions between apple and any of the four berry species during the course of this experiment. With the exception of jostaberry, inoculation with mycorrhizae had no effect on the shoot dry weights, root dry weights or shoot:root ratios of the plant species examined. Jostaberry displayed an antagonistic response to mycorrhizal inoculation with respect to its root dry weight.

Although generally considered mutualistic, there are a few reports of adverse effects of mycorrhizal colonization on plant species. Francis and Read (1994) observed that the survivorship of *Arenaria serpyllifolia* was significantly reduced when grown in association with mycorrhizae. Grime et al. (1987) found that *Arabis hirsuta* and *Rumex acetosa* suffered in terms of biomass when placed in microcosms containing VA fungi. Allen et al. (1989) demonstrated negative effects upon *Salsola kali* when grown in the presence of mycorrhizal fungi.
Hetrick et al. (1991) found that the best single predictor of mycorrhizal dependence was root fibrosity. Plants with relatively coarse root systems displayed high levels of mycorrhizal dependence, while those with fibrous root systems had low levels of dependence. With its highly fibrous root system, it was expected that jostaberry was unlikely to have a high level of dependence on mycorrhizae. However, the detrimental effect of mycorrhizal colonization on jostaberry root growth was unexpected but probably resulted from sink competition. The decrease in root dry weight of jostaberry did not prove harmful to shoot growth, as shoot dry weight was only slightly reduced by mycorrhizal inoculation. This suggests that the external mycelium was able to compensate for the roots with respect to the uptake of nutrients. In addition, the negative effect on jostaberry root dry weight was not sufficient to allow apple to increase its biomass at the expense of jostaberry during the time-frame of this study. Thus, jostaberry’s response to mycorrhizal inoculation may not be as antagonistic as the depression in root growth might, at first glance, suggest.

It is generally accepted that mycorrhizal activity decreases with increasing phosphorus levels (Abbott et al., 1984; Amijee et al., 1990; Li et al., 1991; Marschner, 1995). While not statistically significant, mycorrhizal infection of blackberry, honeyberry, and jostaberry roots decreased when phosphorus was applied. Apple root infection also decreased with phosphorus addition when the companion plant was jostaberry. However, when planted with blackberry or honeyberry, the mycorrhizal infection of apple roots increased with phosphorus addition. While not the typical plant response to mycorrhizal infection in phosphorus sufficient soils, the increased infection...
under those conditions may be due to the ability of blackberry and honeyberry to regulate infection under high phosphorus conditions. Amijee et al. (1990) found an increase in necrotic root infection points in the roots of leek (*Allium porrum*) and a decrease in mycorrhizal infection under high phosphorus conditions, while other researchers found a drastic decrease in the chemotaxis of the root exudates on hyphal growth in plants with high phosphorus supply (Elias and Safir, 1987, as reviewed by Marschner, 1995). This they attributed to the ability of the host plant to finely regulate hyphal growth within its cells.

Blackberry and honeyberry appeared to have a similar ability to regulate hyphal infection at sufficient phosphorus levels, while apple did not appear to share that ability relative to its companion plants. Since the addition of phosphorus increased apple root dry weight, the increase in mycorrhizal infection might simply reflect the increase in root mass available for infection. Or if mycorrhizae were limiting in the experimental pots, and blackberry and honeyberry were able to down-regulate infection at high P levels, while apple was not, the increase in infection in apple roots may be a function of host availability.

Apple roots displayed a high level of mycorrhizal infection but the percentage of root length infected depended on the companion species with which apple was planted. When apple was planted with lingonberry, apple root infection was severely reduced at both levels of phosphorus. Apple infection was also reduced when planted with jostaberry when phosphorus was applied. While the latter reduction might be explained by preferential infection of jostaberry roots by the mycorrhizae, the lack of host plant
regulation ability relative to that of apple, or by the phosphorus induced depression of mycorrhizae, the former cannot, since ericoid plants are non-VA hosts and since the reduction also occurred when phosphorus was limiting. One possible explanation for the lack of apple root infection when planted with lingonberry might be that the ericoid mycorrhizae themselves, had a parasitic or antagonistic effect on the VA mycorrhizae. There is experimental evidence on the suppression of soil-borne fungal and bacterial root pathogens by mycorrhizae (Marschner, 1995). The ericoid mycorrhizae genus, *Oidiodendron*, has also been shown to have anti-mycotic activity (Kathy Demchak, personal communication). While the fungal inhibition by *Oidiodendron* has been observed only on *Penicillium*, it is not improbable that the *Oidiodendron* isolates used in this experiment might also have had anti-mycotic activity on the VA mycorrhizas.

Another possible explanation for the reduction in apple root infection when planted with lingonberry may be due to the presence of the unidentified fungal contaminant present in the pots containing lingonberries. The contaminant may have suppressed VA mycorrhizae activity, thereby reducing the level of infection in the apple roots.

Although lingonberry root infection could not be documented in this experiment, the significant interaction between mycorrhizal inoculation and phosphorus application on the shoot:root ratio suggests that infection occurred at a level necessary to affect growth. Lingonberry displayed the classic plant response to mycorrhizal infection of increased growth under limiting phosphorus levels when mycorrhizae are present (and
slightly decreased growth when inoculated under sufficient phosphorus conditions). This response provided circumstantial evidence of lingonberry root infection by the mix of ericoid mycorrhizae used in this experiment.

The application of phosphorus had a much greater impact on the shoot mass of the species examined than did mycorrhizal inoculation. Apple shoot growth was significantly greater when phosphorus was applied and the companion species were either blackberry, honeyberry or lingonberry. Although apple shoot dry weight also increased when the companion plant was jostaberry, the difference between +P and -P treatments was not significant. This may be due to a greater ability by jostaberry, relative to that of apple, to exploit soil phosphorus supplies. Another explanation might be that the apple plants were being sufficiently shaded by the jostaberry plants that photosynthesis and/or nutrient uptake were negatively affected. Despite the additional supply of phosphorus, apple was not able to significantly increase its above-ground biomass production when planted with jostaberry.

The shoot dry weight of blackberry and jostaberry was significantly affected by phosphorus supply. Both species displayed a marked increased in their above-ground biomass when phosphorus was applied. Conversely, honeyberry and lingonberry were able to maintain (lingonberry) or slightly increase (honeyberry) their shoot mass production at limiting phosphorus levels. Since both these species are native to relatively nutrient poor sites, they may have the ability to tolerate lower resource levels while maintaining biomass production. As such, both honeyberry and lingonberry may qualify as examples of Grime’s (1977, 1988) stress tolerators. By his definition, these are plants
with low growth rates, long-lived, relatively undynamic root systems, low tissue turnover rates, and the ability to accumulate nutrients in plant tissue. These are the characteristics by which stress tolerators can succeed in nutrient poor environments. The fact that both honeyberry and lingonberry were able to maintain above-ground biomass in the -P treatment, while apple shoot growth was significantly reduced (when competing with the former two species) lends further support to the theory that they may be typical examples of Grime's stress tolerator.

Blackberry, jostaberry and apple, by contrast, may be examples of Grime's competitor; those plants with an increased capacity for high growth rate, high morphological plasticity and foraging both above- and below-ground. While the results of this study would rank these species in order of competitive ability: jostaberry, blackberry and apple, it would be interesting to determine if there are differences in the growth rates and/or morphological plasticity among these species. Such knowledge might be able to offer a mechanistic explanation of the competitive interactions between these species.
CHAPTER 6

THE EFFECT OF SHADING ON GROWTH, PHOTOSYNTHESIS AND NUTRIENT UPTAKE OF BLACKBERRY, JOSTABERRY, LINGONBERRY AND HONEYBERRY

INTRODUCTION

Plants typically respond to shade in several ways. Frequently, leaf area ratio, leaf-to-stem mass and stem length increase, while plant dry weight, specific leaf weight and root growth relative to shoot growth decrease with increasing shade levels (Cole and Cole, 2000). Decreased photosynthesis may be important in triggering these responses, but it is also likely that phytochrome and blue light receptors are affected by changes in spectral quality or lowered irradiance (Britz, 1990).

The ratio of shoot to root varies widely among species and is modified by external factors, but the shoot:root ratio has been suggested to represent a functional equilibrium in that there is a general tendency both within and among plant species to maintain a characteristic ratio between shoot and root (Marschner, 1995). Low irradiances can result in the redirection of resource partitioning from the root to the shoots to accommodate the morphological changes necessary to improve light gathering efficiency. While the translocation of photosynthates to the roots is preferentially reduced under shaded conditions, Lambers (1983) has shown that roots still receive an excess of carbohydrates
when shaded, suggesting that regulation of shoot:root ratio is more complex than a functional equilibrium. Britz (1990) suggested that phytochrome and/or blue light receptors were involved in regulating the partitioning of dry matter between the shoot and root of soybean seedlings.

While reduced irradiance lowers the rate of photosynthesis per unit area of leaf and slows growth, there is no correlation between photosynthetic rate or net assimilation rate and the relative growth rate (RGR) of plants (Lambers et al., 1998). This is because assimilation is related to the carbon gain in photosynthesis and carbon loss through respiration. Slow growing species generally use a larger portion of their carbon for respiration, while fast growing species generally invest a greater proportion in new growth, especially leaf growth.

Low light levels can reduce fruit growth and set of many horticulturally important fruit crop species. Shading has been shown to reduce the yield and/or fruit set of many fruit crops including strawberry (Garrison et al., 1991), thornless blackberry (Swartz et al., 1984), black currant (Toldam-Anderson and Hansen, 1993), red raspberry (Waister et al., 1977; Wright and Waister, 1984), black raspberry (Warmund et al., 1995), cranberry (Roper et al., 1995), French American hybrid grape cultivars ‘Chambourcin’ and ‘Seyval’ (Ferreer et al., 2001), apple (Ferreer, 1980; Doud and Ferree, 1980), sour cherry (Flore and Layne, 1990), and pear (Kappel and Brownlee, 2001). The effect of low irradiance on fruit set is often severe even when vegetative growth is only moderately affected. Bepete and Lakso (1998) found that extension shoot growth in apple was a stronger competitor for carbon than fruit early in the season under low light conditions, presumably due to a
survival response of the tree to allow shoot extension and maximize light acquisition. Toldam-Anderson and Hansen (1993) found that fruit drop of black currants was significantly increased when plants were shaded, even though growth parameters were only marginally affected.

Limitations in light availability, through its impact on root activity, may decrease the ability of plants to exploit soil resources. Maximum absorption of nitrate and ammonium ions correlate with maximum photosynthetic rates (Salisbury and Ross, 1992). Thus, shading may impact nitrogen uptake as a function of lower photosynthetic rates. Jackson and Caldwell (1992) found that shading limited the selective increase in the uptake capacity of *Agropyron desertorum* roots in enriched soil patches. Similarly, Donald (1958) found a 20% reduction in the uptake of nitrogen by *Phalaris tuberosa* L. roots when the plants were shaded.

The objective of this study was to determine the effect of shade on the growth of four potential understory berry crops for use in an apple polyculture system: blackberry, honeyberry, jostaberry and lingonberry; and to determine the light response curves for those species and to determine if shading reduced the uptake of nitrogen from the soil.

**MATERIALS AND METHODS**

To approximate the amount of shading under young (4-5yrs) and mature (≥10yrs) apple trees, light levels were measured with a light meter (LI-COR quantum sensor) at 12 different points under and around the base of six different trees at a height of 70cm from the ground. These values were then compared to an equal number of measurements taken under ambient light conditions. Average percent shade was then calculated: 73.2% and
30.3% shade for the mature and young orchards, respectively. This information was used in the design of a greenhouse experiment measuring the effects shade on the growth and nutritional parameters of understory berry plants.

The greenhouse study was conducted during the 2000 and 2001 growing seasons at the Ohio Agricultural Research and Development Center (OARDC) in Wooster, Ohio. To initiate the experiment, one-year old berry plants were potted in 11.4 liter pots filled with an equal mixture of soil, sand, and perlite. Shade cubicles (122 cm tall, 122 cm long and 107 cm wide) were constructed out of PVC pipes and covered with shade cloth that provided 30% or 70% shade. The experiment was designed as a randomized complete block in three treatments (two levels of shade and an unshaded control) and four replicates. Each experimental unit consisted of a group of four pots, each containing one of each berry species. Treatment began on July 25, 2000 by placing experimental units under shade cubicles or on the greenhouse bench (control) according to the experimental design. Plants were watered as needed and fertilized with 100ppm 20-20-20 weekly. Any flowers that developed on the berry plants were removed throughout both growing seasons.

On October 11, 2000, all plants were placed in cold storage for the winter. In January 2001, plants were brought back into the greenhouse and shade treatments were continued. All the honeyberry plants died within 6 weeks of being brought back into the greenhouse from cold storage, so the plants were harvested and the roots and shoots were separated, dried and weighed. The mortality of the honeyberry plants was presumed to be unrelated to the shade treatments, as both control and experimental plants died.
Honeyberry mortality followed a rapid onset of either a disease or inappropriate cultural treatment. The remaining plant species were harvested on October 10, 2001. Shoot biomass, root biomass and shoot:root ratios were analyzed as a split-plot ANOVA with shade as the whole-plot factor and plant species as the split-plot factor.

On August 29, 2001, pairs of soil patches around each plant were treated by using wicks to place 20ml of deionized water on one side of a plant and 20ml of a 6g/L solution of 20-20-20 on the other. Plants were not fertilized 4 weeks prior to treatment injection. After two weeks of continued shading, soil cores approximately 5cm diameter, and 20cm deep were taken from the enriched and control patches. Roots from each core were sieved from the soil, dried and ground for nitrogen content analysis. Root nitrogen content data was analyzed as a split-split-plot ANOVA with shading as the whole-plot factor, plant species as the subplot factor and nutrient enrichment as the sub-subplot factor. A steady-state gas-exchange system (CIRAS-1, PP systems) was used to measure the decrease in photosynthesis caused by shading and to obtain light response curves for the species x shading combinations on June 8, July 1 and August 7, 2001. Two leaves were sampled per replicate plant on each of the days measured. The light compensation points for blackberry, jostaberry or lingonberry were not determined for plants from any of the shade treatments, since the lowest irradiance level measured was 249 µmol m⁻² s⁻¹.

RESULTS

Shade treatments had a significant effect on both shoot and root biomass (Table 6.1). There were also differences among the plant species with regard to shoot and root biomass and shoot:root ratio. Jostaberry had the greatest shoot biomass of all species.
examined. Total shoot biomass did not differ between the control plants and the plants subjected to 30% shade. However, the shoot biomass of jostaberrries grown under 70% shade conditions was reduced by more than half (Figure 6.1).

Blackberry shoot biomass followed the same trend as that observed for jostaberry (Figure 6.1). There was no difference in the control and 30% shaded plants, while the shoot biomass of the 70% shaded plants was nearly half that of the blackberries in the other two treatments.

While honeyberry shoot biomass was not affected by the shade treatments, lingonberry shoot growth was significantly lower in the 30% shade treatment as compared to the control (Figure 6.1). Lingonberries in the 70% shade treatment were significantly smaller than those in either of the other two treatments.

The root mass of all of the species was generally reduced with increasing shade levels (Figure 6.2). Blackberry root mass was reduced from the control at 30% shade, while 70% shade resulted in a further reduction. While jostaberry root mass was not significantly different in the control as compared to the 30% shade plants, 70% shade resulted in nearly a two-fold reduction from the control. Honeyberry root mass was unaffected by shade treatment. Although lingonberry root growth was generally reduced with increasing shade levels, the difference was not significant.

There were no differences in the shoot:root ratios of each species with regard to shade treatment (Figure 6.3). However, blackberry and jostaberry ratios generally
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Table 6.1: Split-plot analysis of variance for the effects of shade treatment (0%, 30%, 70%) and plant species (blackberry, honeyberry, jostaberry, lingonberry) on the shoot dry weight, root dry weight and shoot:root ratios of the plants.
Figure 6.1: Comparison of the shoot biomass of blackberry, honeyberry, jostaberry, and lingonberry when each plant species was grown under full sun (0%), 30% shade or 70% shade conditions. Each plant was kept in the shade regime for two growing seasons, except for honeyberry, which was only kept for one growing season.

increased with increasing levels of shade, while that of lingonberry generally decreased with increasing shade level. The shoot:root ratio for honeyberry was relatively stable across all shade treatments.

The percent nitrogen concentration of roots did not differ from the control or enriched patches. In addition, shade did not affect the nitrogen status of the roots of blackberry or jostaberry (Table 6.2). Lingonberry roots could not be analyzed due to an insufficient sample size. Blackberry and jostaberry roots did not differ in their concentration of nitrogen. Blackberry root nitrogen content was roughly 2% regardless of shade treatment, while that of jostaberry was slightly higher (Figure 6.4).
Carbon assimilation for blackberry and jostaberry was affected by shade treatment, while that of lingonberry was relatively constant across shade regimes (Figure 6.5). The light response curve for blackberry was similar between the unshaded control and 30% shade leaves, although the saturation point of the 30% shaded plants appeared to be slightly lower than that of the control plants. Assimilation rates for blackberry were much lower in leaves from the 70% shaded plants than from those of the other two treatments. The light saturation point was also significantly lower in the 70% shaded plants.
Jostaberry assimilation was lower in the 30% and 70% shade treatments as compared to the control. Unlike blackberry, even the relatively light shade conditions of the 30% shade treatment were enough to significantly reduce photosynthetic rates. A further increase in shade from 30% to 70% resulted in a further, smaller reduction in the photosynthetic rates of jostaberry.

Carbon assimilation was greater in blackberry than either of the other two plant species at all levels of shade. Light saturation for blackberry and jostaberry occurred at similar light levels from control leaves, but that of jostaberry was much lower when exposed to 30% shade. In fact, light saturation and carbon assimilation for jostaberry and lingonberry were nearly identical when each species was grown at 30% shade. At both 30% and 70% shade, maximum assimilation of jostaberry was similar to that of lingonberry.
Figure 6.3: Comparison of the shoot:root ratio of blackberry, honeyberry, jostaberry, and lingonberry when each plant species was grown under full sun (0%), 30% shade or 70% shade conditions. Each plant was kept in the shade regime for two growing seasons, except for honeyberry, which was only kept for one growing season.
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Table 6.2: Split-split-plot analysis of variance on the percent nitrogen content of root tissue for blackberry, or jostaberry with shade treatment (0%, 30%, 70%) as the main factor, plant species as the split factor and fertilizer treatment (control or fertilized) as the split-split factor.
Figure 6.4: Percent nitrogen content of blackberry or jostaberry roots from plants that were either grown at full sun (0%), 30% shade or 70% shade conditions.
Figure 6.5: Light response curves for blackberry, jostaberry and lingonberry when plants were grown at full sun (control), 30% shade or 70% shade conditions.
DISCUSSION

The shading of the four berry species had a significant impact on above and below ground characteristics, as well as on the photosynthetic rates for each plant. In terms of above ground biomass production, lingonberry appeared to be the most sensitive of the four species to shaded conditions. While the shoot dry weight of the other berry species remained constant from the control to 30% shade, that of lingonberry was significantly reduced. This result was surprising, given that lingonberries are native understory plants of alpine forests and sub-arctic environments. However, alpine environments are marked by moderate day lengths and high irradiance levels, while arctic regions have long day lengths with low irradiance levels (Salisbury and Ross, 1992). The shade conditions imposed in this experiment likely exacerbated day length and irradiance differences between its natural environment and that of Ohio. Soil pH may also have affected the response of lingonberries to shade, since the plants were likely already stressed from a higher than optimum pH.

The reduction in lingonberry above-ground biomass occurred despite similar photosynthetic rates between control and shade plants. This suggests that photosynthetic capacities of individual leaves are not well correlated with whole plant performance in terms of biomass production. Pearcy and Sims (1994) found that in Alocasia, photosynthetic capacity per unit area greatly affected carbon gain and growth in high light, but only marginally affected growth and carbon gain when light was limiting.

Shade had little to no effect on the shoot or root dry weights or shoot:root ratio of honeyberry. This data must be viewed cautiously however, since the honeyberry plants
were only exposed to one season of shade, while the remainder of the berries were exposed to two seasons. It is impossible to determine the impact that shading would have had on honeyberry had the experiment been of longer length. With that caveat, it is likely that honeyberry was the most shade tolerant of the berry species examined.

The impact of shade on the biomass of blackberry was similar to that of jostaberry. Shoot biomass was not reduced for either species until shading reached the 70% level. However, the reduction from the control was greater in jostaberry than in blackberry. Blackberry shoot mass was maintained at 30% shade despite a significant reduction in root growth. This indicates that blackberry was probably already diverting carbon to the shoot at the expense of the root, a phenomenon which did not occur in jostaberry until 70% shade. The shoot:root ratios of both species increased with increasing levels of shade, although jostaberry was better able to maintain its “functional equilibrium” than was blackberry. The biomass data suggest that blackberry was more affected by shade than was jostaberry. However, the light response curves for both species show a significant reduction in the photosynthetic rate of jostaberry with as little as 30% shade, while blackberry did not see a similar decrease until 70% shade.

While flowering and fruiting were not measured during the course of the experiment, flowers were removed on plants throughout the growing seasons. The observation was made that while both lingonberry and blackberry still flowered under 30% shade (although to a lesser degree than the control), jostaberry failed to flower at all.
In addition, none of the plants flowered at 70% shade. Although purely observational, it appears as though even slight shading could cause significant reductions in the yield of jostaberry and to a lesser extent in blackberry or lingonberry.

The data on nitrogen root content from the creation of nutrient-enriched patches of soil was somewhat ambiguous. There was not a significant difference in the nitrogen content of roots from control or enriched patches. This might indicate that the roots of jostaberry and blackberry were unable to take advantage of the increased nitrogen supply in the enriched patches, and therefore the N content of the roots was not different from the control. However, there was also no significant interaction between fertilizer and shade treatments. This indicates that neither species was prevented from taking up nitrogen due to shaded conditions. Analyses of the soil from the cores of control and enriched patches also did not show a difference in nitrogen content. This could mean that there was an overlap in the patches between control and enriched. However since the soil was not collected until two weeks after injection, the lack of difference in the soil nitrogen content between the patches could reflect differences in the plant removal of nitrogen from roots within each patch or leaching as a result of continued watering of the plants within that two week period. A more controlled study is needed to address these questions and to determine whether shade has any impact on the ability of blackberry or jostaberry to take up nitrogen or other nutrients from the soil.
CHAPTER 7

CONCLUSIONS

The results from the field study indicate that of the possible apple-berry polyculture systems examined, the apple-honeyberry combination is the only one that shows any promise as a viable system. The apparent success of the apple-honeyberry polyculture primarily stems from the weakness of honeyberry as a competitor. The remainder of this body of research was devoted to offering some mechanistic explanations for the results observed in the field.

Grime and Hodgson (1987) listed several plant characteristics that confer strong competitive ability: (1) a robust perennial life form with a strong branching habit above and belowground, (2) a rapid growth rate, (3) high morphological plasticity in the shoots and roots, and (4) short life span of individual leaves and roots. Conversely, plants from low fertility environments are stress-tolerators that succeed in such habitats because they have low growth rates, long-lived relatively undynamic root systems, low tissue turnover rates, and the ability too accumulate nutrients in plant tissue (thereby uncoupling nutrient uptake from growth).

Honeyberry had much lower growth rates than did blackberry, jostaberry or apple. It seemed to prefer crowded and shaded conditions. While honeyberry allocated more of its biomass below-ground than any of the other plant species, its extensive root system
did not exhibit the plasticity required to take advantage of regions of nutrient enrichment. For these reasons, honeyberry appears to have a life-strategy similar to that of Grime’s stress tolerators. Under the relatively fertile conditions of the horticultural environment, it is unlikely that honeyberry would ever significantly reduce the growth and fruiting behavior of apple to such an extent that the success of the polyculture would be compromised. Furthermore, the apparent shade tolerance of honeyberry indicates that the polyculture would likely remain productive for several more years.

Lingonberry also appeared to be a stress-tolerator. It had a low growth rate with a root system that was incapable of making plastic adjustments, to take advantage of nutrient pulses. However, the apple-lingonberry polyculture is not recommended because of the inherent differences between the species in their soil pH requirements. While typically considered shade tolerant, lingonberry was not capable of maintaining growth under even slightly shaded conditions, presumably because it was already stressed from higher than optimum soil pH or because of inherent differences in daylength and irradiance between its natural alpine environment and the Ohio conditions within which it was placed. As the apple trees mature, it is expected that lingonberry growth would decline, with a concurrent decrease in fruit yield.

Both blackberry and jostaberry appeared to be stronger competitors than was apple, as both species negatively affected both the growth and yield of apple. Both blackberry and jostaberry exhibited high growth rates and the ability to proliferate within zones of soil nutrient enrichment. By contrast, apple did not demonstrate a consistent ability to proliferate its roots in zones of nutrient enrichment. Since neither blackberry or
jostaberry achieved a height capable of severely shading the apple tree, it is concluded that belowground competition (especially for nitrogen) was the primary mechanism by which apple growth and yield were affected. This finding is supported by numerous other studies in which belowground competition was found to be more important than aboveground competition in the interactions between plants (Wilson, 1988). However, competition for light also appeared to be a significant component in the interactions between these plants as berry yield was greatly affected by close spacing and the presence of an apple tree. Although not an effective competitor for nitrogen, the apple, by virtue of its stature, may have been a better competitor for light.

Jostaberry appeared to be particularly sensitive to shaded conditions as its photosynthetic capacity was greatly reduced and it failed to flower even under lightly shaded conditions. Blackberry was also negatively affected by shade, but to a lesser extent than jostaberry. Although the failure of the apple-blackberry and apple-jostaberry polycultures can likely be attributed to the disproportionate reduction in apple yield as compared to berry yield, it is predicted that in future years the polycultures will remain unsuccessful because of a disproportionate reduction in berry yield as shade levels increase.

Mycorrhizal inoculation was unable to mediate the outcome of competition between apple and the four berry crops. Mycorrhizae are most likely to affect plant interaction when the plants in question differ in their dependence on the association, especially if the association is mutualistic for one species and antagonistic for another. Despite the fact that mycorrhizal inoculation had an antagonistic affect on jostaberry

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growth, the difference not great enough to result in the release of apple from the competitive suppression of jostaberry. While not empirically measured, the mycorrhizal dependence of each of the plant species examined is considered to be low, as inoculation did not improve the growth of any of the species.

Growth per se, does not explain the competitive success of a species, rather it is important to examine how a plant invests its dry matter under different environmental conditions (Kuppers, 1994). Blackberry demonstrated a high degree of morphological plasticity with respect to its ability for rapid root proliferation and in its ability to divert resources to its shoots (at the expense of its roots) under even lightly shaded conditions. Overall, blackberry was the most responsive species both above and belowground and is therefore considered the strongest competitor of the species examined.
REFERENCES CITED


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